Phylogeny of wasps of the genus *Mischocyttarus* de Saussure (Hymenoptera, Vespidae, Polistinae)

Orlando Tobias Silveira

Coordenação de Zoologia; Museu Paraense Emílio Goeldi, MPEG/MCT; Av. Perimetral 1901, Terra Firme, 66077-530 Belém-PA, Brazil;
Fone: 55 -91- 3217-6115; orlando@museu-goeldi.br

ABSTRACT. Phylogeny of wasps of the genus *Mischocyttarus* de Saussure (Hymenoptera, Vespidae, Polistinae). A phylogenetic analysis is presented of subgenera and species-groups of *Mischocyttarus* de Saussure, the largest genus of social wasps. The analysis is based on 62 morphological and nest architecture characters, coded for 71 terminals representing much of the taxonomic diversity within the genus, plus three outgroup terminals representing other polistine tribes. The main conclusions about phylogenetic relationships within the genus are based on parsimony analysis under implied weights. Monophyly of *Mischocyttarus* is confirmed as well as that of most of the previously recognized subgenera: *Mischocyttarus* s. str., *Clypeopolybia*, *Monogynoecus*, *Scytokeraia*, *Phi*, *Kappa*, *Megacanthopus* and *Omega* sensu Richards (1978). *Haplometrobius* as conceived by Richards (1978) is not a monophyletic taxon, but some of its species-groups are monophyletic. The groups of *M. artifex* and *M. cerberus* are raised to subgenus level, and a new concept of *Haplometrobius* restricts it to the group of *M. iheringi* (the type species of this subgenus) in the sense of this work. The concept of subgenus *Omega* is widened to include the species-groups of *M. surinamensis* and *M. prominulus*. Besides the new subgeneric classification presented, limits and diagnoses of all species-groups of the subgenera *Phi* and *Haplometrobius* sensu Richards (1978) are discussed, and a new key for all subgenera and species-groups of *Mischocyttarus* is also presented.

KEYWORDS. Systematics; new classification; social wasps.

RESUMO. Filogenia das vespas do gênero *Mischocyttarus* de Saussure (Hymenoptera, Vespidae, Polistinae). O artigo apresenta um estudo filogenético dos subgêneros e grupos de espécies de *Mischocyttarus* de Saussure, o maior dos gêneros de vespas sociais. A análise é baseada em 62 caracteres morfológicos e de arquitetura de ninhos, codificados para 71 terminais representantes da diversidade taxonômica do gênero e mais três terminais correspondentes às outras três tribos de Polistinae. As conclusões principais sobre relações filogenéticas são extraídas de análises usando pesagem implícita de caracteres. O monofiletismo de *Mischocyttarus* é confirmado, assim como da maioria dos subgêneros previamente reconhecidos: *Mischocyttarus* s. str., *Clypeopolybia*, *Monogynoecus*, *Scytokeraia*, *Phi*, *Kappa*, *Megacanthopus* e *Omega* sensu Richards (1978). *Haplometrobius* tal como concebido por Richards (1978) não é um táxon monofilético, mas alguns de seus grupos de espécies são monofiléticos. Os grupos de *M. artifex* e *M. cerberus* são elevados à categoria de subgênero e um novo conceito mais restrito de *Haplometrobius* é adotado, circunscrito ao grupo de *M. iheringi* (a espécie tipo desse subgênero). O conceito do subgênero *Omega* é ampliado para incluir os grupos de espécies de *M. surinamensis* e *M. prominulus*. Além de uma nova classificação subgenérica, acompanhada de chave de identificação, discute-se também os limites e diagnoses de todos os grupos de espécies dos subgêneros *Phi* e *Hamplometrobius* sensu Richards (1978).

PALAVRAS-CHAVE. Sistemática; nova classificação; vespas sociais.

Mischocyttarus de Saussure (1853) is the single genus in Mischocyttarini, one of the four tribes recognized by Carpenter (1993) in the subfamily Polistinae of social wasps. The genus is the largest among social vespids with 245 species distributed in nine subgenera, being essentially a Neotropical taxon with a few species occurring north of Mexico (Carpenter & Wenzel, 1988; Cooper, 1996a, 1996b, 1997a, 1997b, 1998a, 1998b; Raw, 1985, 1996; Richards, 1941, 1945, 1978; Silveira, 1998; Zikán, 1935, 1949). It originally included only those species with a very long petiole between meso and metasoma, and whose nests typically have a circular comb suspended by a long thin central peduncle (de Saussure, 1853; Richards, 1978; Zikán, 1949). Other related morphotypes were initially assigned to *Polybia* Lepeletier (1836) or, some time later, to the newly created genera *Megacanthopus* Ducke (1904) and *Monacanthocnemis* Ducke (1905). Ducke (1913) himself recognized those two names as synonyms of *Mischocyttarus*, thus establishing the modern concept of the genus.

As currently understood, *Mischocyttarus* is recognizable by at least two characters that are exclusive to the genus. In adults, the internal and external lobes of the tarsal segments are asymmetrical, the former being longer. In addition, in mature larvae, the first abdominal sternum presents at least one forwardly directed, appendix-like process (Hunt, 1991; Kojima, 1998; Reid, 1942; Richards, 1978). The biology is similar to that found in species of *Polistes* Latreille (1802), with a dominance hierarchy being established among the females of a colony through physical attacks and oophagy. The nests normally consist of a single unenveloped comb, fastened to the substrate by a peduncle (Gadagkar, 1991; Jeanne, 1972, 1980; Richards, 1971; Wenzel, 1991, 1998).

The genus was revised by Richards (1945), Zikán (1949) and Richards (1978). The history of names applied to subgenera of *Mischocyttarus* by various authors is rather complicated, having been revised in part by Richards (1978) and Carpenter & Day (1988). In his monograph about the Vespidae, Henri de Saussure (1854) used names derived from letters of the Greek alphabet to refer to groups of species (divisions) in the nominotypical subgenus of *Polybia* Lepeletier. Some of these divisions, corresponding in certain measure to groups of species of *Mischocyttarus* as currently conceived, received subsequently new names either at the genus or subgenus level, or simply attained formal recognition at the subgeneric level. Such are the cases of *Monacanthocnemis* Ducke (= *Omega* de Saussure, 1854), *Monocyttarus* Richards (1978) (= *Phi* de Saussure, 1854), and *Kappa* de Saussure (1854). In his book on the social wasps of the Americas, Richards (1978) followed the norm then in force of the International Code of Zoological Nomenclature (2nd edition), which did not give formal status to names that had been originally used below the subgenus level. Richards therefore considered as valid the two names created by Ducke (1904, 1905), and attributed authorship of *Kappa* to Bequaert (1933) who had designated the type species of *Kappa*. In that same work, Richards created the subgenus *Monocyttarus* that coincidentally contained representatives of de Saussure´s division *Phi* (this actually mostly formed by species now placed in the genus *Agelaia* Lepeletier (1836; see also Bequaert, 1943)). More recently, based on the revised ICZN (3rd edition), Carpenter & Day (1988) reestablished validity (and authorship) of the names created by de Saussure. They also pointed out that because Bequaert (1943) had fixed the type species of *Phi* as *Vespa phthisica* Fabricius (1793), incidentally an element of *Monocyttarus*, this name then turned out to be a junior subjective synonym of *Phi*. Finally, Cooper (1997a) created the subgenus *Scytokeraia* for a group of species (with some new additions) that had been placed by Richards (1978) in the subgenera *Monogynoecus* Richards (1941) and *Monocyttarus*.

While Richards (1941, 1945) by the time of his earlier works had already established the foundations of the present-day subgeneric classification, Zikán (1949) largely ignored his concepts. According to Richards (1978) and with the modifications introduced by Cooper (1997a), the subgenera of *Mischocyttarus* are the following:

1) *Mischocyttarus* s. str. de Saussure, 1853. A small group with 12 species, distributed mostly in South America, although the type species *M. labiatus* (Fabricius, 1804) reaches Panama, and *M. melanarius* (Cameron, 1906) occurs only in Central America (Richards, 1945, 1978; Zikán, 1949). *Mischocyttarus acunai* Alayo (1972), from Cuba, was treated by Richards (1978) as a member of *Monocyttarus* (= *Phi* Saussure). However, as explained by Silveira (2002), this species is a member of *Mischocyttarus* s. str., being its endemic and sole element in the Caribbean. Another recent addition to the group is *M. aripuanaensis* described by Silveira (1998) from the Brazilian state of Mato Grosso. Jeanne (1970, 1972) and Litte (1981) respectively published studies about the sociobiology of *M. drewseni* de Saussure (1857) and *M. labiatus* (Fabricius, 1804).

2) *Clypeopolybia* Brèthes, 1923. With *M. flavicans* (Fabricius, 1804) as its type species, this group was referred by Richards (1978) as containing 11 species. However, as shown by Silveira (1998), *Mischocyttarus heliconius* Richards (1945), *M. sericeus* Richards (1978), and *M. piger* Richards (1945) are not proper elements of *Clypeopolybia* (see below). In his first revision of the genus, Richards (1945) treated the species allied to *M. flavicans* as part of the nominotypical subgenus together with *M. labiatus* and allies. Later, in his 1978 book, the author removed the *M. flavicans* group to a separate subgenus for which he used the name *Clypeopolybia* Brèthes, 1923. However, Richards (1978) added to the new subgenus the species of the *M. heliconius* group, which in 1945 he treated as parts of subgenus *Kappa* (see below). Most species of *Clypeopolybia* occur in South America, and detailed studies of the behavior are lacking.

3) *Haplometrobius* Richards, 1978. Erection of this subgenus apparently resulted from Richards decision to confer separate status to the group of *M. collaris* of his previous works (1941, 1945), thus limiting the concept of *Megacanthopus* to its type species and closely related forms. Erection of *Haplometrobius* logically followed for the remaining groups of *M. prominulus* Richards (1941), *M. surinamensis* (de Saussure, 1854), *M. cerberus* Ducke (1918), *M. artifex* (Ducke, 1914) and *M. iheringi* Zikán (1935). The resulting subgenus is hard to diagnose, and is a very large group with 74 species currently recognized, and with *M. iheringi* as its type species. A considerable amount of work has been recently dedicated to this group. Raw (1985) added a new species to the group of *M. artifex*. Cooper (1996b) recognized a new species-group, *M. mendax* Richards (1978), adding six new species. Cooper (1998a) described two species in the group of *M. iheringi*, and in a subsequent paper (1998b), he described five new species in the group of *M. artifex*. Silveira (2004) described the male of *M. nomuare* Richards (1978) and rearranged the group of *M. cerberus*. Most species of *Haplometrobius* occur in South America, but various are found from Panama up to Mexico. The colony cycle and social organization of *M. cerberus* in Brazil has been investigated by Giannotti (1998, 1999).

4) *Kappa* de Saussure, 1854. With 36 described species (Silveira, 2006), this group was created by de Saussure (1854) as an informal division of the nominotypical subgenus of *Polybia*. Bequaert (1933) designated *P. injucunda* de Saussure (1854) as the type species of *Kappa* solely with the intention of synonymyzing it under *Mischocyttarus*. However, Richards (1941, 1945) used the name at the subgeneric level, but with far wider limits than in his 1978 work. Besides the usual member species, the earlier *Kappa* concept also included all species-groups now in *Phi* plus *M. heliconius* Richards. Geographic distribution is Neotropical from Mexico to north of Argentina, most species occurring in the northwest of South America. The group was recently revised by Silveira (2006), and information on the biology and behavior of species can be found in Bequaert (1937), Gorton (1978), London & Jeanne

(1996), O'Donnell (1992), Queller et al. (1992), Rapôso-Filho et al. (1994), Silva (1988), Silva & Oliveira (1989), Silva & Rodrigues (1987), Starr (1988), and Windsor (1972).

5) *Megacanthopus* Ducke, 1904. This name was created for a new genus of social wasps containing all species with asymmetrical tarsal segments, which previous authors had assigned to *Polybia*. While convincingly justifying separation of the new taxon from *Polybia*, Ducke (1904) only very unsatisfactorily distinguished *Megacanthopus* from *Mischocyttarus*. In his key (p. 320), differences between the two taxa refer essentially to body-length related characters. Later, Ducke (1913) recognized the two names as synonyms, and Bequaert (1933) subsequently designated *Mischocyttarus collaris* (Ducke, 1904) as type species of *Megacanthopus*. Richards (1941, 1945) used the name for a subgenus of *Mischocyttarus*, with a concept wide enough to include not only the species more similar to *M. collaris* but all those for which he would subsequently create the subgenus *Haplometrobius* (see Richards, 1978). Thus, it was only in Richards's last revision that the name *Megacanthopus* gained its current meaning, corresponding to a small group of ten species possessing unique morphological features. Cooper (1997b) revised the subgenus, adding three new species, and presented notes on the biology and distribution of the species. They occur mostly in South America, only *M. collarellus* Richards (1940) being recorded from Panama and Costa Rica (Cooper, 1997b; Garcete-Barrett, 1999; O'Donnell, 1999; Richards, 1978).

6) *Monogynoecus* Richards, 1941. This name was created for a small group of three species having *M. lecointei* (Ducke, 1904) as type species. Zikán (1949) described three more species, all showing good correspondence to the original concept. However, Richards (1978) included in *Monogynoecus* some species (described by himself and earlier by Zikán, 1949) that either shared only superficial similarity with typical species of the group in features like the "round" humeral region of pronotum, or primitive widely distributed characters as the presence of a pronotal fovea. The heterogeneous composition of the subgenus was corrected by Cooper (1996a), who removed the outlying species, and subsequently describing a new subgenus for them: *Scytokeraia* Cooper, 1997a. According to Cooper (1996a), all eight species of *Monogynoecus* occur in South America east of the Andes. That author also presented information on the natural history of some species.

7) *Omega* de Saussure, 1854 (= *Monacanthocnemis* Ducke, 1905). Both of these names were created for monotypic groups containing only the species *M. filiformis* (de Saussure, 1854). Synonymy of *Monacanthocnemis* under *Mischocyttarus* was recognized by Ducke (1913). Richards (1941) initially used de Saussure's name to refer to a subgenus composed of *M. filiformis* and allied species, but substituted Ducke's *Monacanthocnemis* in 1978 following the restrictions then imposed by the International Code of Zoological Nomenclature on infrasubgeneric names. The group comprises seven described species (plus several undescribed ones), most of which occurring in South America. Only *M. chalucas* Snelling (1983) and one undescribed species from Panama (UCDC, Bohart Museum) occur in Central America. Detailed work on the behavior of the species is lacking.

8) *Phi* de Saussure, 1854 (= *Monocyttarus* Richards, 1978). As explained in Carpenter & Day (1988), synonymy of *Monocyttarus* under *Phi* Saussure is consequence of the choice by Bequaert (1943) of *Mischocyttarus phthisicus* (Fabricius, 1793) as the type species of *Phi*. Differently from de Saussure's division, however, Richards's taxon is a reasonably homogeneous group, rather easily diagnosable from other subgenera. It is thus ironic that Bequaert chose a *Monocyttarus* species (instead of an *Agelaia* one) as type of *Phi*, and only to make this a synonym of *Mischocyttarus*. With 75 described species, *Phi* is one of the largest groups in *Mischocyttarus* and that with the most extensive geographic distribution. Being mostly Neotropical, four species occur north of Mexico (USA and Canada), four in the Caribbean, and *M. flavitarsis* (de Saussure, 1854) has been introduced in Hawaii. Information on the biology and behavior of the species has been published by Giannotti & Fieri (1991), Giannotti & Silva (1993), Litte (1977, 1979), Machado & Wiendl (1976), Rapôso-Filho (1987, 1989), Rapôso-Filho & Rodrigues (1984 a, and b, 1986, 1987, 1988), Silva & Rodrigues (1987), and Strassmann et al. (1995).

9) *Scytokeraia* Cooper, 1997. As mentioned above, creation of this subgenus was linked to corrections made by Cooper (1996a, 1997a) in *Monogynoecus*. Even Richards (1978) had noted that his species *M. mastigophorus* did not possess the very distinctive male genitalia, typical of the species of *Monogynoecus*. On the other hand, the threadlike shape of the male antenna in *M. mastigophorus* was unique in the genus, only approached by a few *Phi* species like *M. flavitarsis* (de Saussure, 1854) or *M. pallidipectus* (Smith, 1857). After collecting additional material, including the previously unknown males of other species, Cooper (1997a) perceived the correlation between the distinctive male features and the emarginated female clypeus. He noted that, together with a very low and straight pronotal carina such a combination of characters could not be referred to any of the known groups of *Mischocyttarus*, thus justifying creation of *Scytokeraia* with *M. mastigophorus* as type species. The new subgenus also included the species *M. subornatus* Zikán (1949) and *M. stenoecus* Richards (1978), placed by Richards (1978) respectively in the subgenera *Monocyttarus* (= *Phi*) and *Haplometrobius*. *Scytokeraia* comprises 12 species distributed in Central America and northwestern regions of Andean South America, including the Pacific coast of Colombia (Carpenter & Wenzel, 1988; Cooper, 1997a; Richards, 1978). Detailed studies on the biology and behavior of *M. mastigophorus* have been published by O'Donnell (1998, 1999).

Mischocyttarus has been of great importance for the study of sociobiology in wasps (Jeanne, 1970, 1972; Litte, 1981; O'Donnell, 1999; Queller et al, 1992; Strassmann et al, 1995). The open nests facilitate considerably the observation of behavior. However, further success of these studies depends strongly on a parallel effort to reconstruct phylogenetic relationships within the genus. For other vespid taxa, the recent development of phylogenetic hypotheses (Carpenter, 1982, 1987, 1988a, 1991) has made possible the critical evaluation of competing hypotheses on the evolution of several social features (Carpenter, 1991, 1997; Carpenter et al, 1993; Wenzel & Carpenter, 1994). The present work is the first cladistic study specifically designed to investigate the phylogenetic relationships within *Mischocyttarus*. In a recent analysis including various polistine genera, Arévalo et al. (2004) obtained results with some resolution of internal relations within *Mischocyttarus*, but the few species used represent only three of the nine subgenera currently recognized. In fact, the main objective of that study was to investigate relations within the genus *Polistes* Latreille, 1802. Here, I use morphological characters of several species of *Mischocyttarus* from all the subgenera and major species-groups in order to investigate their monophyly and relationships.

MATERIAL AND METHODS

Terminology. The terminology used to describe characters is essentially that of Richards (1978) with some introduced terms, such as the name "tyloid" to designate special areas on the ventral surface of the male antennal flagellomeres (see Bin et al, 1999; Carpenter, 1991). Major divisions of the body are named as in Goulet & Huber (1993).

Selection of Taxa.Complete reference to author and year of publication of taxon names cited in this study are presented in Table 1 and Appendix 1. The analysis was based on 71 terminals (Tables I, II, and Appendix 1) representative of the morphological diversity observed in 181 named species and subspecies of *Mischocyttarus* (plus several undescribed) from all currently recognized subgenera (see Appendix 1). Addition of exemplar species as terminals was preferred as a method of representing the variation within a group. However, for five species-groups within *Mischocyttarus*, ground-plan assumptions or polymorphic terminals were used. Table I shows the list of terminals with the respective species-groups or taxa represented, and other relevant information on taxa or specimens and their depositories.

The three remaining tribes of Polistinae (see Carpenter, 1993) were chosen to compose the outgroup: Polistini (consisting of *Polistes* Latreille, 1802), Ropalidiini (comprising *Ropalidia* Guérin-Menéville, 1831; *Parapolybia* de Saussure, 1854; *Polybioides* Buysson, 1913; and *Belonogaster* de Saussure, 1854), and Epiponini (formed by nineteen Neotropical swarming genera) (Appendix 1). Characters of all four genera of Ropalidiini were used to infer states of the composite terminal representing the group. For the Epiponini, ground-plan characters were inferred based on the conditions observed in *Apoica* Lepeletier and *Agelaia* Lepeletier, two basal lineages in the tribe (Carpenter, 1991).

Providers of specimens for the study. Examined material representative of the taxa cited in Table 1, and Appendix 1 was loaned from various institutions worldwide. For *Mischocyttarus* species, holotypes and/or paratypes were examined in most cases (75%), and complete collecting data and depository for them are available in the works of Richards (1940, 1945, 1978), Silveira (1998, 2006), and Zikán (1935, 1949). In the present work, collecting information is only presented for critical taxa, i.e. undescribed or unidentified forms, and taxonomically problematic species (see Table 1). Contributing collections (abbreviations as in Arnett *et al*, 1993) and their respective curators are as follows: American Entomological Institute, Gainesville (**AEIC**; Dr. David Wahl); American Museum of Natural History, New York (**AMNH**; Dr. James Carpenter); Natural History Museum, London (**NHM**; Ms. Christine Taylor); California Academy of Sciences, San Francisco (**CASC**; Dr. W. Pulawski and Dr. D. Ubick); Carnegie Museum of Natural History, Pittsburgh (**CMNH**; Dr. John Rawlins); Estación de Biologia Chamela, San Patricio, México (**EBCC**; Dra. Alicia Rodríguez-Palafox †; Dr. Ricardo Ayala-Barajas); Essig Museum, Berkeley (**EMEC**; Dr. Cheryl B. Barr); Florida State Collection of Arthropods, Gainesville (**FSCA**; Dr. J. Wiley); Museo Fairchild, Universidad de Panama (**GBFM**; Dr. Roberto Cambra T.); Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Macapá (**IEPA**; Mr. José Madson Gama); Instituto Miguel Lillo, Tucumán (**IMLA**; Dr. Abraham Willink †; Dra. M.aria Virginia Colomo de Correa); Instituo Nacional de Biodiversidad, Santo Domingo (**INBC**; Dr. Jesus Ugalde and Dr. Jorge Carvajal Alfaro); Instituto de Zoologia-Academia de Ciências de Cuba (Dr. Luis F. de Armas); Museo Nacional de Historia Natural del Paraguay, Asunción (**INBP**; Dr. John Kochalka and Dr. Bolivar Garcete-Barret); Instituto Nacional de Pesquisas da Amazônia, Manaus (**INPA**; Dra. Catarina Motta and Dr. Augusto Henriques); Fundação Instituto Oswaldo Cruz, Rio de Janeiro (**IOC**; Dr. Sebastião José de Oliveira †; Dra. Jane Margaret Costa von Sydow); Museum of Comparative Zoology, Cambridge (**MCZC**; Dr. Philip Perkins); Museum National d'Histoire Naturelle, Paris (**MNHN**; Dr. Janine Casevitz-Weulersse and Dr. Claire Villemant); Museu Nacional do Rio de Janeiro, Quinta da Boa Vista (**MNRJ**; Dr. Miguel A. Monné and Dra. Rita Tibana); Museu Paraense Emílio Goeldi, Belém (**MPEG**; Dr. Terezinha Pimentel and Dra. Ana Harada); Museu de Zoologia da Universidade de São Paulo, São Paulo (**MZSP**; Dr. Carlos R. F. Brandão); Museum Für Naturkunde Humboldt-Universität, Berlin (**ZMB**; Dr. Koch Wessel); National Zoological Collection of Suriname (**NZCS;** Dr. H. Hiwat-van-Laar); Naturhistoriska Riksmuseet, Stockholm (**NHRS**; Dr. Lars-Ake Janzon); Rice University, Texas (Dr. Joan Strassmann); Bohart Museum, University of California at Davis, Davis (**UCDC**; Dr. S. L. Heydon); Universidade Federal do Maranhão, S. Luís (**UFMA**; Dra. Gisele Garcia); Universidade Federal do Paraná, Curitiba

(**UFPR**; Dr. Gabriel A. R. de Melo); University of Ibaraki, Mito (Dr. Dr. Jun-ichi Kojima); Smithsonian Institution, Washington (**USNM**; Dr. Ronald J. McGinley and Dr. David G. Furth); Zoologische Saamlung des Bayerischen Staates, Munich (**ZSMC**; Dr. Johannes Schuberth); Dr. Carlos E. Sarmiento, Colômbia.

Preparation of Specimens. Most characters were studied under a stereomicroscope, and drawings were made with a camera lucida. For preparations of the male genitalia, the terminal part of the metasoma was softened with 10% KOH and removed with forceps, and then heated in KOH for 10 minutes. After cleaning in distilled water and dehydration, the pieces of the terminalia were preserved in plastic microvials containing a 1:1 mixture of 70% alcohol and glycerin. Observation of the genitalia was made under the microscope in a Petri dish filled with alcohol, and with the help of a small positioning support made with an extra-fine electric copper wire conveniently twisted (suggested by S. T. P. Amarante).

Ventral surface of the male flagellomeres and other parts were studied with scanning electron microscopy (SEM). Part of the images were obtained in the "Departamento de Microscopia Eletrônica da Universidade de São Paulo", with ZEISS equipment, and captured as computer files or KODAK 5-PXP 120 film. Most of the SEM's were made in the "Departamento de Fitopatologia da EMBRAPA", in Belém, with JEOL equipment and image reproduction by POLAROID 667 film. Dirty specimens were bathed for 24h in commercial synthetic detergent (VEJA), washed in slow current water, cleaned with a soft brush, and then put to dry in a stove at 50°c. Critical point drying was not considered necessary, and in some cases a chloroform bath was used prior to air-drying.

Larval characters were observed in alcohol preserved specimens or, in a few instances, in dry mummified specimens removed from nests in collections. In spite of the larval collections gently provided by Dr. Garcete-Barrett (Paraguayan specimens) and Dr. J. Kojima (Ropalidiini specimens), scoring the states for a number of terminals depended on information from the literature (Cooper, 1996*a*, 1996*b*, 1997*a*, 1997*b*; Dias-Filho, 1975; Kojima, 1998; Reid, 1942; Richards, 1945, 1978).

Information on *Mischocyttarus* species not directly examined was obtained from the literature, especially Richards (1941, 1945, 1978), Zikán (1949), Raw (1985, 1996) and Cooper (1996a, 1996b, 1997a, 1997b, 1998a, 1998b). In one case, occurrence of an expected condition (male antenna lacking hairs) was inferred in *M. chanchamayoensis*, in spite of being not explicitly mentioned by Cooper (1998a). It is judged that occurrence of the alternative state would certainly be noted by the author. Information about the genera composing the outgroup was found in the works of Richards (1973, 1978), Kojima (1982, 1984, 1998), Kojima and Kojima (1988), and Carpenter (1991, 1996).

Character Coding. Characters used in this study were constructed in three ways: (1) simple alternative conditions (e. g., presence/absence of pronotal fovea); (2) more complex shapes constituted by two or more correlated elements of form (composite coding of Wilkinson, 1995); (3) by recognizing a very different extreme condition among a set of otherwise poorly differentiated forms considered to be one same alternative state (e.g., the deep lateral indentations of the female clypeus as a putative synapomorphy of *Clypeopolybia*). Multistate characters are ordered in cases where a linear series of related shapes was evident. Missing information (mostly about males and larvae) is represented in the matrix (Table II) by a question mark (?). Ambiguity is scored as a minus sign (-).

Polymorphic Terminals. None of the subgenera of *Mischocyttarus* could be represented in the study by a single terminal. In general, the recommendation of Nixon & Davis (1991) was followed, i.e. to increase the number of representative terminals (species). In some cases, however, polymorphic terminals had to be used when treating the occurrence of a character with more than one state within a single species (e.g., *M. immarginatus*) or in a composite terminal representing a group of species (e.g., Ropalidiini, or the *M. punctatus* group).

Phylogenetic Analysis. The data matrix was analyzed by both unweighted standard parsimony and parsimony analysis under implied weights (Goloboff, 1993a). WinClada 1.00.08 (Nixon, 2002) was used for editing the matrix and inspection of trees generated by NONA 2.0 and Pee-Wee 3.0 (Goloboff, 1993b). Character support for groups was evaluated in WinClada using option "unumbiguous changes only" (as to methods of optimization of character changes). Matrix was run in NONA and Pee-Wee with options amb-, mult*50. Command "jump*" was used to jump between islands of trees separated by specified differences in fit or number of steps. The program TNT 1.0 (Goloboff et al, 2005) was also used for exploring the data. Any presented consensus tree is the strict consensus. Absolute and relative Bremer supports (Bremer, 1994; Goloboff & Farris, 2001) were estimated in NONA and Pee-Wee using the following command sequence (as suggested by P. Goloboff to J. Carpenter; in lit.):

```
  "first find shortest trees, and then..."
     > out filename; <enter>
     > hold 1000 ; sub 1 ; find * ; <enter>
     > hold 2000 ; sub 3 ; find *; <enter>
     > hold 4000 ; sub 5 ; find * ; <enter>
```

(in this work expanded until collapsing of basalmost branches of the ingroup)

```
     > hold 6000; sub 7; find *; <enter>
     > hold 8000; sub 9; find*; <enter>
     > bsupport ; bsupport*; <enter>
     > quit <enter>
```

(and for implied weights)

```
     > hold 1000; sub 10; find*; <enter>
     > hold 2000; sub 30; find*; <enter>
     > hold 4000; sub 50; find*; <enter>
     > bsupport ; bsupport*; <enter>
     > quit <enter>
```

Implied weights analysis performed with Pee-Wee with the constant of concavity “k” set to 1 is considered main reference regarding the phylogenetic knowledge attained in the study (character changes presented on Appendix 2 refer to trees found under this concavity value). However, other values of “k” are also evaluated, and with the purpose of making classificatory changes, results of weighted analyses with “k” varying from 1 to 3 are taken as reference. Bremer support values for Pee-Wee trees are presented for these analyses only.

RESULTS

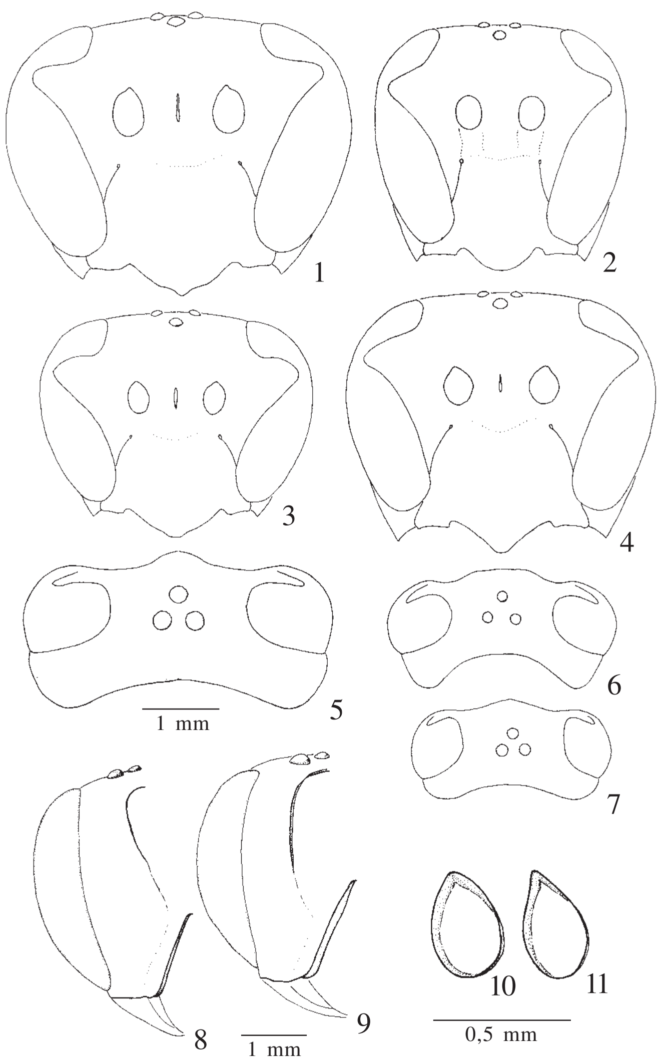
Character analysis (complete data matrix presented in Table II)

HEAD

1. Occipital region: (**0**) with salient carina dorsally and laterally; (**1**) just compressed dorsally and laterally; (**2**) compressed only dorsally; (**3**) occiput unmargined. (Ordered 0-1-2-3).

State 0 occurs in all the genera used as outgroups. In *Mischocyttarus*, however, a carinate occiput occurs only in groups probably distantly positioned from the base of the phylogeny, as in some species of the *heliconius* and *iheringi* groups, in the *prominulus* group, in the subgenus *Omega* (*Monacanthocnemis* of Richards, 1978), and in most species of *Kappa*. Cooper (1996a) recently described *M. onorei*, a species in the subgenus *Monogynoecus* presenting a carinate occiput. This is a remarkable finding since all other species in that subgenus lack an occipital carina. The description of *M. onorei* is incomplete in respect of many of the characters used in this work, so that it could not be included as an independent terminal in the analysis. According to Cooper, *M. onorei* has a pointed clypeus, the pronotal carina is acute at sides, and the pronotal fovea is absent. No other species in *Monogynoecus* presents a similar combination of characters. *Mischocyttarus insolitus* has a pointed clypeus and the pronotal fovea is absent, but the pronotal carina is almost completely reduced at sides, similar to the condition in *M. lecointei*. Inclusion of the states occurring in *M. onorei* as polymorphisms in one of the three species-groups used as terminals in *Monogynoecus* would be too much tentative since that species does not fit easily in any of these groups.

2. Dorsal part of the head behind eyes and ocelli (degree of lengthening backwards, elevation, and profile in dorsal view): (**0**) surface behind ocelli curved and strongly dipping backwards, occipital margin (or the corresponding region) very low, distinctly positioned below the plane of the vertex, dorsal profile variably concave (Fig. 6); (**1**) surface behind ocelli reasonably planar and lengthened backwards, region corresponding to occipital margin quite elevated and practically in the same plane of the vertex, dorsal profile only a little concave (Fig. 5); (**2**) all the posterior dorsal part (and gena) of the head very narrow, surface behind eyes and ocelli very short and with a strong dip backwards, dorsal profile gently concave (Fig. 7). (Unordered)



Figs. 1-11. Frontal view of female head in 1, *M. laurae*; 2, *M. acunai*; 3, *M. metathoracicus*; 4, *M. flavitarsis*; dorsal view of female head in 5, *M. aripuanaensis*; 6, *M. cerberus*; 7, *M. stenoecus*; lateral-posterior view of female head showing hypostomal lamella in 8, *M. ornatus*; 9, *M. chanchamayoensis*; female left antennal socket in 10, *M. malaris*; 11, *M. buyssoni*.

State 1 occurs typically in *M.* (*Mischocyttarus*) *aripuanaensis*, and in *M. flavicans* and *M. carbonarius* of *Clypeopolybia*. Similar shapes were observed in some species of *Polistes* and *Ropalidia*, which nonetheless have an evident occipital carina. State 2 is a putative synapomorphy of *Scytokeraia*.

3. Posterior part of the head around occipital foramen: (**0**) produced into a shallow cavity with a smoothly rounded boundary; (**1**) produced into a deep cavity below, its ventral portion nearly horizontal but not sharply margined; (**2**) produced into a deep cavity below, its ventral portion horizontal, sharply margined, like a shelf (Fig. 135). (Ordered 0-1-2)

State 2 typically occurs in *Omega* and most species of

Table I. Ingroup and Outgroup (OG) terminals used in phylogenetic analyses.

1) *Polistes* Latreille, 1802. (OG)
2) Ropalidiini sensu Carpenter (1993). (OG)
3) Epiponini sensu Carpenter (1993). (OG)

Subgenus *Kappa* de Saussure, 1854.
4) *Michocyttarus immarginatus* Richards, 1940.
5) *Michocyttarus laurae* Silveira, 2006. A species described by Silveira (2006) based on the female holotype only (Venezuela, Merida, Guarunes, no date, P. Anduze; AMNH).
6) *M. tolensis* Richards, 1941.
7) *M. latior* (Fox, 1898).
8) *M. metathoracicus* (de Saussure, 1854).
9) *M. funerulus* Zikán, 1949.

Subgenus *Haplometrobius* Richards, 1978.
10) *M. cerberus* Ducke, 1918; representing *M. nomurae* Richards, 1978 and *M. peruanus* Zikán, 1949.
11) *M. dimorphus* Zikán, 1949 and *M. narinensis* Cooper, 1998. Two quite similar species, characters of male genitalia observed in *M. narinensis* (Colombia, Valle, Buenaventura, Rio Calima, 40m, 8/ix/1995, C. Sarmiento coll.); referred to in matrix as "dimorphus-narinensis".
12) group of *M. mendax* Richards, 1978, sensu Cooper (1996*b*). Material examined: female, holotype of *M. mendax*; female and male, Peru (no date), Ducke collection (MPEG), corresponding respectively to descriptions of *M. montivagus* and *M. reclusus* Cooper (1996*b*); female, Brasil, Pará, Caxiuanã, 18/x/1998 (Silveira & Pena) (MPEG), corresponding to description of *M. tectus* Cooper (1996*b*).
13) group of *M. heliconius iperuae* Richards, 1978. A small group of very similar forms, part of them mistakenly referred by Richards (1945, 1978) to his concept of *M. undulatus* (Ducke, 1904) (see Carpenter, 1999). Material examined: female, Colombia, Putumayo, Mocoa, 25/viii/1978, female, Bolivia, Beni, Rurrenabaque, 270m, 26/iv/1979 (M. Cooper) (NHM); female, Brasil, Pará, S. Norte, Manganês, 1-3/vii/1985 (M. Zanuto), male, Brasil, Acre, P. N. Serra do Divisor, 9/iii/1997 (E.F. Morato) (MPEG); referred to in matrix as "iperuae group".
14) *M. heliconius* Richards, 1945.
15) *M. chanchamayoensis* Richards, 1978. The male was not examined but some characters were obtained in Cooper (1998a).
16) *M. artifex* (Ducke, 1914).
17) *M. interjectus* Zikán, 1935; representing *M. capichaba* Zikán, 1949.
18) *M. sylvestris* Richards, 1945; representing *M. lemoulti* (Buysson, 1908).
19) *Mischocyttarus* (*Haplometrobius*) sp1. Unidentified species similar to *M. peruviensis* Richards, 1945. Material examined: female, Brasil, Amapá, Amapari, Tucano 2, 9-11/xi/1993 (F. F. Ramos) (MPEG); male, Brasil, Amazonas, Estirão do Equador, R. Javarí, ix/1979 (Alvarenga) (MZSP); referred to in matrix as "gr artifex sp".
20) *M. oecothryx* Richards, 1940; representing *M. synoecus* Richards, 1940, *M. nigroclavatus* Zikán, 1949, *M. reflexicollis* Zikán, 1949, *M. undulatus* (Ducke, 1904) and *M. interruptus* Richards, 1978.
21) *M. mirificus* Zikán, 1935; representing *M. ypiranguensis* Fonseca, 1926, *M. schadei* Zikán, 1949, and *M. thrypticus* Richards, 1945.
22) *M. cooperi* Richards, 1978; possibly representing *M. naumanni* Richards, 1978, and *M. vredeni* Richards, 1978.

Table I. Cont.

23) *M. ornatus* Zikán, 1949; representing *M. longicornis* Zikán, 1949.
24) *M. weyrauchi* Zikán, 1949.
25) *M. iheringi* Zikán, 1935; representing *M. travassosi* Zikán, 1949, *M. curytibanus* Zikán, 1949, and *M. saussurei* Zikán, 1949.
26) *Mischocyttarus* (*Haplometrobius*) sp.2 (= *M. undulatus* sensu Richards, 1978; in part). Material examined: Brasil, Mato Grosso, 1 female, 2males, 10/ix/1968, 2 females, 12/ix/1968 (O. W. Richards) (NHM). This is a distinct unnamed species, one of the forms that have been confounded by Richards (1978) under the name "undulatus"; referred to in matrix as "gr iheringi sp"
27) *M. nigropygialis* Zikán, 1949; possibly representing *M. macarenae* Cooper, 1998.
28) group of *M. elegantulus* Zikán, 1949. This terminal combines characters of the female of *M. elegantulus* and those of a male specimen from Colombia, Meta, Villavicencio, 530m, 30/iv/1995 (C. E. Sarmiento, private collection), possibly the same species; representing *M. prominulus* Richards, 1941.
29) *M. silvicola* Zikán, 1949.
30) group of *M. alboniger* Richards, 1978. Small group of unidentified species with morphology and color similar to *M. alboniger*. Material examined: Brasil, female, Amazonas, Rod. AM-010 Km 31 Embrapa, 30/x/1991 (L. F. Albuquerque & J. Hinda), female, Roraima, R. Uraricoera, I. de Maracá, 21-30/xi/1987 (J. A. Rafael e equipe) (INPA); Pará, Bujarú, female, 30/vi/1977 (P. Waldir & L. Braack), female and male, 14/viii/1977, female, 15/viii/1977 (P. Waldir), female, 16/iv/1982 (W. França), Moju, 3 females, 10/viii/1977 (P. Waldir), Belém, Utinga, female and male, 16/x/1996 (O. T. Silveira) (MPEG).
31) *M. confusus* Zikán, 1935; representing part of the species of the group of *M. surinamensis* (de Saussure, 1854) possessing the first metasomal segment short, as in *M. ignotus* Zikán, 1949, *M. hoffmanni* Zikán, 1949, and *M. garbei* Zikán, 1935.
32) *Mischocyttarus* (*Haplometrobius*) sp. 3. Unidentified species, with examined specimens from Panama and other countries of Central America. The male has the antennal apex very short, an atypical condition in the group of *M. surinamensis*. Material examined: Costa Rica, female, Go. Ifito, 14/vii/1957 (Truxal & Menke) (UCDC); México, female, Quintana Roo, nr. Coba Ruins, 20/xii/1982 (S. Meredith) (EMEC); Panamá, 2 females, Rancho Frio, Cerro Pirre Darien, 7/iv/1986 (D. Windsor) (GBFM), Barro Colorado, female, 12/ii/1955 (C. Rettenmeyer), female, 23/vii/1963 (Cavagnaro & Irwin), male 10/viii/1981 (R.B. & L. S. Kimsey) (UCDC); referred to in matrix as "gr surinamensis sp".
33) group of *M. surinamensis* (de Saussure, 1854): This terminal represents the forms more strictly similar to *M. surinamensis*, with a more elongated first metasomal segment, as in *M. bahiaensis* Zikán, 1949, *M. decimus* Richards, 1978, and *M. tricolor* Richards, 1945.

Subgenus *Phi* de Saussure, 1854 (sensu Richards, 1978)
34) *M. itatiayaensis* Zikán, 1935; representing species of the group of *M. alfkenii* (Ducke, 1904) in which the male has the clypeus narrowly separated from the eyes, and the antennomere 13 is two times longer than wide, as in *M. costalimai* Zikán, 1949, *M. araujoi* Zikán, 1949, *M. scitulus* Zikán, 1949, *M. infrastrigatus* Zikán, 1949, and *M. riograndensis* Richards, 1978.
35) *M. alfkenii* (Ducke, 1904); representing *M. flavicornis* Zikán, 1935.
36) *M. basimacula* (Cameron, 1906).

Table I. Cont.

37) *M. mexicanus* (de Saussure, 1854). This and the next two species represent a set of species of the group of *M. flavitarsis* in which the male has a very short antenna, with the apex normal, not “hook-like”, the antennomere 13 being typically very short and wide, as in *M. phthisicus* (Fabricius, 1793), *M. costaricensis* Richards, 1945, and “*M. angulatus* morph *ictericus*” Richards (1945).
38) *M. angulatus* Richards, 1945.
39) *M. mexicanus cubicola* Richards, 1978.
40) *M. extinctus* Zikán, 1935. This species is similar to *M. crypticus* Zikán, (1949) both with the clypeal ventral angle very acute and the apex perfectly rounded. However, *M. crypticus* has the pronotal carina with a distinct lamella and the tyloids of the male antenna are reduced as in remaining species of *Phi*. In *M. extinctus*, the tyloids are larger and well defined as in the other subgenera.
41) *M. consimilis* Zikán, 1949.
42) *M. cassununga* (von Ihering, 1903).
43) *M. pallidipectus* (Smith, 1857). This and the next four species share marked similarities regarding the very wide male gena, and very strong and robust male mandible.
44) *M. flavitarsis* (Saussure, 1854).
45) *M. marginatus* (Fox, 1898).
46) *M. hirtulus* Zikán, 1949.
47) *Mischocyttarus* (*Phi*) sp. Undescribed species very similar to *M. hirtulus*. Material examined: female and male, Colombia, Antioquia, Heliconia, Humareda 1, 15/i/1997 (Y. Vargas) (MPEG); referred to in matrix as “nr hirtulus sp”.
48) *M. tarmensis* Richards, 1945 (= *M. huacapistanus* Zikán).
49) group of *M. hirsutus* Richards, 1945. This terminal represents several examined forms from Colombia similar to *M. hirsutus* Richards, for which no types or identified specimens were available. Material examined: female and male, Nariño, Barbacoas, 1.200m, 22/vii/1995, 2females, Valle, Anchicayá, Hiodroelectrica bajo Anchicayá, El engaño, 260m, 24/iii/1995, female, Caldas, Aguadas La Herencia, 2.170m, 23/i/1996, female, Parque Nacional Tatamá, Risaralda, R. San rafael, 4/1/1993 (C. E. Sarmiento, private collection).
50) *M. wagneri* (Buysson, 1908).
51) *M. alternatus* Zikán, 1949; representing *M. confirmatus* Zikán, 1949.
52) *M. campestris* Raw, 1985. Information about characters of the male were obtained in Raw (1985); representing *M. chapadae* (fox, 1898).

Subgenus *Clypeopolybia* Brèthes, 1923 (sensu Silveira, 1998)

53) *M. richardsi* Zikán, 1949; representing the smaller species of *Clypeopolybia*, like *M. wygodzinkyi* Zikán, 1949, *M. clypeatus* Zikán, 1935, and *M. adjectus* Zikán, 1935.
54) *M. duckei* (Buysson, 1908).
55) *M. flavicans* (Fabricius, 1804).
56) *M. carbonarius* (Saussure, 1854).
57) *M. carbonarius tibialis* Richards, 1978. This form is in fact distinct from the nominotypical taxon. Material examined: Brasil, Amazonas, male, Serra de Parintins, 15/ix/1907 (A. Ducke) (MPEG); Costa Rica, Heredia, 2 females, Est. El Ceibo, PN Braulio Carrillo, 400-600m, ii/1990 (C. Chaves & R. Aguilar) (INBC).

Subgenus *Mischocyttarus* de Saussure, 1853 (sensu Silveira, 2002)

58) *M. acunai* Alayo, 1972.

Table I. Cont.

59) *M. aripuanaensis* Silveira, 1998; male, larva, and nest are unknown.
60) *M. smithii* de Saussure, 1853.
61) *M. drewseni* de Saussure, 1857.
62) *M. tomentosus* Zikán, 1935; representing those species with the first metasomal segment very elongate, as in *M. labiatus* (Fabricius, 1804), *M. melanarius* (Cameron, 1906) and *M. rotundicollis* (Cameron, 1912).

Subgenus *Monogynoecus* Richards, 1941 (sensu Cooper, 1996)

63) *M. lecointei* (Ducke, 1904); representing *M. insolitus* Zikán, 1949.
64) *M. montei* Zikán, 1949; representing *M. foveatus* Richards, 1941.
65) *Mischocyttarus* (*Monogynoecus*) sp. Undescribed species from Brazilian Amazonia. Material examined: Brasil, Amazonas, 3 females, Paraná do Xiboreninho, 7/viii/1979 (Adis e equipe) (INPA), Pará, female and male, Belém, Faz. Velha, 20/vii/1977 (P. Waldir) (MPEG); referred in matrix as “Monogynoecus sp”.

Subgenus *Omega* de Saussure, 1854.

66) group of *M. punctatus* (Ducke, 1904). This terminal combines the female characters found in *M. punctatus* and *M. vaqueroi* Zikán (1949) and the male characters of an undescribed form from Bolivia which Richards (unp. manuscript) labeled with a manuscript name. Material examined: Bolivia, 2 females, Beni, Rurrenabaque, 23/iv/1979, female and male, La Paz, Caranavi, 600m, 16/v/1979 (M. Cooper) (NHM); Brasil, Maranhão, female, lectotype of *M. punctatus* (MPEG), Pará, 2 females, Óbidos, xii/1913, female and male (lacking part of the metasoma) R. Cuminá Mirim, Trombetas, 13/xii/1906 (Ducke) (MPEG), female, Pará (without locality and date) (Baker) (UCDC), Amazonas, female, 60 Km N Manaus, 22/ii/1979 (Montgomery *et al*), female, C. Univ., 4/vi/1982 (J. A. Rafael) (INPA); Panama, female, Barro Colorado, 29/vii/1956 (C. W. & M. E. Rettenmeyer) (UCDC); female, Peru, holotype of *M. vaqueroi* (IOC).
67) group of *M. buyssoni* (Ducke, 1906). Includes at least two undescribed forms and *M. napoensis* Richards (1978). Material examined of the two undescribed species: Brasil, Pará, Serra Norte, 2 females, Serraria, 15/vi/1985 (R. D. Thomaz); 3 females, Fofoca, 16/ix/1985 (M. F. Torres); 2 males, Fofoca, 16/ix/1985 (M. F. Torres) (MPEG).
68) *M. filiformis* (de Saussure, 1854).

Subgenus *Megacanthopus* Ducke, 1904

69) *M. collarellus* Richards, 1940; representing most of species of the subgenus, in which the male has the antennomere 13 strongly enlarged and compressed.
70) group of *M. malaris* Richards, 1978. This terminal represents a smaller subset of species in which the male has the antennomere 13 normal, not enlarged and compressed, as in *M. malaris* Richards, *M. inexpectatus* Cooper (1997) and a third undescribed species from Brasil, Mato Grosso, Buriti, 8/ii/1961 (J. & B. Bechyné) (MPEG). Characters of the male antenna in the analyzed matrix correspond to a specimen from Pará, Belém, Utinga, 9/iii/1977 (A. Y. Harada) (MPEG) similar in general to *M. malaris* (Richards, 1978; Cooper, 1997*b*).

Subgenus *Scytokeraia* Cooper, 1997.

71) *M. stenoecus* Richards, 1978.
72) *M. subornatus* Zikán, 1949.
73) *M. mastigophorus* Richards, 1978.
74) *M. alienus* Richards, 1978.

Kappa. An intermediate condition (state 1) is present in *M.* (*Kappa*) *immarginatus*, and in *Megacanthopus* species.

4. General shape of the head in frontal view: (**0**) head nearly as wide as high, its contour roughly quadrangular or circular (Figs. 2, 4); (**1**) head much wider than high, its contour being laterally prominent at the level of ocular sinus, roughly triangular (Figs. 1, 3).

State 1 is observed only in the subgenus *Kappa*.

5. Hairs on posterior ventral part of the gena: (**0**) short and rarefied, inconspicuous; (**1**) longer and more numerous; (**2**) produced into very long and dense often silvery pilosity. (Ordered 0-1-2)

State 0 occurs in the outgroup and in most species-groups in *Mischocyttarus*. State 2, the extreme condition occurs in *Omega* (*Monacanthocnemis* of Richards, 1978), *Kappa*, and in part of *Phi*. In the latter subgenus, however, one can see an intermediate condition (state 1) in some species like *M. alfkenii* and *M. basimacula*, and in similar way also in the subgenus *Scytokeraia*, and in part of *Megacanthopus*.

6. Frontal region of the head in female: (**0**) not or not remarkably protuberant; (**1**) strongly protuberant.

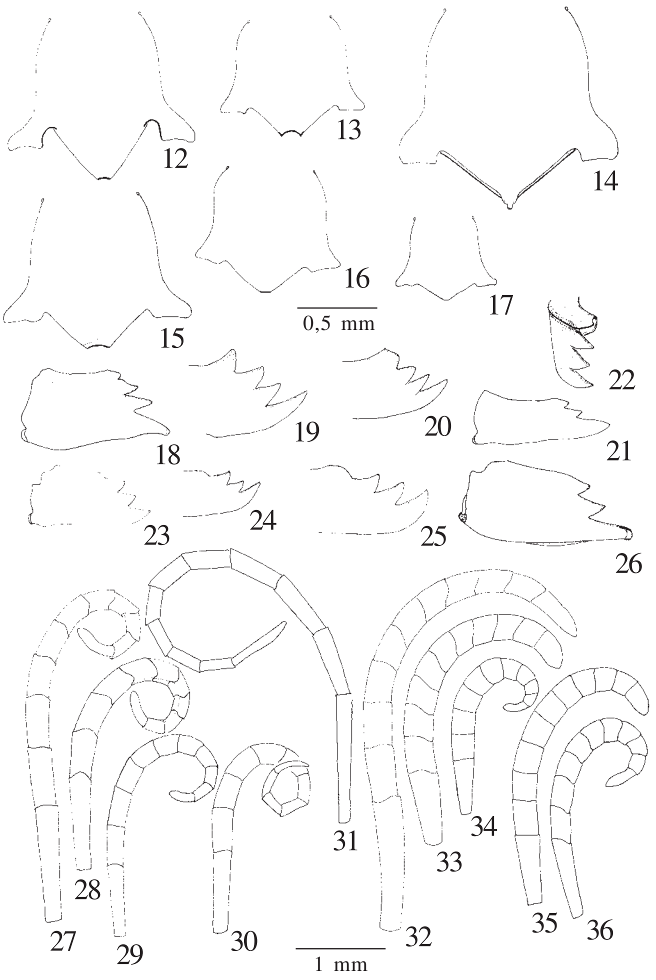
State 1 occurs in the species of the *prominulus* group, and in the *punctatus* group (*Omega*). Maybe this character is correlated with miniaturization of the body. In the *punctatus* group, frons shape looks more inflated in the smaller individuals, as is the case in specimens of *M. vaqueroi*.

7. Distal margin of the clypeus in female (presence and shape of a pre-marginal carina related topologically to the distal transversal row of bristles): (**0**) pre-marginal carina undeveloped, only indicated by a low edge, true margin of clypeus well apparent in frontal view as an acute border (Fig. 136); (**1**) carina developed but receded medially, margin of clypeus as a thin border; (**2**) carina developed, margin of clypeus wider looking as a round border (Fig. 137); (**3**) carina well developed, and projecting downwards beyond true margin of clypeus so delimiting a shallow marginal sulcus (Figs. 138-140). (Unordered)

State 0 occurs in outgroups but was not observed in *Mischocyttarus*. State 1 occurs in three species of the nominotypical subgenus and state 2 occurs in this and in *Clypeopolybia*. State 3 occurs in the remaining subgenera.

8. Apex of the clypeus in female: (**0**) narrowly truncate (Fig. 16); (**1**) pointed lobe (Fig. 14); (**2**) widely truncate (Fig. 15); (**3**) bidentate (Figs. 12-13); (**4**) narrowly rounded (Fig. 17); (**5**) widely rounded (Fig. 2). (Unordered)

State 1, occurring only in the Ropalidiini and Epiponini is uninformative about relationships within *Mischocyttarus*. This state could well correspond to the (unobserved) pointed clypeus of *M. onorei*, as described by Cooper (1996a), a species that also has the occiput carinate, a plesiomorphic character in Polistinae.



Figs. 12-36. Frontal view of female clypeus in 12, *M. duckei*; 13, *M. mastigophorus*; 14, *Parapolybia indica*; 15, *M. drewseni*; 16, *M. iheringi*; 17, *M. elegantulus*; aspect of male mandible in 18, *M. tarmernsis*; 19, *M. pallidipectus*; 20, *M. costalimai*; 21, *M. dimorphus*; 22, 23, *M. richardsi*; 24, *M. labiatus*; 25, *M. imitator*; apical view of female mandible in 26, *M. tolensis*; lateral aspect of male antenna in 27, *M. stenoecus*; 28, *M. interjectus*; 29, *M. surinamensis*; 30, *M.* (*Omega*) sp. (MPEG); 31, *M. subornatus*; 32, *M. duckei*; 33, *M. acunai*; 34, *M.* (*Omega*) sp. (NHM); 35, *M. costalimai*; 36, *M. montei*.

9. Lateral symmetric indentations of the female clypeus: (**0**) indentation shallow or only moderately deep, contour of median lobe of the clypeus continuous with the lateral parts (Figs. 13-17); (**1**) indentation very deep, median lobe of the clypeus appearing detached from the lateral parts (Fig. 12).

State 1 occurs typically in *Clypeopolybia*, but some species in other groups present similar conditions as *M.* (*Phi*) *pallidipectus*, and *M. tectus* of the *mendax* group (*Haplometrobius* sensu Richards, 1978). The latter species-group is treated as polymorphic for this character in the matrix.

10. Margin of hypostoma: (**0**) margin with a low lamella (Fig. 8); (**1**) margin with a very high lamella, particularly ventrally near mandible articulation (Fig. 9).

Table II. Matrix of observed character states in *Mischocyttarus* and other polistine tribes (1 – 62). Symbols: (?) unknown; (-) ambiguous; (*) polymorphism (see footnote list).

	5 10 15 20 25 30 35 40 45 50 55 60
Polistes	0*000000001000000110000000000001200000000*000100000*000000*00
Ropalidiini	0*00000100**000001*0000000*000012-0000001000010000*1-000*0000
Epiponini	0000000100001000002100000000000012-000000102001000011-00040—---
immarginatus	30112034001211012123000210300011333000 2*01000110211012012100 0
laurae	010110340111111010130002103000113330002 00??????????????????????
tolensis	00212034011211002013000210300111333101220100031021001202 12????
latior	30212034001200012013000210300111333101220100011021001202121000
metathoracicus	00212034001200002013000210300112333101220100021021101202121000
funerulus	00212034001200022013000210300112333101220100031021001202121000
cerberus	30000030001100022011021210100011121000000100021021041002012000
dimorphus-narinensis	30000030001100022011021210100012121000000100021021041002 01?000
mendax group	3000003 3*0100000001000021010001212100000001000210110210020 42-00
iperuae group	*0000034 0*11001010100002101000 1*12100000001000210110112020 4????
heliconius	00000340111001010100002101000121210000000???????????????????????
chanchamayoensis	00000340110001010100002101000121210000000?0?0210?1?????????000
artifex	10000033001000121011031210100012121000000010013101101124204?300
interjectus	10000033001000121011001210100012121000000010013102101104204?200
sylvestris	30000033001000020011001210100012121000000010003102101104204 2*00
gr *artifex* sp	30000033001000020011001210100012121000000010002102101104204????
oecothrix	20000033001000121011021210100012121000000010013102101104204 2300
mirificus	30000033001000021011001210100012121000000010001101101104203?300
cooperi	10000030001000111011001210100012121000000010012101101132203 2400
ornatus	10000030001000101011001210100012121000000010012101102132203?500
weyrauchi	10000030001100101012021210100011121000000010012101102132203 2400
iheringi	10000030001000121011001210100012121000000010012101102132203?500
gr *iheringi* sp	00000030001100121011000210100012121000000010012101102132203 2000
nigropygialis	00000030001000121011001210100012121000000010012101102132203?300
elegantulus group	00000134001000202011021210100012121000000010011101103150 10??000
silvicola	00000134001010202011031210100012121000011100111011031501022???
alboniger group	0000013400100020201102121010 0*1222100000110001101103150 1022000
confusus	20000034001010202011021210100012121000000010012101103150102?000
gr *surinamensis* sp	30000034001000002011021210100012121000000010011101101150102?000
surinamensis group	30000034001000102011021210100012121000000010012101103150 1022000
itatiayaensis	30001030001100021012020210100011231000220111001010001002 00?000
alfkenii	30001030001100021012020210100011231000220101001010001002 002000
basimacula	30001030001100021022020210100011231000220101001010001002 00?000
mexicanus	30002030001100011022000210100011232000220101001010001002 002200
angulatus	30002030001100001022020210100011232000220101001010001002 00????
mexicanus cubicola	30001030001100011022000210100011232000220101001010001002 00?000
extinctus	30001034001100021023000210100011232000210100011010001002 00?000
consimilis	30000030001100021013000210100011232000220101011010001002 002000
cassununga	30001030001100021013020210100011232000220101011010001002 002*00
pallidipectus	30002034101100000023000110100011233000220 0*1021110001002 002000
flavitarsis	30002034001100000023000110100011333000220011021110001002 002000
marginatus	30001034001100000013000110100011233000220011011110001002 00?000
hirtulus	30002034001100000023000010100011131000020001011110001002 00?000
nr *hirtulus* sp	30002034001100000023000010100011131000220001011110001002 00?000
tarmensis	30002034001100000023000110110011131000220101011010001002 00?000
hirsutus group	30002030001100010012020110100011232000220101011010001002 002000
wagneri	30001030001100021023000210100011232000220101011010001002 00?000
alternatus	30001030001100021023000210100012232000220101011010001002 00?000
campestris	30000033001100000012000110100011233000220?1?011??0?010??00?000
acunai	30000015000100000012000200110111000010000100001001050112032101
richardsi	20000023101000000001000000111001212100010010000100100000200?000
duckei	20000023100000000001000000111001212100010010010100000000200?000
flavicans	21000023100000000001010000111001111?000100100101000000000 2003000
carbonarius	21000023100000000001010000111001111?000100100101000000000 2003001
carbonarius tibialis	20000023100000000001000000111001112100000010010100000000 02002???
aripuanaensis	21000023000000000001010000011001100000010 0??????????????????????
smithii	300000100000000000010000000110011000010100100001001050112 00????
drewseni	30000012000100000001200000011001100001010010000100101011 2002101
tomentosus	30000023000000000001010000011001200001010010000100102011 2002101
lecointei	30000034000000000102104121010001012100000001000110000214320 32000
montei	30000030000000001101104021010001112100000001000110000214320 32000
Monogynoecus sp	30000030000000002101000021010001112100000001001310000214320 32000
punctatus group	0020213000110*20210103121 0*0011222*00022110001101112150 204?300
buyssoni group	002020300012000202011031210201111 2*2000321100020011111*0104?000
filiformis	002020300012000202001031210201112212000321100020011111501042000
collarellus group	201010300011002020110112101000121210000000100131011011002032*10
malaris group	2010103000 1000?0201101121010001212100000001001010110110020 32310
stenoecus	32001033001000000002100001010001112100000001000230000110020 02300
subornatus	32001033001000000002100001010001112100000001000220000110020 0?200
mastigophorus	32001033001000000001100001010001112100000001000230000210020 0?000
alienus	320010-300100000000110001101000111210000101001230000210020 02300

---

* List of polymorphisms (terminal/character/states): *Polistes* 2(0,1); 43(0,1); 53(0,1); 60(0,3); Ropalidiini 2(0,1); 12(0,1); 13(0,1); 20(0,1); 28(0,1); 52(0,2); 58(0,4); *immarginatus* 40(1,2); *mendax* group 9(0,1); *iperuae* group 1(0,1); 10(0,1); 32(1,2); *sylvestris* 60(0,3); *alboniger* group 30(0,1); *cassununga* 60(0,2); *pallidipectus* 43(0,1); *punctatus* group 14(0,1); 27(2,3); 35(1,2); *buyssoni* group 34(1,3); 54(0,5); *collarellus* group 60(0,3)

State 1 was observed in the species of the *heliconius* group, and in three species of *Kappa*.

11. Antennal sockets and adjacent areas of face and frons in the female: (**0**) frons looking depressed, scarcely swollen, antennal sockets close to each other, separated by distance no longer than their height, socket aperture facing well forwards, with an almost perfectly circular contour, its margin as a freely outstanding elevated lamella, interantennal area variably raised (Figs. 2, 141); (**1**) frons and upper portion of interantennal area more swollen and raised, socket aperture oriented more laterally, contour further apart of a circular shape, often angularly narrowed above, marginal lamella looking as if turned and compressed outwards (Figs. 1,3-4, 10-11, 142).

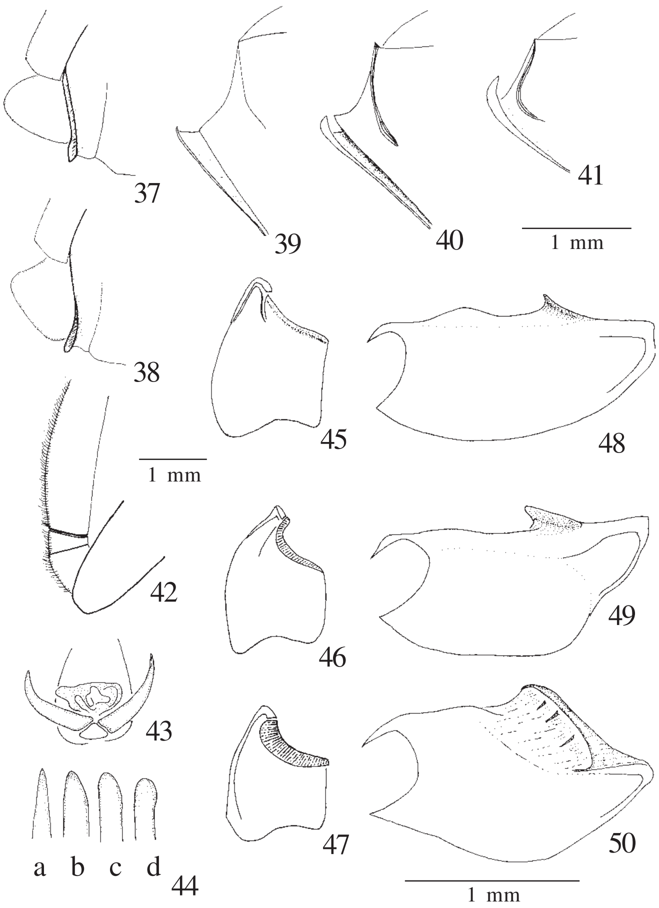
State 0 occurs in all the outgroup genera except *Belonogaster*. Within *Mischocyttarus*, it was observed in the subgenera *Mischocyttarus* s. str., *Clypeopolybia* (excepting the smaller species akin to *M. richardsi*), and *Monogynoecus*. State 1 occurs in all remaining groups in somewhat variously appearing conditions. In *Kappa* and most species of *Phi*, the interantennal area is comparatively wider and more raised, the upper portion shaped as a sloping surface that is continuous with the frontal region. In *Megacanthopus* and in the groups of *M. cerberus*, *M. surinamensis*, *M. prominulus*, and most of the *artifex* group, the interantennal area tends to be much more planar and vertical, presumably correlated with a narrower less swollen clypeus. But the rather subtle nature of the variation in form, and the occurrence of intermediate shapes restrict the recognition of additional states.

12. Distance between posterior ocelli: (**0**) posterior ocelli distinctly approximated, often separated by less than one diameter; (**1**) posterior ocelli well-separated (but not exaggeratedly) by more than one diameter, the three ocelli positioned as the vertices of an equilateral triangle; (**2**) posterior ocelli separated by nearly two (or more) diameters, the three ocelli distinctly positioned as the vertices of a low triangle. (Ordered 0-1-2)

State 1 occurs in *Polistes* and *Ropalidia*, and in various groups within *Mischocyttarus*, typically in the subgenus *Phi*. State 0 also has a wide distribution. State 2 is observed only in part of *Kappa* and part of *Omega*.

13. Hairs on the eye of the female: (**0**) eye with sparse and very short hairs, not or scarcely visible at the dissection microscope; (**1**) eye with more numerous and longer hairs, distinct at the dissection microscope even at medium magnification.

In the outgroup genera, state 1 could be observed in some species of *Ropalidia*, in *Agelaia* and *Apoica*. Within *Mischocyttarus*, it occurs in a few species of *Kappa*, and of the *surinamensis* and *prominulus* groups.



Figs. 37-50. Aspect of mesoscutal lamella in 37, *M. flavitarsis*; 38, *M. carbonarius*; lateral aspect of pronotum in 39, *M. flavitarsis*; 40, *M. reflexicollis*; 41, *M.* (*Omega*) sp. (MPEG); basal ring-like sulcus on femur in 42, *M. carbonarius*; last hind tarsal segment and claw in 43, *M. lecointei*; apex of inner hind tarsal claw in 44a, *M. aripuanaensis*; 44b, *M. carbonarius*; 44c, *M. wygodzinskyi*; 44d, *M. interjectus*; ventral aspect of proepisternum in 45, *M. sylvestris*; 46, *M. montei*; 47, *M. confuses*; lateral aspect of female coxa in 48, *M. labiatus*; 49, *M. flavitarsis*; 50, *M. laurae*.

14. Anterior face of the mandible in the female: (**0**) distal portion of the anterior face of the mandible without a prominent external edge, the transition between the anterior and lateral main surfaces appearing rounded and continuous in apical view; (**1**) distal portion of the anterior face of the mandible with a prominent external edge, distinct in apical view (Fig. 22).

State 1 was observed in the *Kappa* species *M. immarginatus*, *M. tolensis* and *M. laurae*, and in a few forms of the *punctatus* group of subgenus *Omega*.

MESOSOMA

15. Anterior margin of the pronotum: (**0**) margin with the lamella not reflexed (Fig.39); (**1**) margin with the lamella reflexed (not more than 180 degrees) (Fig. 40); (**2**) margin with the lamella wide and strongly reflexed, especially at the center (more than 180 degrees) (Figs. 41, 52, 55-56, 58, 144). (Ordered 0-1-2)

State 2 is an extreme condition with a rather narrow distribution, occurring in the subgenus *Omega* (*Monacanthocnemis* of Richards, 1978*)*, and in the *prominulus* group and part of the *surinamensis* group. A similar form was observed in most species of *Megacanthopus*, represented in the analysis by *M. collarelllus*. In *Megacanthopus*, however, the shape of the lamella seems to be correlated with the presence of a lateral spine that is unique within the genus *Mischocyttarus* (Fig. 56). Cooper (1997b) recently described *M. inexpectatus*, which lacks several apomorphies typical of the *collarellus* group as well as of *Megacanthopus* sensu Richards (1978). In spite of the very characteristic pronotal carina, clearly indicating a close relationship with remaining *Megacanthopus* species, *M. inexpectatus* does not present a lateral pronotal spine, and the anteromedian lamella is not typically wide and reflexed (Cooper's figure 1). Because this species could not actually be examined, the state in terminal "malaris group" was coded as ambiguous ("?"). State 1 is an intermediate condition observed in several *Haplometrobius* groups (sensu Richards, 1978), and in *M. laurae*.

16. Secondary margin behind the anteromedian lamella of the pronotum: (**0**) absent (Figs. 39, 41); (**1**) present as a low obtuse carina not projecting forwards; (**2**) present as a high acute carina strongly projecting forwards (Fig. 40). (Ordered 0-1-2)

This character was widely used by Richards (1978) in the recognition of species-groups, especially in *Phi* and *Haplometrobius*. However, it is highly homoplasious.

17. Anterior margin of the proepisternum: (**0**) margin low, not reflexed, lateral portion shaped as a narrow collar without an acute border directed backwards (Fig. 45); (**1**) margin low, not reflexed, lateral portion shaped as a wider collar with an acute border directed backwards, but not really detached or raised (Fig. 46); (**2**) margin elevated and strongly reflexed, lateral collar very wide and quite freely detached (Fig. 47). (Ordered 0-1-2)

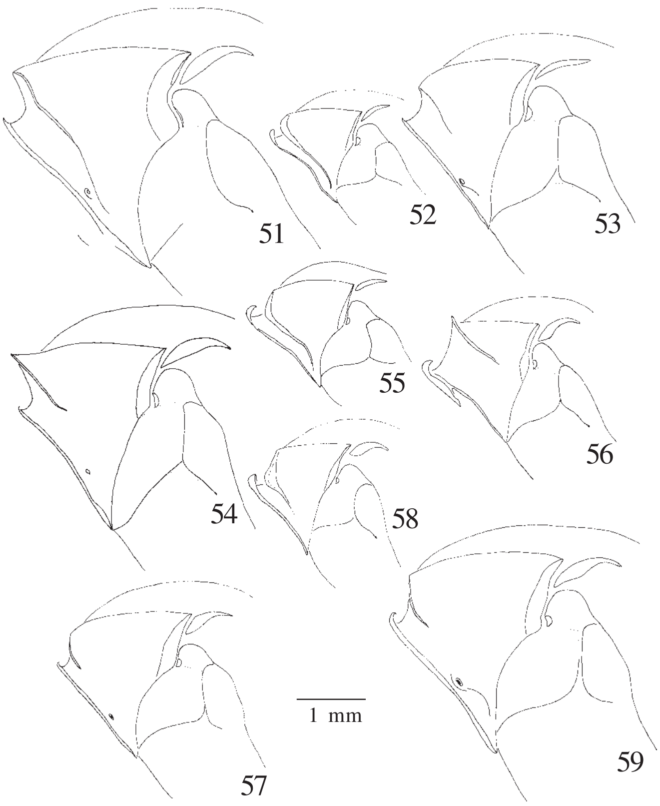
State 0 occurs in the outgroup genera, and in *Mischocyttarus* s. str., *Clypeopolybia*, *Scytokeraia* and some species of *Phi* and *Haplometrobius* (sensu Richards, 1978). State 1 is observed in *Monogynoecus*, most species of *Phi* and *Haplometrobius*, and in *M. laurae*. State 2 occurs in *Megacanthopus*, *Omega* and *Kappa*, and a few groups of *Haplometrobius* (sensu Richards, 1978).

18. Pre-marginal raised crest on proepisternum ("double-margined" condition of Richards, 1978): (**0**) absent; (**1**) present.

State 1 occurs only in *M.* (*Kappa*) *immarginatus* and in the *punctatus* group of the subgenus *Omega*.

19. Pronotal carina at sides: (**0**) lamellate and extending downwards; (**1**) lamellate not extending downwards; (**2**) obtuse, lamella reduced (Fig. 143). (Ordered 0-1-2)

State 2 has a scattered distribution, certainly the result of multiple origins, but it is probably useful in the recognition of less inclusive groups. One can see the reduced condition in part of *Phi*, part of *Scytokeraia*, in *M.* (*Kappa*) *immarginatus*, and in the *lecointei* group of the subgenus *Monogynoecus*.



Figs. 51-59. Lateral aspect of pronotum and mesopleuron in 51, *Polistes testaceicolor*; 52, *M.* (*Omega*) sp. (NHM); 53, *M. flavitarsis*; 54, *M. flavicans*; 55, *M.* (*Omega*) sp. (UCDC); 56, *M. saturatus*; 57, *M. metathoracicus*; 58, *M. filiformis*; 59, *M. laurae*.

20. Central portion of the pronotal carina: (**0**) carina well developed, angularly raised at the center; (**1**) carina evenly raised from side to side; (**2**) carina partially reduced at center, without a distinct lamella but its linear course still perceptible; (**3**) carina completely reduced at center. (Ordered 0-1-2-3)

State 2 occurs typically in part of the species of *Phi*, but similar conditions are observable in *M. drewseni* and *M. acunai* (subgenus *Mischocyttarus* s. str.), and the two unrelated species *M. interruptus* (*artifex* group) and *M. weyrauchi* (*iheringi* group). State 3 also occurs in *Phi*, and in all species of *Kappa*.

21. Slope of the antero-dorsal part of the pronotum (including carina) in lateral view: (**0**) nearly vertical (Fig. 53, 56, 57, 59); (**1**) with a strong negative slope, antero-dorsal face distinctly projecting forwards as a roof over the region of the anterior margin (Fig. 51, 54).

Within *Mischocyttarus*, state 1 was observed only in the larger species of *Clypeopolybia* (*M. flavicans* and *M. carbonarius*), and two species of *Mischocyttarus* s. str. (*M. aripuanaensis* and *M. tomentosus*). A similar but certainly unrelated form was observed in one species of *Polistes* (Fig. 51).

22. Humeral region of the pronotum: (**0**) well developed,

angular but without a prominent lobe (Fig. 60); (**1**) humeral region with a distinctly rounded contour (Fig. 61); (**2**) with well developed and laterally produced lobe (Fig. 62); (**3**) with greatly developed lobe projecting forwards (Fig. 63); (**4**) humeral region strongly reduced, its contour seen from above nearly continuous with the anterior region of the pronotum (Fig. 64). (Unordered)

State 0 occurs in almost all of the outgroup genera, with the exception of *Polybioides* where the humeral region is strongly reduced and the pronotal carina is completely absent, this being an autapomorphy of the genus. In *Belonogaster*, which also lacks a pronotal carina, the humeral region is more produced and angular, a feature corresponding well to state 0. States 1 is an autapomorphy of *Megacanthopus*, state 3 is typically observed in subgenus *Omega* (*Monacanthocnemis* of Richards, 1978*)*, and state 4 is observed in most species of *Monogynoecus*.

23. Pronotal fovea: (**0**) present; (**1**) absent.

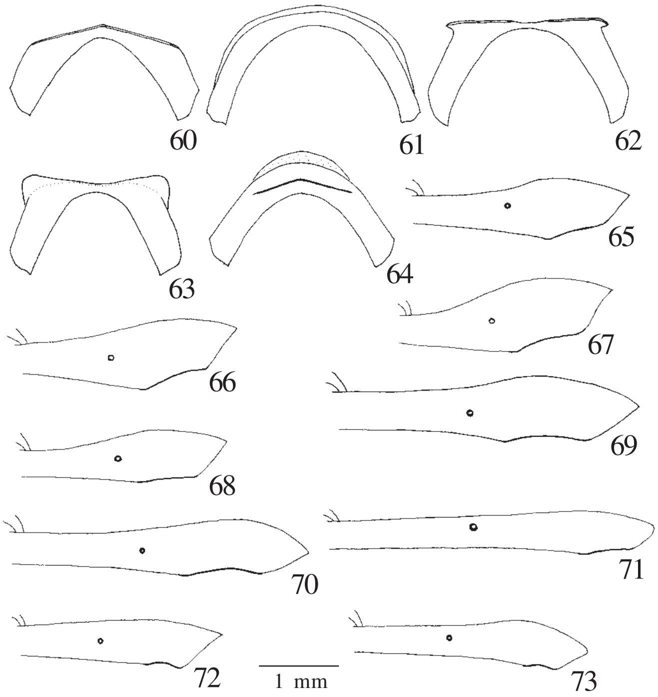
State 0 occurs primitively in most of the outgroup genera, with exception of *Ropalidia* and *Belonogaster*. State 1 had probably at least two independent origins in *Mischocyttarus*.

24. Inner margin of the anterior coxa. (**0**) very low (Fig. 48); (**1**) more raised but weakly reflexed (Fig. 49); (**2**) raised and strongly reflexed (Fig. 50). (Ordered 0-1-2)

This was one of the two main characters used by Richards (1978: 273; first dichotomy of the key for the *Mischocyttarus* subgenera) to differentiate *Mischocyttarus* s. str. and *Clypeopolybia* from the remaining subgenera. Richards did not notice (neither did Cooper, 1997a) that state 0 occurs in *M. mastigophorus* and related species, as well as in some *Phi* species like *M. hirtulus* and *M. spadiceus* Zikán (= *M. commixtus* Richards). Furthermore, in some other species of *Phi*, such as *M. flavitarsis*, *M. pallidipectus*, and *M. marginatus* the margin of the anterior coxa presents an intermediate condition here referred to as state 1. Finally, to make things worse, *M. acunai*, considered by Richards (1978) as part of *Monocyttarus* (= *Phi*), but an evident member of *Mischocyttarus* s. str. (see Silveira, 2002) has a raised and reflexed inner margin. This character has a far more complicated distribution than previously considered by other authors.

25. Ring-like sulcus on the base of the fore and mid femora: (**0**) present (Fig. 42); (**1**) absent.

This is the other main character used by Richards (1978) to distinguish *Mischocyttarus* s. str. and *Clypeopolybia* from the remaining subgenera. State 0 occurs in the outgroup, in all species of *Mischocyttarus* s. str., and in *Clypeopolybia* sensu Silveira (1998). State 1 is then a putative synapomorphy of a major clade comprising all remaining groups of *Mischocyttarus*, including the *heliconius* group of Richards (1945). It is indeed intriguing that, given the perfectly consistent distribution of this character, Richards (1978) nevertheless decided to include *M. heliconius* and related species (that lack a basal sulcus) in *Clypeopolybia*.



Figs. 60-73. Dorsal aspect of pronotum in 60, *M.* (*Monogynoecus*) sp. (INPA); 61, *M. saturatus*; 62, *M. weyrauchi*; 63, *M.* (*Omega*) sp. (NHM); 64, *M. foveatus*; lateral aspect of first metasomal segment in 65, *M. mastigophorus*; 66, *M. lecointei*; 67, *Mischocyttarus* sp. gr. *heliconius* (MPEG); 68, *M. cassununga*; 69, *M. mexicanus*; 70, *M. basimacula*; 71, *M. filiformis*; 72, *M. buyssoni*; 73, *M.* (*Omega*) sp. (MPEG).

26. Fore femur in the female: (**0**) fore femur in section with a roughly round contour, not noticeably flattened posteriorly; (**1**) fore femur with its posterior surface strongly flattened, with a longitudinal sharp edge ventrally, this sometimes appearing "lamellate".

State 1 is an extreme condition occurring in *Clypeopolybia* only. A moderate degree of flattening could be observed in a few species of *Mischocyttarus* s. str., *Phi*, and *Kappa*.

27. Pronotum and mesopleuron in lateral view: (**0**) posterior margin of the pronotum laterally strongly curved below the pronotal tubercle, the ventral angle being positioned just below the tubercle; dorsal mesepisternal plate oblique, pleuron not strongly protuberant (Fig. 51); (**1**) posterior margin of the pronotum laterally nearly straight below the pronotal tubercle, the ventral angle being in a more anterior position; dorsal mesepisternal plate oblique, pleuron not strongly protuberant; humeral region short, distance between the extremity of the pronotal carina and tubercle equal to or less than the distance between the latter and the posterior angle of the pronotum (Figs. 53, 54, 56); (**2**) posterior margin of the pronotum laterally nearly straight below the pronotal tubercle, the ventral angle being in a more anterior position; dorsal mesepisternal plate shortened below, pleuron strongly protuberant; humeral region short, distance between the extremity of the pronotal carina

and tubercle equal to or less than the distance between the latter and the posterior angle of the pronotum (Figs. 52, 58); (**3**) posterior margin of the pronotum laterally strongly curved below the pronotal tubercle, the ventral angle, however, being in a position more anterior than that of the tubercle; dorsal mesepisternal plate wide and "horizontal", pleuron strongly protuberant; humeral region longer, distance between the extremity of the pronotal carina and tubercle clearly longer than the distance between the latter and the posterior angle of the pronotum (Figs. 55, 57, 59). (Unordered)

State 0 occurs only in the outgroup genera, being typically observed in *Polistes*. State 1 is a putative synapomorphy of *Mischocyttarus* as a whole, and states 2 and 3 are putative synapomorphies respectively of *Omega* (*Monacanthocnemis* of Richards, 1978*)* and *Kappa*, but one form in the *punctatus* group of *Omega* (a female from Panamá; UCDC, Bohart Museum) presents a morphology similar to the condition observed in *Kappa* species. So the *punctatus* group is scored as polymorphic for this character.

28. Margin of the mesoscutum adjacent to tegula: (**0**) with a complete laterally projecting margin (Fig. 37); (**1**) anterior two-thirds of the margin reduced (Fig. 38).

State 0 occurs primitively in *Polistes* and the other genera of the outgroup, with the exception of *Ropalidia* and *Parapolybia*. In *Mischocyttarus* it can be observed in a great majority of groups and species. State 1 occurs typically in *Mischocyttarus* s. str. and *Clypeopolybia*, but similar forms were observed in the *Phi* species *M. tarmensis*, and *M. spadiceus* Zikán (= *M. commixtus* Richards).

29. Number of spurs on mid-tibia: (**0**) two; (**1**) one.

State 1 is a putative synapomorphy of a clade comprising most species of *Omega* (*Monacanthocnemis* of Richards, 1978*)* except those of the *punctatus* group.

30. Ventral surface of the hind femur in the female: (**0**) surface planar or slightly round; (**1**) surface with a shallow longitudinal sulcus.

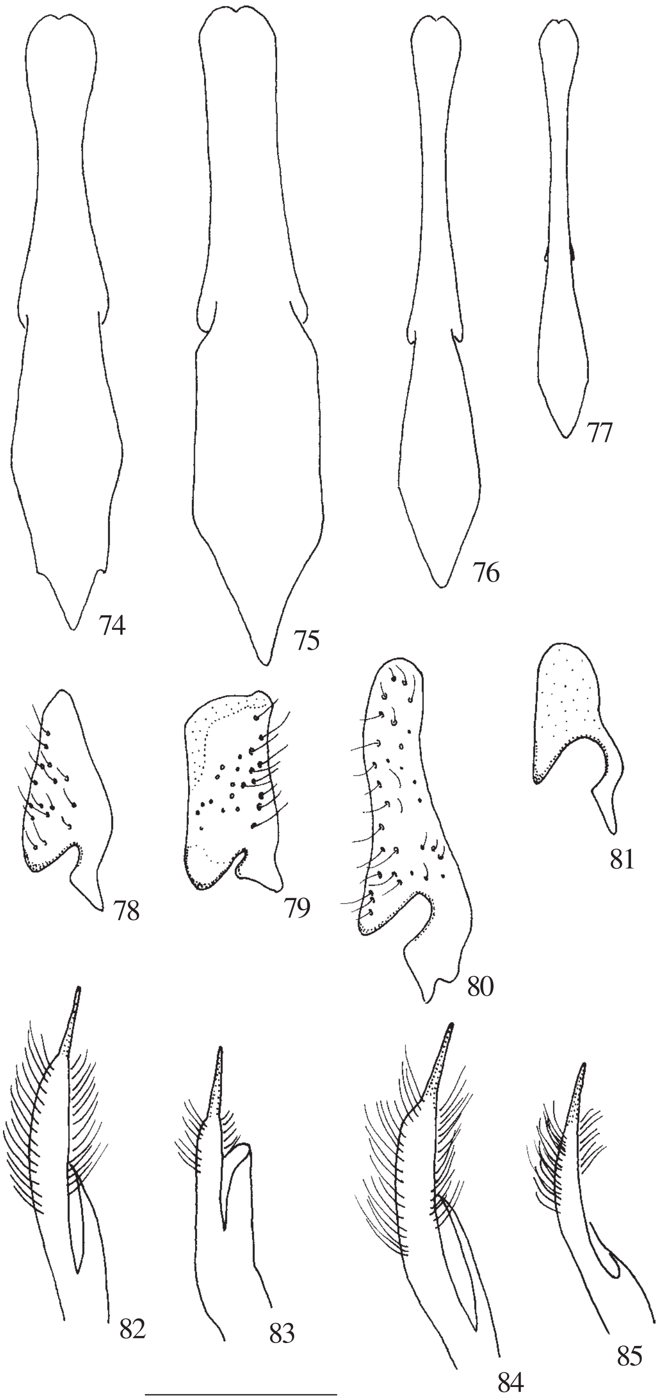
State 1 is observed in *M. acunai*, in all species of *Omega* (*Monacanthocnemis* of Richards, 1978*)* and in part of *Kappa*, and also in some forms of the *prominulus* group represented in the analysis by the terminal "alboniger group".

31. Symmetry of tarsal inner and outer lobes: (**0**) tarsal segments with symmetric lobes; (**1**) tarsal segments with asymmetric lobes, the inner one larger.

State 1 is a putative synapomorphy of the genus *Mischocyttarus*.

32. Hind tarsal claws: (**0**) symmetric or nearly, sharply pointed (Fig. 43); (**1**) asymmetric, the internal one larger and presenting the apex sharp or narrowly pointed (Figs. 44 a and b); (**2**) asymmetric, the internal one larger and presenting the apex wide and rounded (Figs. 44 c and d). (Ordered 0-1-2)

State 0 occurs in the outgroup, and in the group of *M. lecointei* of subgenus *Monogynoecus*. None of the other two states present consistent distributions, but state 1 most often occurrs in the subgenera *Mischocyttarus* s. str., *Clypeopolybia*, *Monogynoecus*, *Scytokeraia*, *Phi*, and



Figs. 74-85. Male aedeagus in 74, *M. drewseni*; 75, *M. acunai*; 76, *M. duckei*; 77, *M. mastigophorus*; male digitus in 78, *M. drewseni*; 79, *M. acunai*; 80, *M. flavicans*; 81, *M. mastigophorus*; male parameral spine in 82, *M. drewseni*; 83, *M. acunai*; 84, *M. flavicans*; 85, *M. mastigophorus*.

Kappa, whereas state 2 is more frequently observed in the subgenera *Megacanthopus*, *Haplometrobius*, and *Omega*.

33. Shape of propodeum: (**0**) with anterior medial surface raised and "horizontal", planar at sides and without lateral posterior concavity; (**1**) with anterior medial surface not noticeably raised, oblique, lateral surface planar and without lateral posterior concavity; (**2**) anterior medial surface not noticeably raised, oblique, lateral surface inflated and with lateral posterior concavity; (**3**) with anterior medial surface raised and "horizontal", lateral surface inflated and with lateral posterior concavity. (Ordered 0-1-2-3)

State 0 is restricted to *Mischocyttarus* s. str. State 1 is observed in the outgroups and various subgenera and species-groups within *Mischocyttarus*, whereas 2 and 3 are generally observed in *Phi* and *Kappa* respectively.

34. Propodeal median furrow: (**0**) deep and triangular; (**1**) deep and linear; (**2**) shallow linear or absent; (**3**) wide and triangular. (Ordered 0-1-2-3)

State 0 is restricted to *Mischocyttarus* s. str. and state 1 is observed in the two *Clypeopolybia* species *M. flavicans* and *M. carbonarius*. State 2 occurs in the outgroups and various subgenera and species-groups within *Mischocyttarus*, while 3 is generally observed in *Phi* and *Kappa*.

35. Shape of metanotum: (**0**) transversal; (**1**) triangular and flattened or very low; (**2**) triangular and moderately convex; (**3**) triangular and strongly convex. (Ordered 0-1-2-3)

State 0 occurs in *Polistes* and in *Mischocyttarus* s. str. State 1 occurs is the smaller species of *Clypeopolybia* and in several other species-groups in *Mischocyttarus*. State 2 occurs in most *Phi* species and in *Omega* (*Monacanthocnemis* of Richards, 1978*)*, whereas state 3 was observed in all species of *Kappa* and some of *Phi*, related to *M. flavitarsis*. Shape of the propodeum is variable "within" the two *Clypeopolybia* species *M. flavicans* and *M. carbonarius*, and was then considered inapplicable in these cases. Such was also the treatment given to ropalidiines and epiponines where considerable variation exists between species, with shapes evidently unrelated to those observed in *Mischocyttarus*.

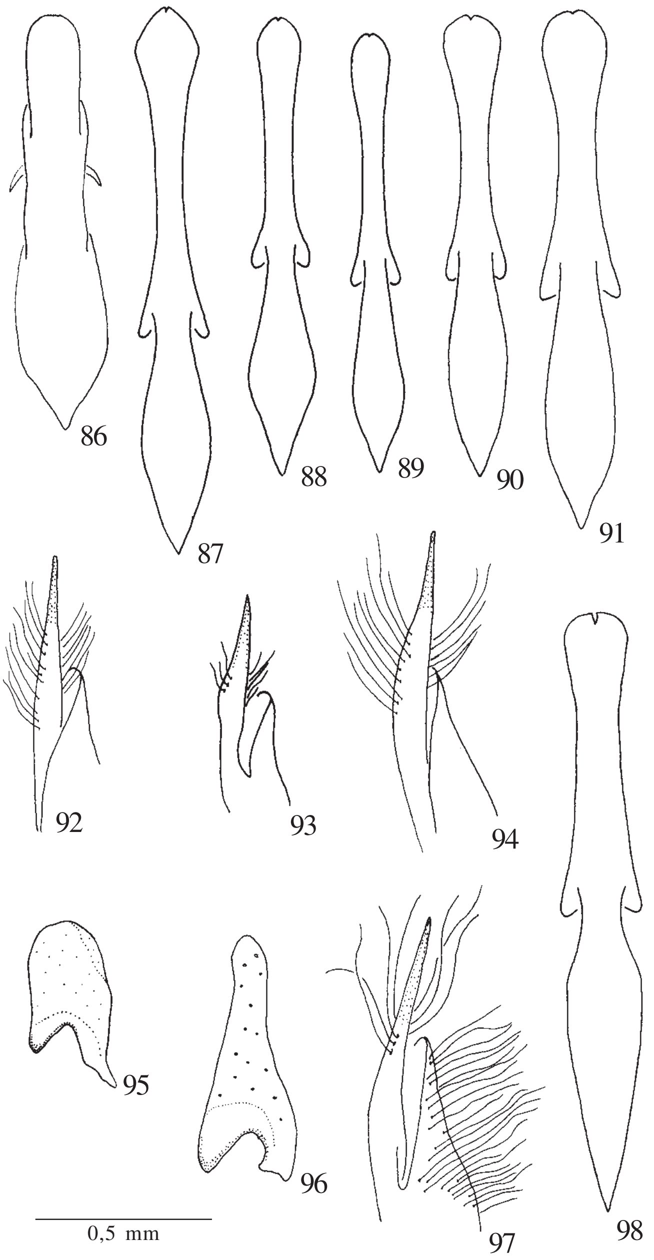
36. Upper edge of the propodeal lateral posterior concavity: (**0**) smoothly rounded, edge not actually defined (Figs. 165-166); (**1**) upper edge well defined and sharp, continuous with the posterior margin of the propodeum adjacent to valvular region, clearly separating the lateral concavity from the central dorsal portion of the propodeum (Figs. 167).

State 1 occurs exclusively and in most species of *Kappa*, being absent only in *M. immarginatus* and in *M. laurae*.

METASOMA

37. Metasoma in cross section: (**0**) with a circular or dorso-ventrally flattened contour; (**1**) narrow, with a laterally compressed contour.

State 1 was found in most species of *Mischocyttarus* s. str., which typically have an elongate first metasomal segment.



Figs. 86-98. Male aedeagus in 86, *M.* (*Monogynoecus*) sp. (MPEG); 87, *M. marginatus*; 88, *M. alfkenii*; 89, *M.extinctus*; 90, *M. bertonii*; 91, *M. tolensis*; 98, *M. immarginatus*; male parameral spine in 92, *M. extinctus*; 93, *M.* (*Monogynoecus*) sp. (MPEG); 94, *M. marginatus*; 97, *M. immarginatus*; male digitus in 95, *M.* (*Monogynoecus*) sp. (MPEG); 96, *M. immarginatus*.

38. Lateral aspect of petiolar portion of the first metasomal segment: (**0**) limit between tergum and sternum rounded, sometimes demarcated by a sulcus; (**1**) limit between tergum and sternum produced into a prominent shining edge, sternum distinctly flattened.

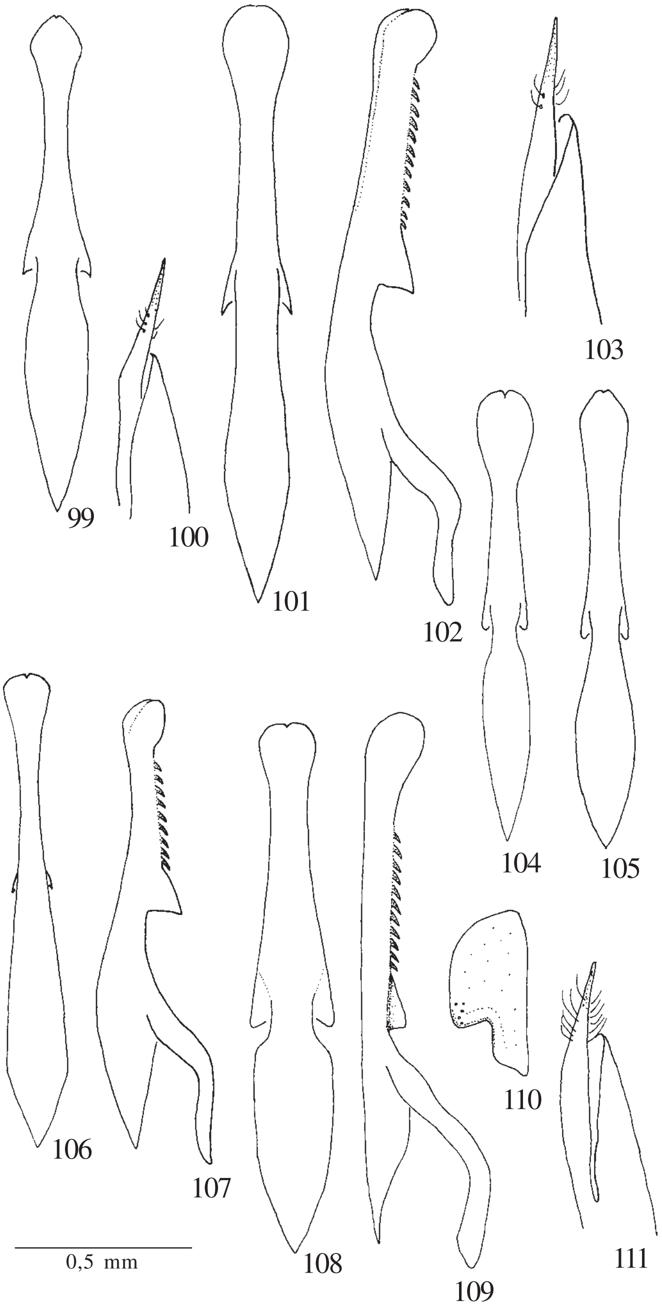
State 1 is a putative synapomorphy of a clade comprising most species of *Kappa*, being absent only in *M. immarginatus* and *M. laurae*.

39. General shape of the first metasomal segment: (**0**) profile of the segment with a distinct ventral angle at a point positioned posteriorly to the spiracle, tergal margins not too closely approximated below at this point, distal portion of the segment in lateral view oriented obliquely "upwards" (Figs. 65-67); (**1**) segment strongly compressed, its profile very deep ventrally with a quite prominent ventral angle positioned posteriorly to the spiracle, tergal margins closely approximated ventrally at this point, so that the sternum has a constricted appearance, distal portion of the segment in lateral view oriented obliquely "upwards"; (**2**) segment with a shallow profile, ventrally with a poorly developed angle at a point positioned posteriorly to the spiracle, tergal margins not noticeably approximated at this point, distal portion of the segment lengthened backwards and oriented in line with the petiole, the distal expanded portion of the sternum in lateral view always longer than a distance measured in forward direction from the beginning of the expanded part up to the spiracle (Figs. 68-70); (**3**) segment long and very narrow, even distally, its profile sometimes slightly curved downwards, no ventral angle posterior to the spiracle, but distal portion of the segment not noticeably lengthened backwards, the distal portion of the sternum in lateral view shorter than a distance measured in forward direction from the beginning of the expanded part up to the spiracle (Figs. 71-73). (Unordered)

In spite of the distinct "subsessile" aspect of the first metasomal segment in *Polistes*, the condition in this genus is considered equivalent to state 0 found in other outgroup genera and in various groups within *Mischocyttarus*. In *Ropalidia* the shape of the segment seems highly variable, being in some instances very similar to that typically observed in *Polistes*. In these cases, the fundamental aspect considered was the presence of a ventral angle in the profile of the segment situated posteriorly to the spiracle. State 1 is characterized by the compressed aspect of the ventral part of the segment, occurring in *Mischocyttarus* s. str. and part of *Clypeopolybia*. Sate 2 occurs in the subgenera *Phi*, *Kappa*, and in the *punctatus* group of *Omega* (*Monacanthocnemis* of Richards, 1978). State 3 was found only in the remaining species of *Omega*.

40. Lateral margin of the distal expanded portion of the first metasomal sternum: (**0**) margin raised and sharp (Fig. 170); (**1**) margin reduced for the most part, sharp only on its distal extremity; (**2**) margin completely reduced (Figs. 171-172). (Ordered 0-1-2)

State 0 occurs in the outgroup genera and in most groups of *Mischocyttarus*. States 1 and 2 occur in *Phi*, in most of the species of *Kappa*, and in *Omega* (*Monacanthocnemis* of Richards, 1978). The intermediate state 1, however, could also be observed in the *prominulus* group, and in some species of *Scytokeraia*, like *M. alienus*.



Figs. 99-111. Male aedeagus dorsal in 99, *Mischocyttarus* sp. gr. *artifex* (MZSP); 101, *M. artifex*; 104, *M. weyrauchi*; 105, *M. cooperi*; 106, *M. interjectus*; 108, *M. nigropygialis*; male aedeagus lateral in 102, *M. artifex*; 107, *M. synoecus*; 109, *M. nigropygialis*; male parameral spine in 100, *Mischocyttarus* sp. gr. *artifex* (MZSP); 103, *M. artifex*; 111, *M. nigropygialis*; male digitus in *M. nigropygialis*.

41. Hairs and tegument of the basal portion of the first metasomal sternum: (**0**) sternum with a dense cover of short hairs, also presenting longer more scattered ones; (**1**) sternum without a dense cover of short hairs, tegument shining, with few and scattered long hairs (Figs. 168-169).

State 1 occurs in part of the species of the *prominulus* group, and in subgenus *Omega* (*Monacanthocnemis* of Richards, 1978).

MALE CHARACTERS

42. Width of gena in the male: (**0**) wide, similar to condition in the female; (**1**) distinctly narrower than in the female.

State 0 occurs in *Polistes*, *Belonogaster*, and in a few species of the *flavitarsis* group of *Phi*. State 1 is the prevalent condition both in the outgroup genera and within *Mischocyttarus*, being certainly the primitive state in the genus.

43. Separation between clypeus and eye in the male: (**0**) contiguous; (**1**) separate.

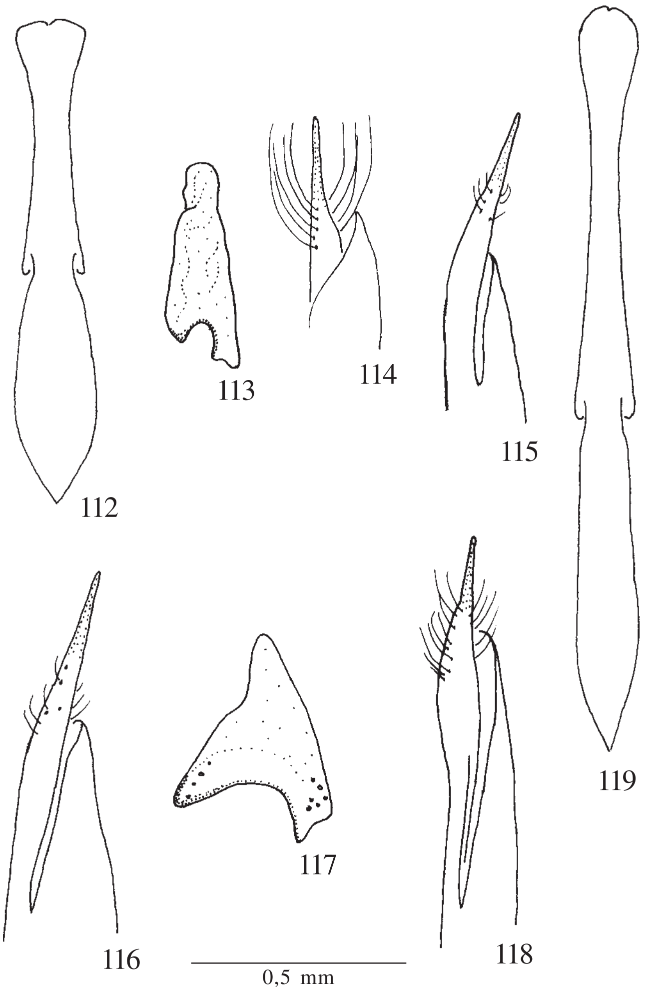
Some species in *Polistes*, especially in the subgenus *Aphanilopterus*, present a narrow separation between clypeus and eye in the male, but the primitive condition in the genus is that in which the two structures are contiguous (Carpenter, 1996). In *Mischocyttarus*, state 1 could be observed in some species of subgenus *Phi*.

44. Tyloids on the ventral surface of flagellomeres of the male antenna: (**0**) well defined, elongate, with rectangular or oval shape (Figs. 145-155, 157-158); (**1**) present but smaller or very reduced, their limits imprecise, sometimes fragmented, not very shining (Figs. 156, 159-161); (**2**) absent. (Ordered 0-1-2)

Antennal tyloids appear at the dissection microscope as areas with a different texture, often more raised and shining than circumjacent areas of the flagellomeres. At the scanning microscope they are characterized by the absence (or extreme rarity) of placoid sensilla and also of those bristle-like sensilla with spiraled cuticular patterns typical of other zones of the flagellomeres. This may be seen especially in figures 146 and 149 showing in detail the limit between tyloid and circumjacent area in *Ropalidia romandi* and *Mischocyttarus* (*Scytokeraia*) *mastigophorus*. State 1 occurs in the great majority of *Phi* species, with the only noted exception of *M. extinctus* (Fig. 158). In some species of *Ropalidia* and *Polybioides*, tyloids may be quite small, with a circular shape, but they also have a more raised and shining aspect than in *Phi* species (Fig. 146). Furthermore, according to currently accepted relationships among the basal lineages of Polistinae (Carpenter, 1991, 1993), the occurrence of well developed tyloids in *Polistes*, *Parapolybia* and *Belonogaster* indicate indeed that the conditions observed in *Ropalidia* and *Polybioides* are convergently derived. In some species of *Kappa*, the tyloids of basal segments appear reduced and fragmented, as in *M. immarginatus* (Fig. 156), but those on more distal segments have a normal aspect. The complete absence of tyloids in *Apoica* and *Agelaia* represents one of the autapomorphies of Epiponini (Carpenter, 1991).

45. Erect conspicuous hairs on the ventral surface of the flagellum of the male antenna: (**0**) absent (Figs. 145-147, 149-150, 153, 156-161); (**1**) present (Figs. 148, 151-152, 154, 155).

Richards (1978) used the name “cilium” (pl. cilia) to refer to the hairs on the antenna of males specially in groups like *Haplometrobius* and *Megacanthopus*, in which hairs tend to be longer and more numerous. However, reasonably conspicuous erect hairs can be found in other groups too, presenting a somewhat continuous variation in length and density of occurrence, making it difficult to recognize more than one “ciliate” state.



Figs. 112-119: Male aedeagus in 112, *M. narinensis*; 119, *Mischocyttarus* sp. gr. *heliconius* (MPEG); male digitus in 113, *M. narinensis*; 117, *M. collarellus*; male parameral spine in 114, *M. narinensis*; 115, *M. reclusus*; 116, *Mischocyttarus* sp. gr. *heliconius* (MPEG); 118, *M. collarellus*.

46. General shape of the antenna in the male: (**0**) antenna with an essentially linear shape, not much elongate, apical articles cylindrical, not much narrower than basal ones (Figs. 32, 33, 36); (**1**) antennal apex strongly shortened, with a hook-like shape, apical articles cylindrical, distinctly narrower than basal ones (Figs. 34-35); (**2**) antenna elongate, apical part very narrow and spirally rolled, apical segments cylindrical, distinctly longer than wide in dorsal view (Figs. 27, 29, 30, 31); (**3**) antenna moderately elongate, narrower at the apex, but with distal segments distinctly flattened below and not much longer than wide in dorsal view (Fig. 28). (Unordered)

State 0 occurs in the outgroup genera, in the subgenera *Mischocyttarus* s. str. and *Clypeopolybia*, and probably convergently in part of *Megacanthopus*. State 1 has a widespread occurrence in *Mischocyttarus*, and is present also in part of the outgroup genus *Polistes*. It tends to occur in most *Monogynoecus* and *Phi* species, but is also found in *Kappa*, and *Haplometrobius* and *Omega* (*Monacanthocnemis* of Richards, 1978*)*. State 2 is likewise widely distributed, occurring in the outgroup genera *Parapolybia* and *Belonogaster*, and in the subgenera *Scytokeraia*, *Phi*, *Kappa*, *Haplometrobius*, and *Omega*. State 3 is typically observed in the *artifex* group and in most species of *Megacanthopus*, but a similar shape can also be observed in some species of *Kappa* and in one undescribed species of *Monogynoecus* (MPEG collection).

47. Article 13 of the antenna in the male: (**0**) narrow, laterally compressed, distinctly curved downwards (Figs. 30). (**1**) length variable, slightly flattened ventrally at the base, apex with a conical shape, dorsal profile curved (Figs. 31-36); (**2**) very long, straight, and laterally compressed (Fig. 29); (**3**) long or very long, straight, laterally compressed, distinctly tapering to the apex (Fig. 27); (Ordered 0-1-2-3)

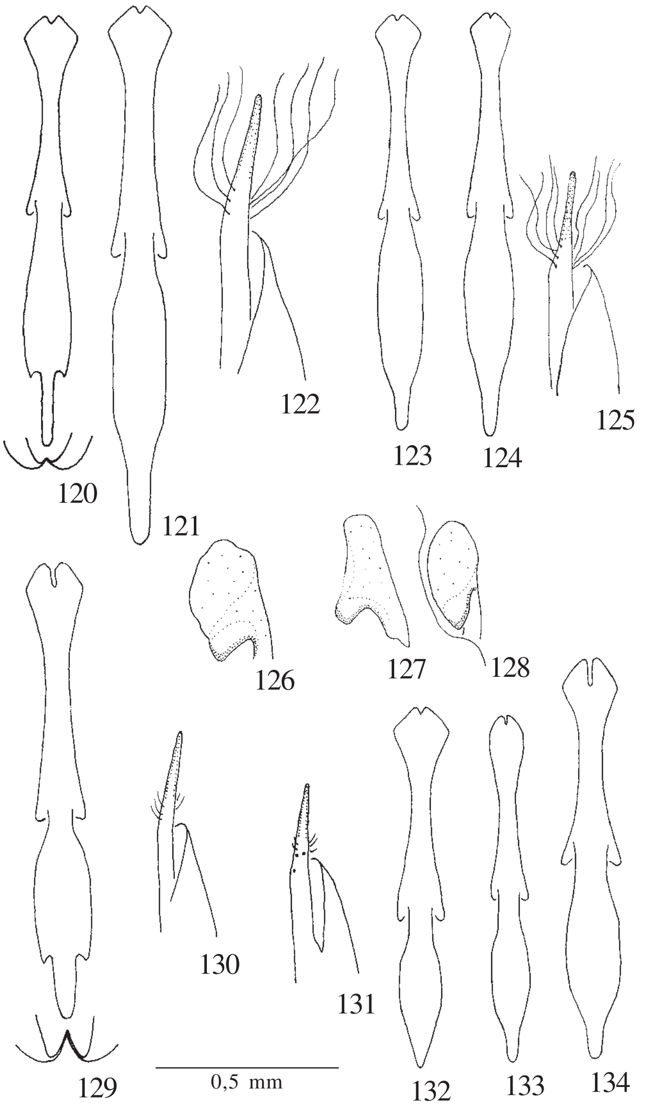
State 1 represents a set of shapes not always very similar regarding general proportions, but it is assumed that such differences are the result of other more general differences related to variation in length of the antenna and diameter of the apical segments, and occurs in outgroups and most *Mischocyttarus* species. States 0, 2 an 3 are synapomorphies of some species-groups, state 0 being a putative synapomorphy between the *filiformis* and *buyssoni* groups of *Omega*, and states 2 and 3 occurring in *Scytokeraia* only.

48. Male mandible: (**0**) reasonably elongate and sclerotized; (**1**) very wide and robust, strongly sclerotized, apical tooth 4 (anteriormost) excessively developed and prominent (Figs. 19).

State 1 occurs only in some species of the *flavitarsis* group of subgenus *Phi*.

49. Apical tooth 1 (posterior-most) of the mandible in the male: (**0**) with external surface quite convex (similar to female), its posterior border curved (Figs. 23-24); (**1**) planar, distal portion often with a linear aspect, apex rounded, posterior border not really sharp and often with a concave profile (Fig. 18); (**2**) very long, much more than tooth 2, plane, distal portion often with a linear aspect, apex rounded, posterior border not really sharp and often with a concave profile (Figs. 21, 26). (Ordered 0-1-2)

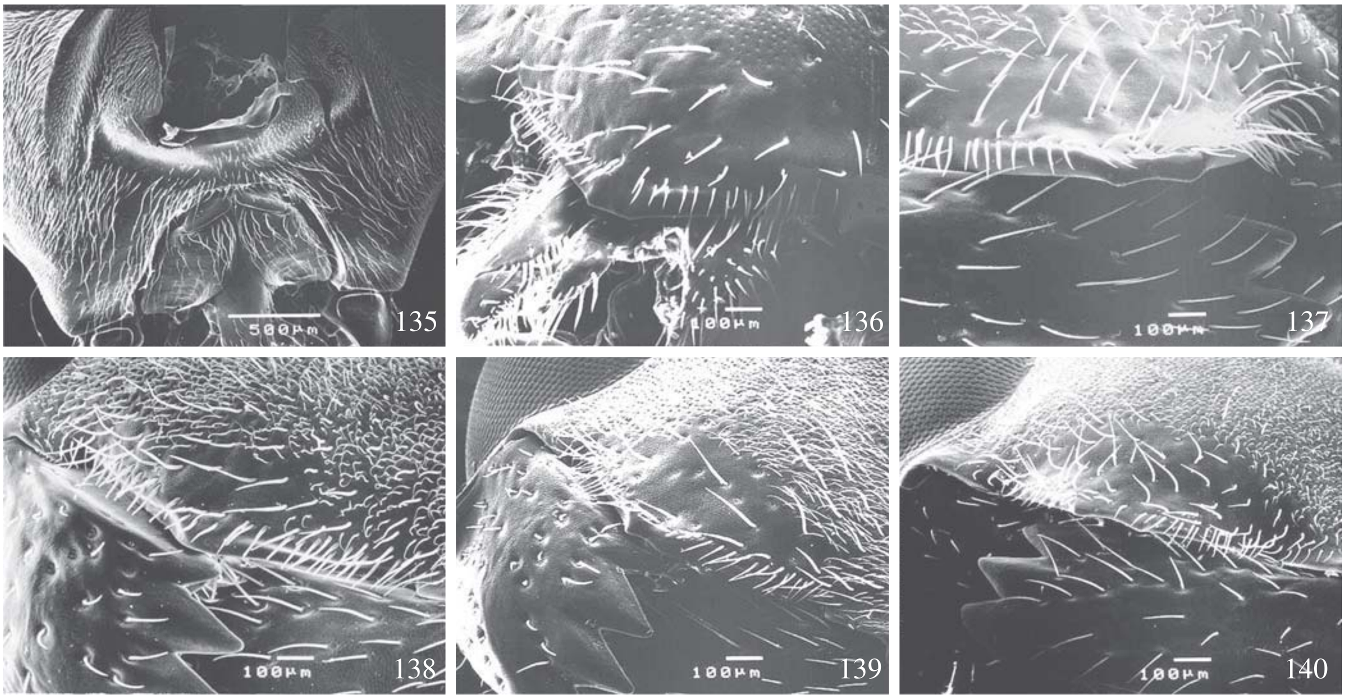
State 0 occurs in the outgroup genera, and in the subgenera *Mischocyttarus* s. str., *Clypeopolybia*, *Monogynoecus*, and *Scytokeraia*. State 1 occurs widely in the other groups of *Mischocyttarus* with few instances of noticeable variation in shape. In those species related to *M. flavitarsis* that have a wide and robust mandible, the tooth 1 has a more solid, less altered form than in remaining *Phi* species. But its shape is not really similar to that in the female as in state 0, and seems to be just a particular aspect of the extreme robustness of the mandible. In *M. weyrauchi* of the *iheringi* group, tooth 1 has a quite pointed apex, and it is not as planar as in the other species presenting state 1. However, in *M. weyrauchi* the posterior margin of the mandible has a strong angle that typically occurs in association with state 1. State 2 is recognized by the extreme elongation of tooth 1, and is observed in *M. cerberus* and *M. dimorphus*, most species of the *artifex* group, and in the species of *Kappa*.



Figs. 120-134. Male aedeagus in 120, *M. surinamensis*; 121, *Mischocyttarus* sp. gr. *surinamensis* (UCDC); 123, *M. silvicola*; 124, *Mischocyttarus* sp. gr. *alboniger* (MPEG); 129, *M. buyssoni*; 132, *M.* (*Omega*) sp. (NHM); 133, *M.* (*Omega*) sp. (MPEG); 134, *M. filiformis*; male parameral spine in 122, *Mischocyttarus* sp. gr. *surinamensis* (UCDC); 125, *Mischocyttarus* sp. gr. *alboniger* (MPEG); 130, *M. buyssoni*, 131, *M.* (*Omega*) sp. (MPEG); male digitus in 126, *M. silvicola*; 127, *Mischocyttarus* sp. gr. *surinamensis* (UCDC) lateral; 128, same species ventral.

50. Tooth 4 of the mandible in the male: (**0**) well developed (Figs. 18-20); (**1**) reduced (Figs. 21-26).

State 1 occurs in the subgenera *Kappa*, *Haplometrobius*,



Figs. 135-140. (SEM). Posterior view of the head showing occipital foramen in *M. imitator*; apical view of female clypeus in 136, *Polistes pacificus*; 137, *M. flavicans*; 138, *M. immarginatus*; 139, *M. mexicanus*; 140, *M. mastigophorus*.

Megacanthopus, *Omega*, in the smaller species of *Clypeopolybia* (cf. *M. richardsi*, *M. wygodzinskyi*) and in *Mischocyttarus* s. str.

51. External surface of the fore coxa of the male: (**0**) convex; (**1**) flattened.

State 1 occurs in *Omega* (*Monacanthocnemis* of Richards, 1978) and in part of the species of *Kappa*. In *Omega*, however, the flattened aspect is more accentuated, extending over the whole anterior leg.

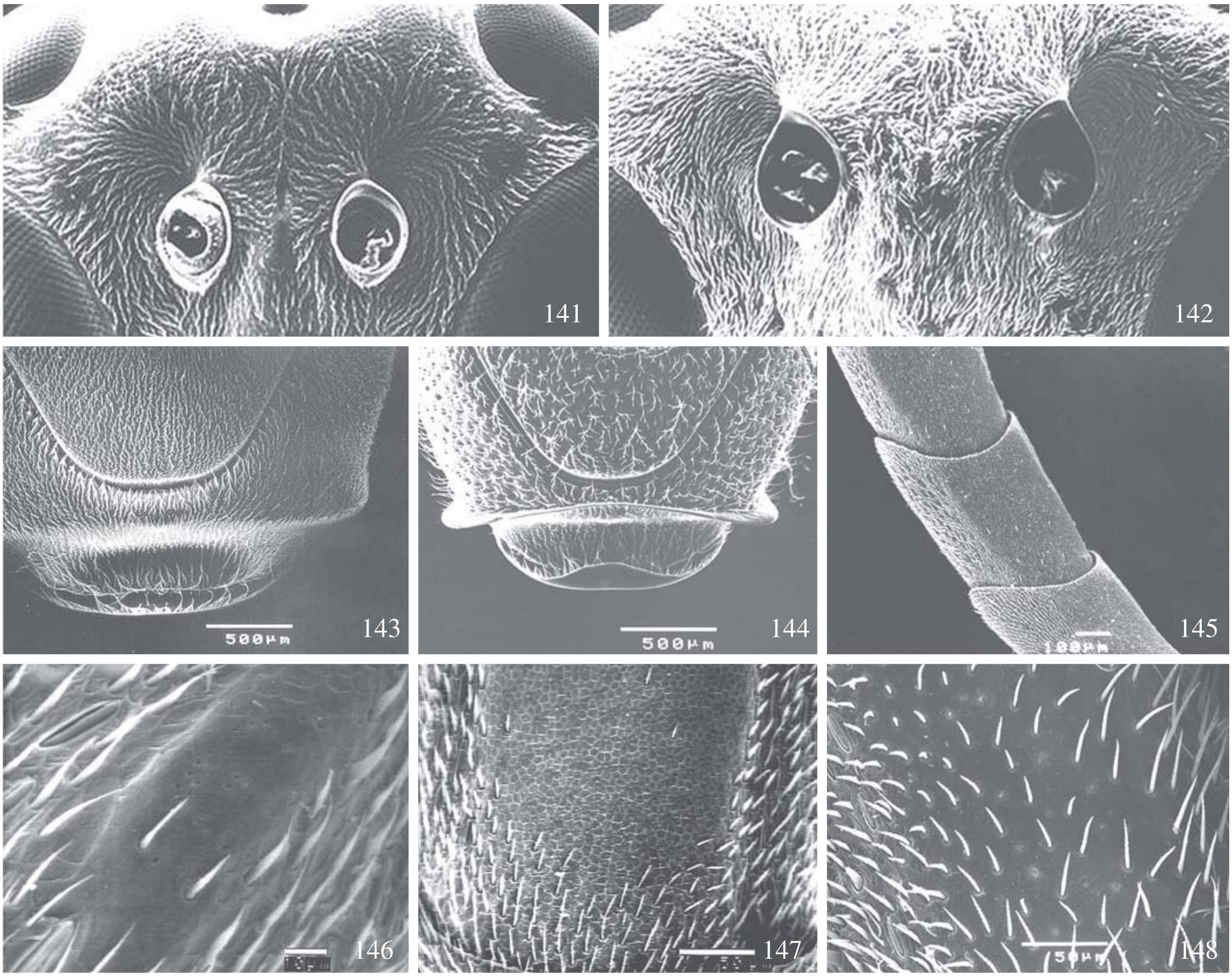
52. Digitus of the male genitalia: (**0**) very long, distally with a finger-like shape (Figs. 80, 96); (**1**) not very long, triangular in lateral view (Figs. 78, 117); (**2**) very short, with a rounded shape (Figs. 81, 95, 110); (**3**) not very long, basal part flattened ventrally, distal part triangular or with a more rounded shape, often folded like pleated bellows (Figs. 126-128); (**4**) very long, shape poorly defined distally, as a wrinkled paper bag (Fig. 113); (**5**) not very long, with a rectangular shape in lateral view (Fig. 79). (Unordered)

State 0 occurs widely in the outgroup genera *Polistes* and *Ropalidia*, and is certainly primitive in these genera (see Richards, 1973; Kojima, 1982, 1984; Kojima and Kojima, 1988, Carpenter, 1996). Within *Mischocyttarus*, state 0 occurs invariably in the subgenera *Clypeopolybia*, *Phi*, and *Kappa*. State 1 is a putative synapomorphy of a small clade comprising *M. cerberus*, *M. nomurae*, and *M. dimorphus*. States 2 and 3 are more variable in form, and certainly had multiple origins in the outgroup genera and in various *Mischocyttarus* groups and species. State 4 occurs only in part of the *surinamensis* group and in the *prominulus* group. State 5 was found in *M. smithii* and *M. acunai* of the subgenus *Mischocyttarus* s. str.

53. Hairs on the digitus of the male genitalia: (**0**) digitus with long and conspicuous hairs quite distinct at the dissection microscope (Figs. 78-80, 162); (**1**) digitus bare or with very small whitish hairs visible only at high magnification (Figs. 81, 95-96, 110, 113, 117, 126-128).

This character is variable in *Polistes*, and was not mentioned by Carpenter (1996), so the genus is here treated as polymorphic. Species of the other outgroup genera presented the glabrous condition (state 1). Within *Mischocyttarus*, state 0 was observed in the nominotypic subgenus and in *Clypeopolybia*, other groups presenting state 1.

54. Aedeagus of the male genitalia: (**0**) curved in lateral view; seen from above, with the distal portion narrow, then abruptly expanding to form a well differentiated apex whose lateral contour is more or less round (Figs. 76-77, 87-89, 99, 106-107, 112, 133); (**1**) curved in lateral view; seen from above, very wide from base to apex, the latter somewhat poorly differentiated with a broad round lateral contour (Figs. 74-75); (**2**) curved in lateral view; seen from above, with the distal portion wide, apex with a broad round lateral contour (Figs. 90-91, 98, 101-102, 119); (**3**) short and absolutely straight in lateral view; seen from above, apex with a broad round lateral contour (Figs. 104-105, 108-109); (**4**) curved in lateral view; seen from above, very wide from base to apex, distal portion extremely short and dorsally flattened, with parallel sides (Fig. 86); (**5**) curved in lateral view; seen from above, with the distal



Figs. 141-148. (SEM). Frontal view of female head showing antennal sockets in 141, *M. montei*; 142, *M. mexicanus*; dorsal anterior view of pronotum in 143, *M. immarginatus*; 144, *M. punctatus*; general view of male antenna showing tyloids in 145, *Polistes* (*Polistes*) sp.; detail of male antennal tyloid in 146, *Ropalidia flavobrunnea*; 147, *M. labiatus*; 148, *M. duckei*.

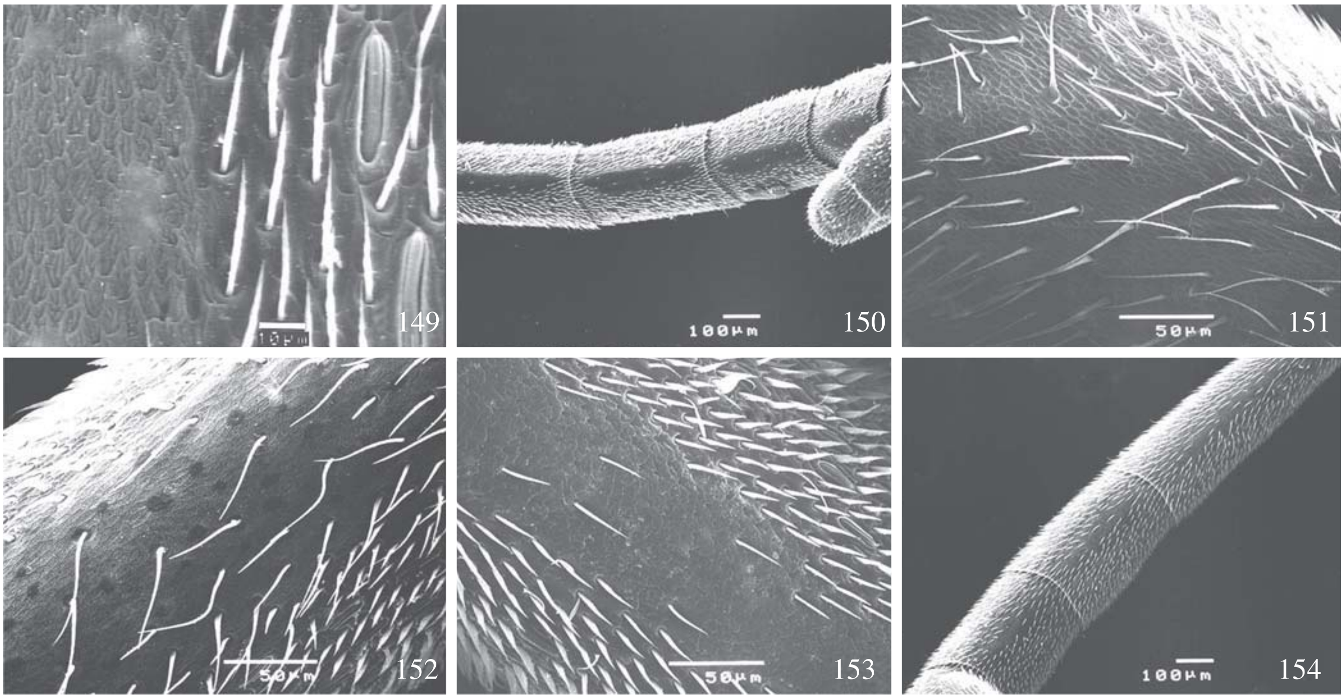
portion narrow, then suddenly expanding to form a well differentiated apex whose lateral contour is distinctly angular (Figs. 120-121, 123-124, 129, 132, 134). (Unordered)

In the outgroup, forms corresponding to state 0 were observed in *Polistes*, *Ropalidia*, *Belonogaster*, and *Polybioides*. In *Parapolybia indica*, the aedeagus presented an extremely divergent shape, and *Apoica* and *Agelaia* also presented different forms of the aedeagus, certainly unrelated to the other states observed within *Mischocyttarus*. In this genus, state 0 occurs in *Clypeopolybia*, *Scytokeraia*, *Phi*, *Megacanthopus*, one undescribed species of *Omega* (male Brasil, PA, Serra Norte, Fofoca, 16/ix/1985, M. F. Torres; MPEG), and in part of *Haplometrobius*. State 1 occurs only in *Mischocyttarus* s. str. State 2 was observed in species of the *heliconius* group, in *Kappa* species and in *M. artifex*. State 3 occurs only in the *iheringi* group. State 4 is a putative synapomorphy of *Monogynoecus* (sensu Cooper, 1996a). State 5 was observed in the *surinamensis* and *prominulus* groups, and in most species of *Omega* (excepting the undescribed one mentioned above).

55. Ventral process of the aedeagus: (**0**) a rounded lobe, not very large but quite visible from above (Figs. 76, 87, 112, 119); (**1**) a small narrow lobe, contorted inwards, with small teeth (Fig. 162); (**2**) a rounded lobe, contorted inwards, without teeth (Figs. 109, 163); (**3**) a very long narrow lobe (Fig. 86); (**4**) a large angular lobe (Figs. 99, 101-102, 107, 164). (Unordered)

States 1, 2, 3, and 4 are putative synapomorphies respectively of *Mischocyttarus* s. str., the *iheringi* group, *Monogynoecus*, and the *artifex* group.

56. Basal area of the aedeagus: (**0**) completely sclerotized, continuous with the paramere basal processes; (**1**) sclerotized portion of the base of the aedeagus a linear elongate lobe



Figs. 149-154. (SEM). Detail of male antennal tyloid in 149, *M. mastigophorus*; 151, *M. synoecus*; 152, *M. ornatus*; 153, *Mischocyttarus* sp. gr. *heliconius* (MPEG); general view of male antenna showing tyloids in 150, *M. montei*; 154, *Mischocyttarus* sp. gr. *surinamensis* (UCDC).

developed anteriorly up to the paramere basal processes (Figs. 120-121, 123-124, 129, 133-134); (**2**) sclerotized portion of the base of the aedeagus with a round or angular shape, not much developed anteriorly, not reaching the paramere basal processes. (Ordered 0-1-2)

State 0 was found in the outgroup genera only. State 1 was observed in most species of *Omega* (excepting an undescribed one of the *punctatus* group; male; Bolivia, La Paz, Caranavi, 600m, 16/v/1979, M. Cooper; BMNH), and in the *surinamensis* and *prominulus* groups. State 2 was found in all other *Mischocyttarus* groups.

57. Long hairs on the external surface of distal part the paramere of the male genitalia: (**0**) absent (Figs. 82-85, 92-94, 100, 103, 111, 114-115, 116, 118); (**1**) present (Fig. 97).

State 1 is a putative synapomorphy of *Kappa* sensu Richards (1978).

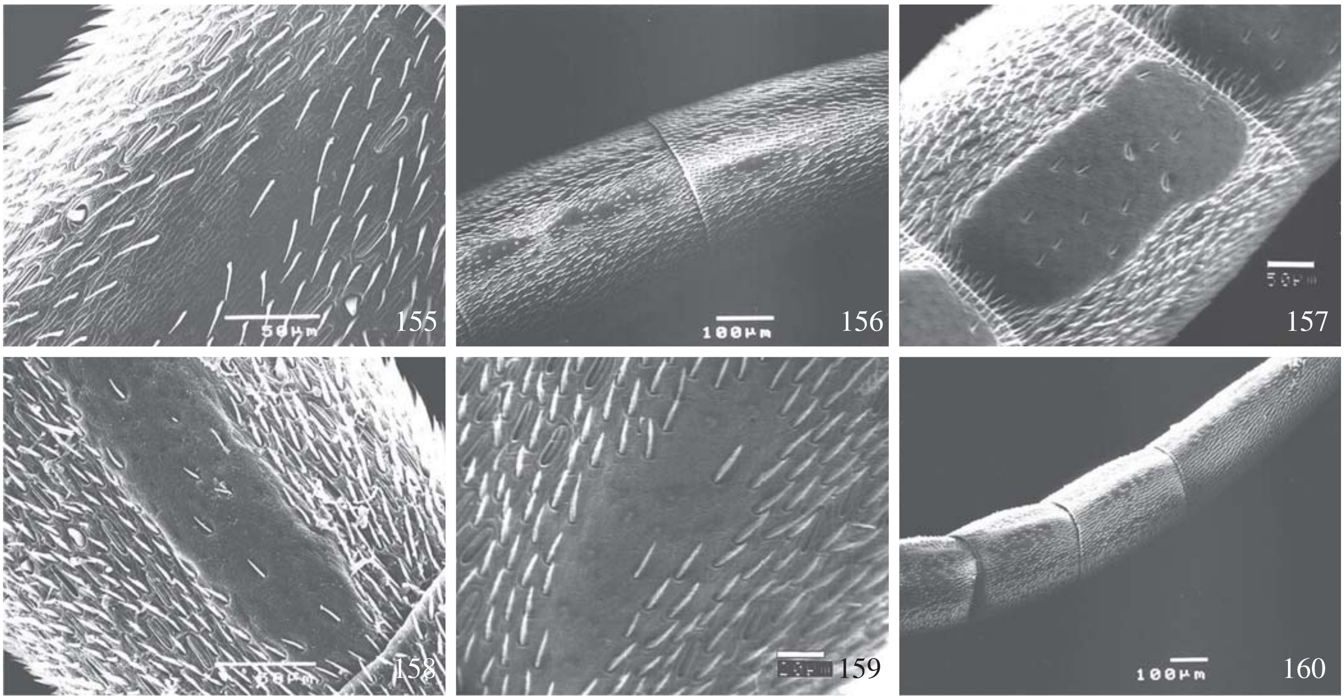
58. Hairs on the parameral spine of the male genitalia: (**0**) long and numerous hairs, distributed over an extensive zone of the parameral spine (Figs. 82-85, 92, 94); (**1**) long but less numerous hairs (Fig. 114); (**2**) a few very long hairs restricted to the apical part of the parameral spine (Figs. 97, 122, 125); (**3**) a few short, but reasonably conspicuous hairs restricted to the apical part of the parameral spine (Figs. 93, 111, 118); (**4**) a few extremely short inconspicuous hairs, parameral spine nearly glabrous (Figs. 100, 103, 115-116, 130-131). (Unordered)

Another character that is variable in the outgroup. *Polistes* spp. and *Parapolybia indica* presented state 0, while in most of the other outgroup genera the hairs on the parameral spine are strongly reduced in number and size (state 4). In *Ropalidia*, the examined species *R. flavobrunnea* and *R. fasciata* present state 4, but several drawings in Charnley (1973) show that state 0 also occurs in the genus. The Ropalidiini were thus scored as polymorphic. Within *Mischocyttarus*, a condition similar to the state in *Polistes* was observed in *Mischocyttarus* s. str., *Clypeopolybia*, *Scytokeraia* and *Phi*. In *M. acunai* (Fig. 131), the hairs on the parameral spine are less developed than in other species of *Mischocyttarus* s. str., this being an autapomorphy of the species. In the other subgenera, the hairs are always less developed than the condition in state 0, this being often associated with more or less differentiated shapes of the parameral spine. State 1 is a putative synapomorphy of a group constituted by *M. cerberus*, *M. nomurae*, *M. dimorphus*, and *M. peruanus*. State 2 occurs typically in *Kappa*, but a quite similar condition was observed in the *surinamensis* and *prominulus* groups of *Haplometrobius*. State 3 was found in species of the *ihering* group of *Haplometrobius*, in *Monogynoecus* and *Megacanthopus*. State 4, the nearly glabrous condition, was observed in the *heliconius*, *mendax*, and *artifex* groups, and in *Omega*.

MATURE LARVA

59. First abdominal segment of the mature larva: (**0**) without any ventral processes; (**1**) with one ventral median process; (**2**) with two ventral processes; (**3**) with three ventral processes. (Unordered)

Occurrence of ventral processes on the first abdominal segment of the larva is only known in *Mischocyttarus*. For this very reason, it is impossible to infer which of states 1-3 is



Figs. 155-160. (SEM). Detail of male antennal tyloid in 155, *Mischocyttarus* sp. gr. *surinamensis* (UCDC); 157, *M. imitator*; 158, *M. extinctus*; 159, *M. itatiayaensis*; general view of male antenna showing tyloids in 156, *M. immarginatus*; 160, *M. cassununga*.

plesiomorphic in the genus using outgroup argumentation. State 2 has the widest distribution, in most of the subgenera, but occurring in somewhat diverse forms. State 1 occurs only in the subgenus *Kappa*. State 3 is only known from two species of *Clypeopolybia* (*M. flavicans* and *M. carbonarius*). Recently, Kojima (1998) described the larva of *M. carbonarius tibialis* Richards reporting the occurrence of only two ventral processes, which is incongruent with the information available for typical *M. carbonarius*. But Richards (1978) indeed noticed the existence of morphological differences between his new subspecies and *M. carbonarius*, apparently deciding to give subspecific status to the former by virtue of the small number of specimens available from a single locality. Altough types of *tibialis* were not available for this study, two females from Costa Rica (INBC) agree very well with Richards' description of *tibialis*, and a male specimen collected by Ducke in Brazil, Amazonas state (MPEG) is probably the same species. The differences noticed by Richards in respect to body size and shape of the pronotal carina are confirmed, and clearly indicate (jointly with information from Kojima, 1998) that *tibialis* is a distinct valid species.

NEST CHARACTERS

60. Nest comb: (**0**) irregular polygonal or suboval cluster; (**1**) circular cluster with central attachement to peduncle; (**2**) vertically elongated cluster several rows wide; (**3**) vertically elongated 1-3 rows-wide comb with cell displacement; (**4**) 1-3 interconnected (nonadjacent) rows parallel to substrate; (**5**) polygonal cluster facing substrate, bottom with moss particles. (Unordered)

State 1 is a putative synapomorphy of *Mischocyttarus* s. str. State 2 occurs in several species of *Phi* like *M. mexicanus*, *M. cassununga*, *M. crypticus*, and *M. cryptobius*, and also of other subgenera, like *M. interjectus* (*artifex* group of *Haplometrobius* sensu Richards, 1978), and *M. subornatus* (*Scytokeraia*) (see Zikán, 1949, figs. 365, 370, 379, 385, 386, 394, 401; Cooper, 1997a). It is similar to state 3, but does not have the extreme cell displacement observed typically in nests of *M. punctatus* or most species of the *artifex* group (see Cooper, 1998b; Ducke, 1914; Wenzel, 1991). State 4 is only found within the group of *M. iheringi*, in species like *M. weyrauchi*, *M. naumanni*, and *M. cooperi*. The nest may be constituted of a single (see Zikán, 1949; Fig. 369) or multiple combs, at times resulting in rather strange forms (Cooper, 1998a; figs. 1-2). State 5 is also typical of some species of the *iheringi* group.

61. Comb external walls: (**0**) convex; (**1**) flattened.

State 1 occurs typically in the subgenus *Megacanthopus*.

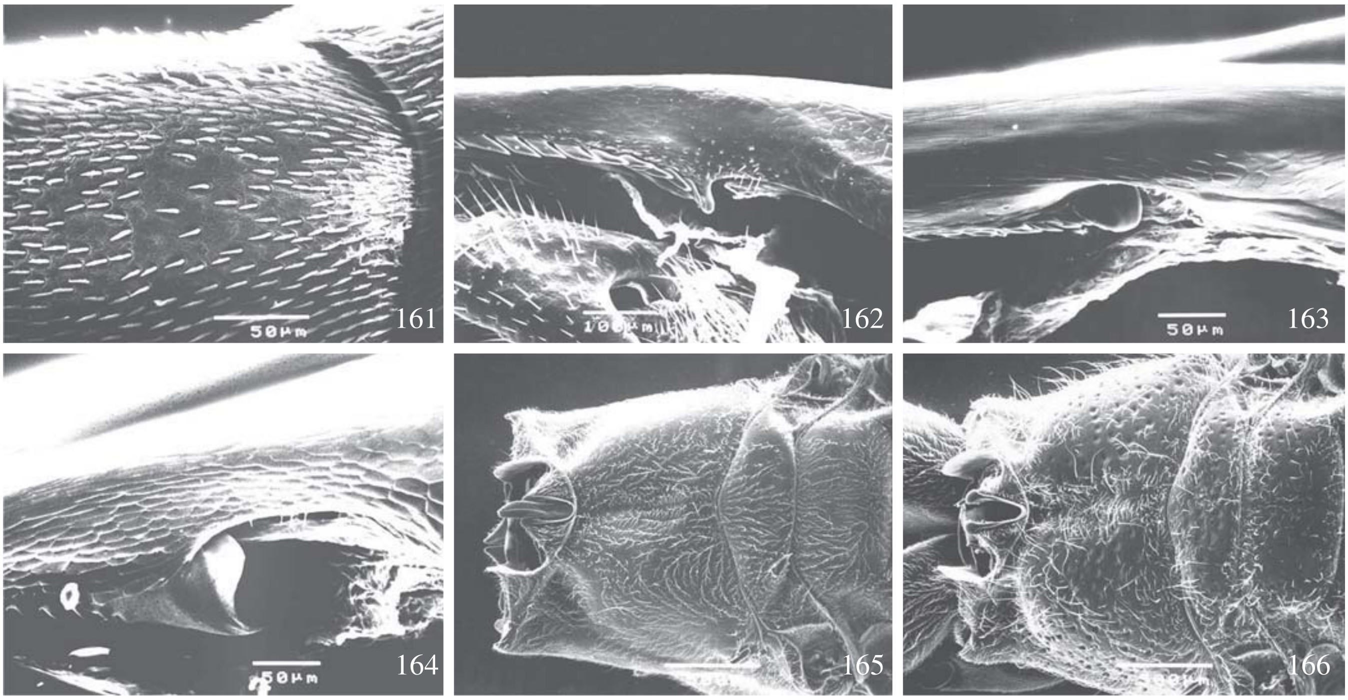
62. Nest pedicel: (**0**) short and wide; (**1**) long and thin, thread-like.

State 1 is typically seen in *Mischocyttarus* s. str., but a similar condition was observed in several nests of *M.* (*Clypeopolybia*) carbonarius.

Phylogenetic Results

Unweighted-analysis

Searches of the uniformly weighted data set using the program NONA 2.0 yielded 32 trees of length 339, CI= 36



Figs. 161-166. (SEM). Detail of male antennal tyloid in 161, *M. cassununga*; lateral aspect of male aedeagus and digitus in 162, *M. drewseni*; lateral detail of male aedeagus showing ventral process in 163, M. iheringi; 164, M. synoecus; dorsal view of propodeum in 165, *Mischocyttarus* sp. gr. *alboniger* (INPA); 166, *M. punctatus*.

(ensemble consistency index), RI= 81 (ensemble retention index). TNT 1.0 found the same trees. The strict consensus is presented in figure 173 along with clade support values (absolute and relative Bremer supports).

The tree in figure 173 is in reasonable agreement with the current internal classification of *Mischocyttarus* (Cooper, 1997a; Richards, 1978). The basal split involving *Mischocyttarus* s. str. and *Clypeopolybia* species at one side, and a large component (*mastigophorus-iheringi*) formed by remaining groups of the genus is somewhat reminiscent of the earlier classification by Ducke (1904) who created the genus *Megacanthopus* for all "Polybia" species with asymmetric tarsal lobes that were not strictly similar to *M. labiatus*. This component is supported in all trees by transformations in four characters (1: 2>0, 11: 0>1, 25: 0>1, and 46: 0>2), the most reliable being the unique loss of a basal sulcus on fore and mid femora (character 25).

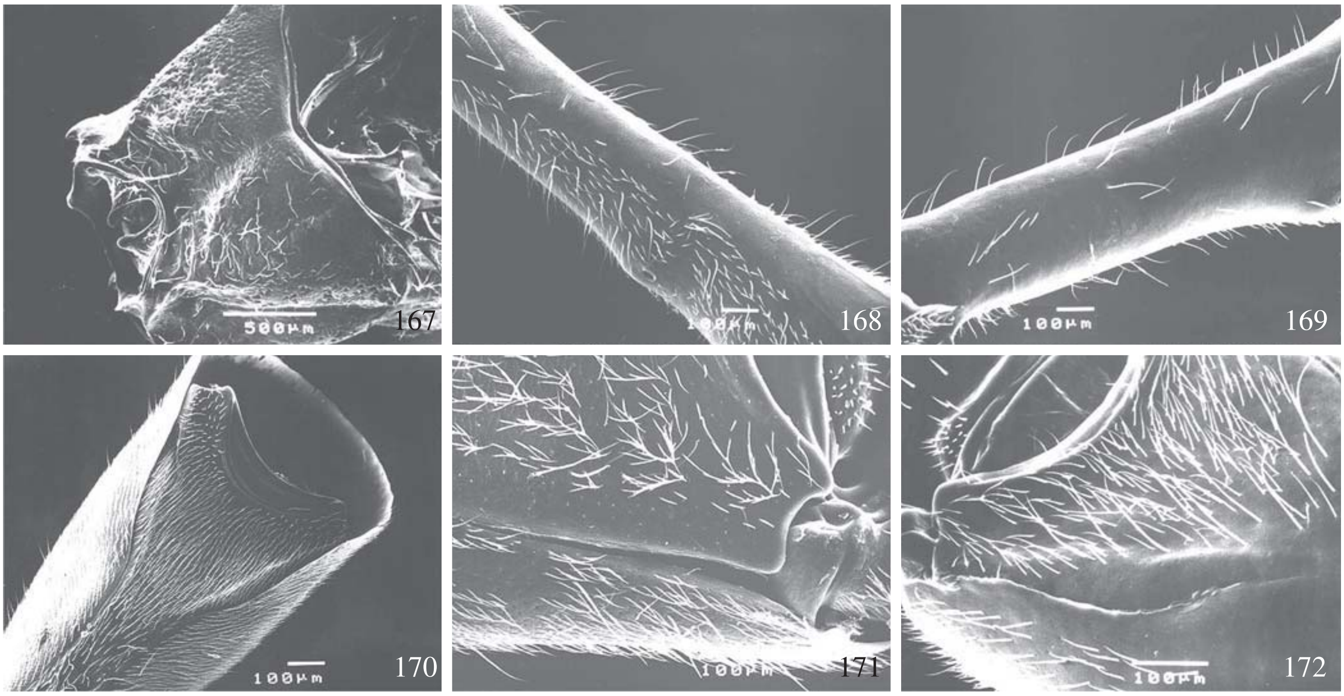
Six of the nine recognized subgenera appear in the consensus tree as monophyletic groups, with the notable exceptions of *Clypeopolybia*, *Phi* and *Haplometrobius*. As to the first subgenus, four topological solutions exist among the 32 trees found, two of them presenting the group as paraphyletic with respect to *Mischocyttarus* s. str. The latter configurations show a closer relationship between the larger species of *Clypeopolybia* (*M. flavicans* and *M. carbonarius*) and the species of *Mischocyttarus* s. str., being supported by shared similarities either in the shape of the pronotum (character 21: 0>1) and the propodeal median furrow (character 34: 2>1), or additionally in the shape of nest pedicel (between *M. carbonarius* and *Mischocyttarus* s. str.; character 62: 0>1). Alternatively in the other trees found, *Clypeopolybia* appears as a monophyletic group supported by the flattened anterior femur (character 26: 0>1), and the deep clypeal lateral indentations (character 9: 0>1).

Regarding subgenus *Phi*, all trees showed it as paraphyletic with respect to *Kappa* (*M. extinctus* is sister to the subgenus *Kappa*). While such an improbable relation is only supported by a homoplastic transformation in the clypeal apex (character 8: 0>4; narrowly truncate to narrowly round), the remaining *Phi* component (*consimilis-flavitarsis*) is supported by the unique reduction of the male antennal tyloids (character 44: 0>1) and the homoplastic reduction of the lateral margin of the distal portion of the first metasomal sternum (Character 40: 1>2).

Problems with the subgenus *Haplometrobius* seem far more extensive and complicated because keeping such a widely inclusive group in the consensus tree (*mendax-nigropygialis*) would necessarily embrace representatives of five other subgenera.

Weighted-analyses

Under implied weights (option k=1) with program Pee-Wee 3.0, 464 trees of fit 294.9 were found. These trees are 17 to 22 steps longer (length: 356 – 361) than those found under equal weights. The strict consensus is presented in figure 174 along with absolute and relative Bremer supports estimated with Pee-Wee. Appendix 2 shows a list of character changes supporting each node of this consensus tree, but only those



Figs. 167-172. (SEM). Dorsal view of propodeum in 167, M. injucundus; ventral view of petiolar first metasomal segment in 168, *Mischocyttarus* sp. gr. *alboniger* (INPA); 169, *M. punctatus*; ventral distal view of first metasomal segment in 170, *M. montei*; same part, lateral detail in 171, *M. mexicanus*; 172, *M. punctatus*.

(unambiguous) changes appearing in "all trees". The consensus shows still better agreement with traditional classification, all subgenera now appearing as monophyletic except *Haplometrobius*. The basal split between *Mischocyttarus* s. str. + *Clypeopolybia* and a large component formed by remaining groups is again apparent, the latter being supported by the unique loss of a basal sulcus on fore and mid femora (character 25: 0>1), and the homoplastic loss of the occipital carina (character 1: 2>3).

Major differences in respect to the consensus tree obtained under equal weights (paraphyly of *Phi* aside) are the positions of subgenera *Monogynoecus* and *Kappa*, and of the species-groups of *M. mendax* and *M. heliconius*. In the first analysis, a putative sister-group relation between *Monogynoecus* and a component formed by species of *Haplometrobius*, *Megacanthopus* and *Omega* (*mirificus*-*ornatus*; Fig. 173) seems to be problematic. Some plesiomorphic features occur in *Monogynoecus* like the fairly circular antennal sockets in female (character 11) and characters of the male mandibula (characters 48, 49, and 50; state 0 in all these cases) suggesting a more basal position for the group. Under implied weights (k=1), the shape of antennal sockets is indeed the character supporting the relationship between *Scytokeraia* and a large component formed by several subgenera (Fig. 174) to the exclusion of *Monogynoecus* (and of *Mischocyttarus* s. str. and *Clypeopolybia*).

With respect to the subgenus *Kappa*, implied weights (k=1) render it member of a small group also comprising elements of the *M. heliconius* group (Fig. 174), this group itself being part of a larger clade including the *M. mendax* group and other elements of subgenera *Haplometrobius*, *Megacanthopus* and *Omega*. These relationships are very different from those obtained under equal weights (in which *Kappa* appears as closely related to part of *Phi*), and must be due mainly to the reduction of the fourth tooth of male mandible in *Kappa* (character 50, state 1).

There are four possible configurations in trees for the three terminals representing *M. chanchamayoensis* and other species of the *M. heliconius* group, two of these arrangements being paraphyletic relative to *Kappa*. Support for this component comes from a set of six characters (1: 3>0, 8: 3>4, 10: 0>1, 12: 0>1, 15: 0>1, and 54: 0>3), but only characters 1 (occipital carina present) and 8 (clypeal apex narrowly rounded) support the group in all trees. Interestingly, Richards (1945) considered *M. heliconius* as part of *Kappa* (then with a much wider concept) before transferring the species-group to subgenus *Clypeopolybia* (Richards, 1978; see also Silveira, 1998). As to the terminal representing the group of *M. mendax*, under implied weights (k=1) it appears in trees as sister-group either of the clade formed by species of the *M. heliconius* group and *Kappa*, or of the whole large component involving *Kappa*, parts of *Haplometrobius*, *Megacanthopus* and *Omega*.

The consensus tree of the weighted analysis (k=1; Fig. 174) shows most species-groups of *Haplometrobius* (*cerberus*, *surinamensis*, *prominulus*, *artifex*, and *iheringi* groups) as parts of a component which also includes the subgenera *Megacanthopus* and *Omega*, and whose prominent supporting character in all trees is the absence of the pronotal fovea (character 23: 0>1). In some trees, characters 45: 0>1 (erect hairs of male antenna) and 58: 4>3 (hairs of male paramere spine) also support the group. A rather similar group was obtained in the analysis under equal weights, except for the inclusion of *M. chanchamayoensis* and the other species of the *M. heliconius* group as a small clade sister to the *M. ihering* group (Fig. 173). This latter pattern of relationships is suggestive of Richards's (1978) concept of the *M. iheringi* group, i.e. including also *M. chanchamayoensis* and *M. undulatus* sensu Richards (1945). However, support for such a group is meager, based on particular transitions in the homoplastic characters 1: 2>1 (occipital region just compressed dorsally and laterally) and 17: 2>1 (anterior marginf of proepisternum low, not reflexed, lateral portion shaped as a wide collar).

In the weighted analysis (k=1), the large clade supported by absence of the pronotal fovea appears in four different topologies according to the different arrangements of its major internal elements (Fig. 175). In all these topologies, the species-groups of *M. surinamensis* and *M. prominulus* appear as nested paraphyletic assemblages, with one element of the *prominulus* goup being more closely related to subgenus *Omega*. Species of the group of *M. artifex* form a monophyletic group in some topologies (Figs. 175a, b, c), but a paraphyletic one in some trees in which a major part of it (*artifex-sylvestris*) appears as sister of the *iheringi* group, to the exclusion of *M. mirificus* (and related species *M. ypiranguensis*, *M. schadei* and *M. thrypticus*) (Figs. 175d). The species-groups of *M. iheringi* (in the sense of present work) and *M. cerberus* are monophyletic in all trees (see also Silveira, 2004).

Analysis with different values of the constant "k" of concavity

Using alternative (less stringent) values for the constant of concavity "k" in the program Pee-Wee resulted in different topologies, but some important congruence is apparent. Consensus trees obtained with values of "k" equal to 2 and 3 (the latter being the default value in Pee-Wee) are showed in figures 176 and 177 respectively (with absolute and relative Bremer supports). As in the analysis with "k" equal to 1, all subgenera are again monophyletic except *Haplometrobius*. Topological relations in the basal part of the trees are also similar to previous weighted analysis in that *Mischocyttarus* s. str. plus *Clypeoplolybia* are sister to a large component formed by remaining subgenera, and that *Monogynoecus* and *Scytokeraia* occupy basal (and consecutive) positions in this large component. Furthermore, all weighted analyses found a clade composed of "afoveate" species-groups of *Haplometrobius* and the subgenera *Omega* and *Megacanthopus*. Differences in internal relationships within this clade mainly refer to monophyly/paraphyly of the species-group of *M. artifex*, and differing positions of *Megacanthopus*. However, using larger values of "k" resulted in hypotheses of a sistergroup relationship between the subgenera *Kappa* and *Phi* (Figs. 176, 177, 178, 179 and 180), similar to the configuration verified under equal weights. In some trees obtained with "k" equal to 4 and in all trees obtained with "k" larger than this value (5 and 6), the relative positions of *Monogynoecus* and *Scytokeraia* are changed in the basal sector of trees.

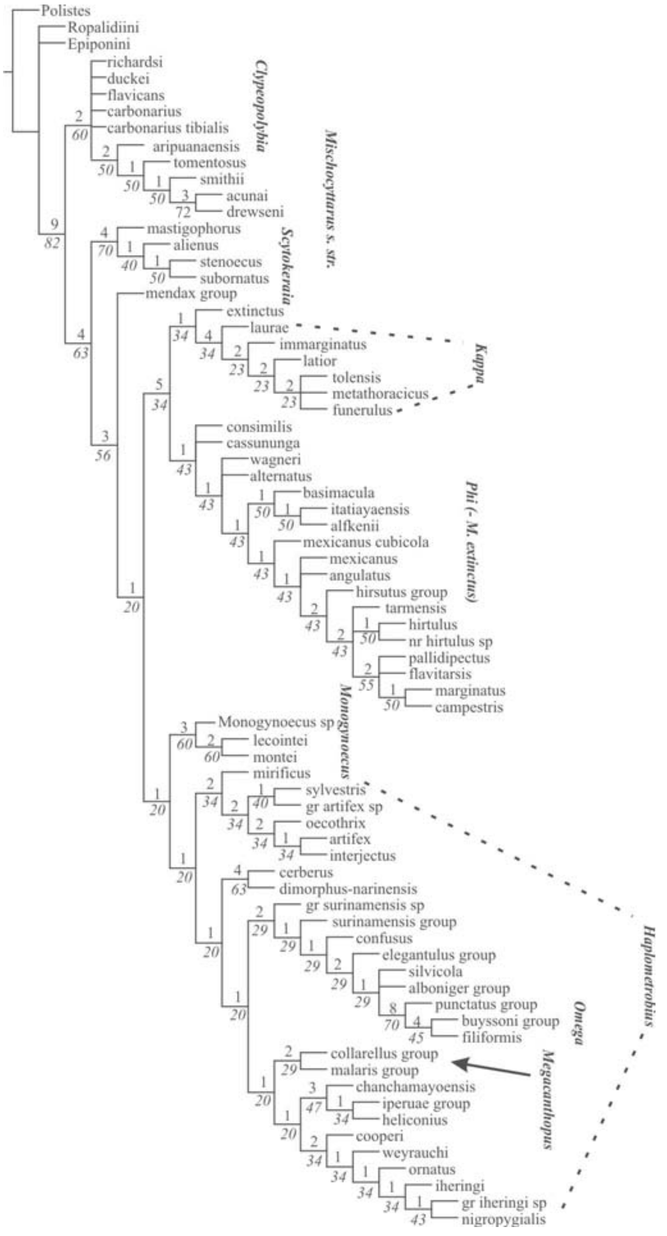


Fig. 173. Strict consensus of 32 trees (L= 339; CI 36; RI 81) found under equal weights with NONA 2.0 for *Mischocyttarus* major species groups. Absolute (above) and relative (below) Bremer supports are presented for ingroup branches, except when the value exceeded the upper limit considered (i.e. >100%).

Analysis with TNT 1.0 under implied weights produced a same set of just 3 trees irrespective of the value of the concavity function "k". The strict consensus of these trees is presented in figure 181. It is very similar to consensus trees obtained with Pee-Wee with larger values of "k" (equal to 5 or 6; compare with figures 179 and 180), except that with Pee-Wee *Megacanthopus* is never placed "within" the *M. surinamensis* group. According to documentation of TNT (Goloboff et al, 2005; file TNT.htm), the fit for discrete additive characters is calculated by decomposing the character into binary variables, and it is possible that the fits calculated by TNT were different from those of Pee-Wee. Whether such recoding may produce a "more meaningful evaluation of the relative weights" of characters (see also Carpenter, 1988b), actual support for the relationship between *Megacanthopus* and some elements of the group of *M. surinamensis*, and of these with the group of *M. prominulus* and *Omega* (shape of occipital region: 3>2; anterior margin of pronotum with the lamella wide and strongly reflexed: 1>2) should hardly be considered robust evidence. *Megacanthopus* does not have some distinctive apomorphies of the male genitalia that were found uniquely in the *M. surinamensis* and *M. prominulus* groups and most species of *Omega*. Overall evidence thus indicates that the particular relationship inferred with TNT is probably incorrect.

DISCUSSION

Conclusions of this work about phylogeny within *Mischocyttarus*, and a new classification for the genus are mainly founded on weighted analysis. Goloboff (1993*a*, 1997) presents convincing justification for using implied weights in cladistic analysis. Quoting Farris (1983) and Carpenter (1988*b*), he argues that inferring weights *a posteriori* based on the homoplasy that characters show in examined trees makes use of "all the evidence" contained in a given set of characters. Differences on cladistic reliability of characters revealed during the analysis are thus used to choose the hypotheses reflecting the strongest evidence. Goloboff´s method has since been widely used, and some authors have preferred it over equal weights (Melo, 1999; Fontal-Cazalla et al, 2002).

In spite of the admirable work of earlier authors like Ducke, Zikán and Richards, we still had no good ideas on phylogenetic relationships within *Mischocyttarus*, except for the general and untested hypotheses implied by the classification of subgenera and species-groups, constructed with traditional taxonomic methods. The present work brings a wealth of new information to the subject, but is still limited in some important ways. The number of characters is relatively small relative to the large number of terminals used. In addition, crucial information on morphology of males, larvae and nests were lacking for a number of species, many of them only known from one or a few female specimens. So we are centainly still far from a satisfactory knowledge of the species phylogeny of the genus, stable and detailed enough to give support to the rich spectrum of opportunities on comparative research of behavior.

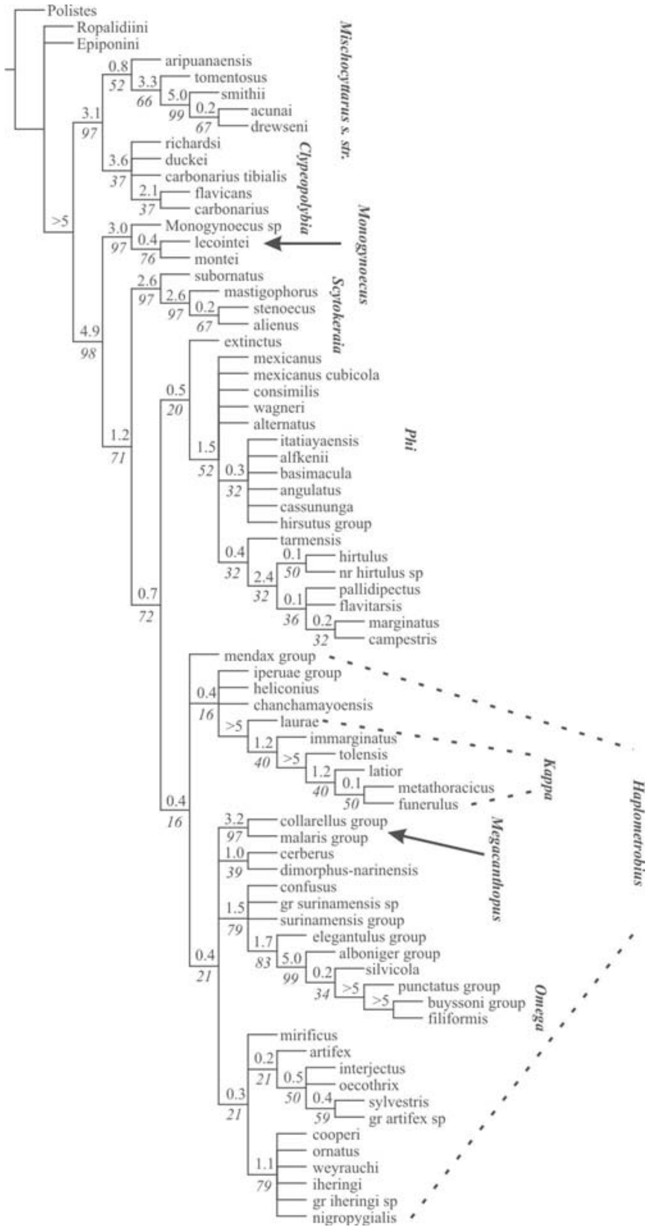


Fig. 174. Strict consensus of 464 trees (Fit= 294.9) found under implied weights (k=1) with Pee-Wee 3.0 for *Mischocyttarus* major species groups. Absolute (above) and relative (below) Bremer supports are presented for ingroup branches, except when the value exceeded the upper limit considered (i.e. >100%).

Monophyly of *Mischocyttarus*

The outstanding character of the genus traditionally used in keys is the asymmetry of lobes of more distal tarsomeres of mid and hind legs. Importance of this character (unique in Polistinae) was already evident in the key presented by Ducke (1904:.320), couplet 2 leading to both *Mischocyttarus* s. str. and the new genus *Megacanthopus*. However, in the paper that established the modern concept of the genus, Ducke (1913) did not discuss details about characters, just mentioned that his genera *Megacanthopus* and *Monacanthocnemis*, by morphological and ethological criteria should belong in fact to *Mischocyttarus* de Saussure. Quite interestingly, asymmetry of tarsal lobes received no mention in the description of *Mischocyttarus* s. str. presented by de Saussure (1853). A larval feature referring to the presence of one or more processes on the first abdominal segment has also been recognized as a character typical of the genus (Richards, 1978). In the present

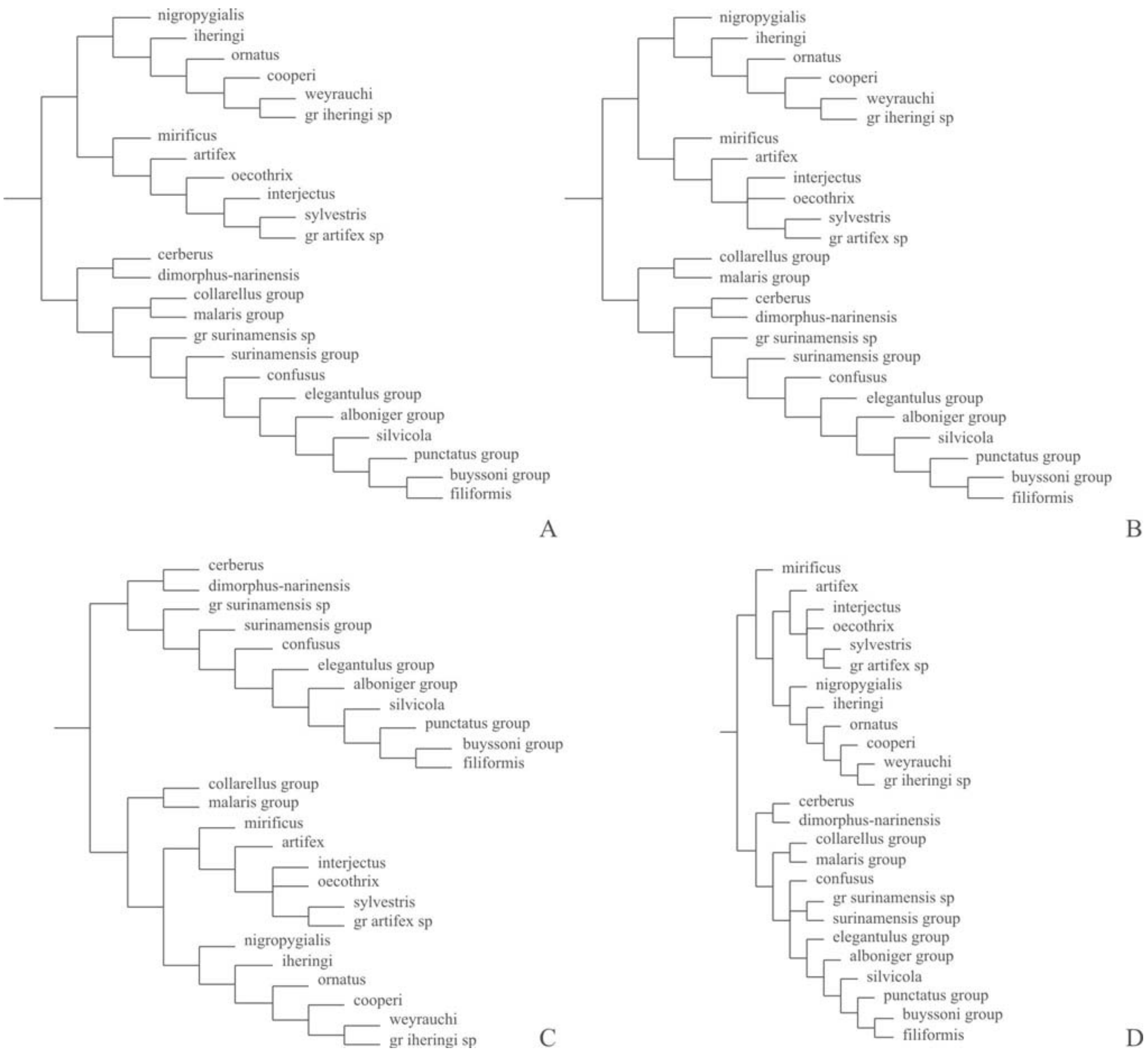


Fig. 175. The four types of topologies found under implied weights (k=1) with Pee-Wee 3.0 for “afoveate” *Mischocyttarus* species.

study, character state 2 (larva with two ventral processes) was inferred as the primitive condition in the genus in all the analyses. Weigthed and unweighted analyses resulted in nearly identical sets of characters supporting monophyly of *Mischocyttarus*. Besides the two mentioned above, newly discovered synapomorphies of the genus (unique in Polistinae) are the posterior margin of the pronotum laterally nearly straight below the pronotal tubercle, with the ventral angle being in a fairly anterior position (character 27, state 1; Figs. 53, 54, 56), and the sclerotized basal portion of the aedeagus less extensive, with a round or angular shape, not reaching the paramere basal processes (character 56, state 2; Figs. 74-77, 86-91, 98-99, 101-102, 104-109,112, 119, 132).

Relationships of Mischocyttarini with other closely related polistine tribes were not the main focus of this work, and the characters studied indeed shed no new light on the subject.

Monophyly of subgenera

Seven of the nine currently recognized subgenera resulted as monophyletic taxa in all analyses: *Mischocyttarus* s. str., *Clypeopolybia*, *Monogynoecus*, *Scytokeraia*, *Kappa*, *Megacanthopus* and *Omega*. *Phi* showed up as a paraphyletic group in the unweighted analysis, but as a monophyletic one in all the weighted analyses. *Haplometrobius* proved to be an unnatural catch-all taxon for rather heterogeneous species-groups left behind after formal recognition by Richards of better defined less inclusive subgenera (i.e. *Megacanthopus* sensu Richards, 1978, and *Omega*). This study found no evidence in favor of its monophyly. A clade including all species of *Haplometrobius* would also have to comprise species of

Kappa, *Phi*, *Omega* and *Megacanthopus*, or at least *Omega* and *Megacanthopus*.

Relationships between subgenera and species-groups

The basal dichotomy in the phylogeny of *Mischocyttarus* appeared in all analyses (figs 173, 174, 176, 177, 178, 179, 180, 181). There seems to be no doubt on the existence of two major clades, one formed by *Mischocyttarus* s. str. and *Clypeopolybia*, and the other by all remaining species-groups. Weighted analyses showed that *Monogynoecus* and *Scytokeraia* occupy basal and (in most analyses) consecutive positions in this second component (fig 174, 176, 177, 178, 179, 180). As already stated, a sister-group relationship between *Monogynoecus* and a large component formed by species of *Haplometrobius*, *Megacanthopus* and *Omega* as obtained in unweighted analysis (Fig. 173) is very improbable. The circular antennal sockets and features of the male mandibule in *Monogynoecus* suggest a more basal position. Weighted analyses with the constant of concavity "k" equal or larger than 4 caused inversion of relative positions of *Monogynoecus* and *Scytokeraia* (Figs. 179 and 180). This is mainly due to weighting conditions favoring characters 17 (anterior margin of the proepisternum) and 24 (inner margin of the anterior coxa), of which *Scytokeraia* has the ancestral state. Other limited evidence coming from a larval feature not used in this study may favor the opposite situation, i.e. with *Monogynoecus* splitting off first. In this subgenus, mature larvae normally possess a dorsal process on abdominal segment 10 (dorsal knob of Richards, 1978), the same structure being observed in *Polistes*, in at least one species of *Apoica*, in the subgenus *Clypeopolybia* and in some species of *Mischocyttarus* s. str. (see Dias-Filho, 1975; Kojima, 1998; Reid, 1942; Richards, 1945, 1978). Such a structure has not been reported in other groups of *Mischocyttarus*, and its absence might well constitute an additional synapomorphy of a clade composed by *Scytokeraia* and remaining subgenera. However, it seems to be too much variable, possibly even between larvae of one same colony. Furthermore, larval forms of many species of *Phi*, especially in Richards´s group of *M. flavitarsis* remain unknown.

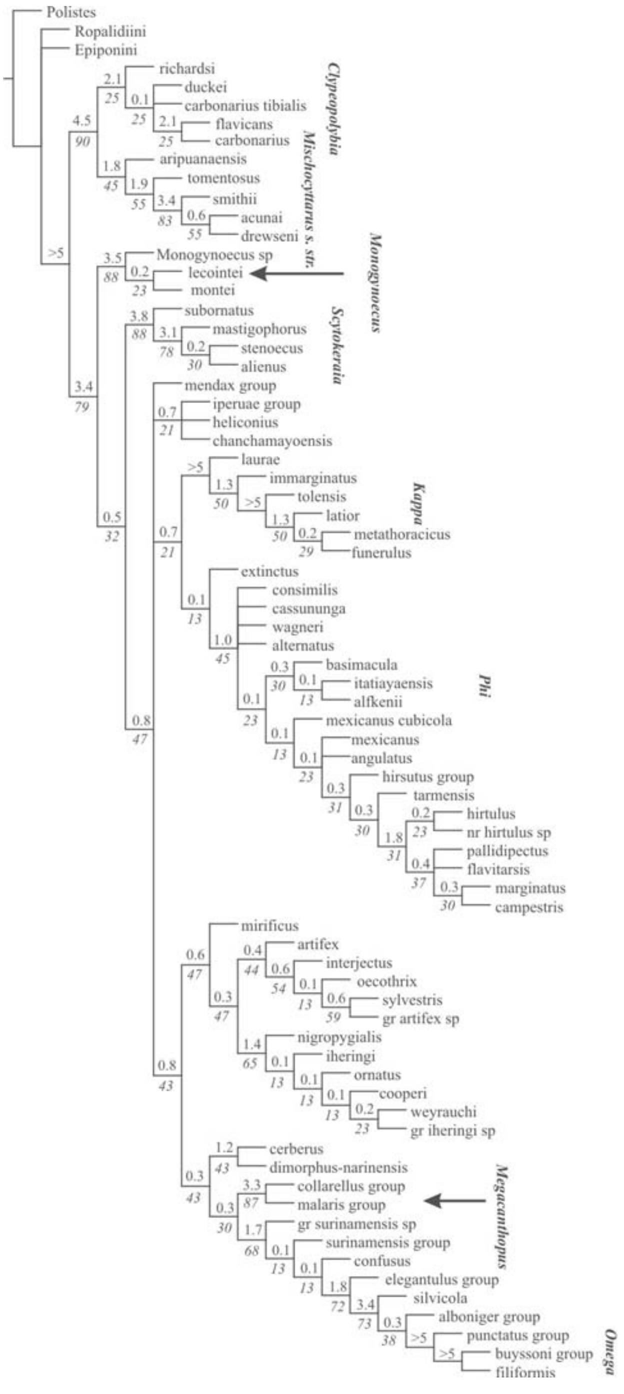


Fig. 176. Strict consensus of 6 trees (Fit= 351.2) found under implied weights (k=2) with Pee-Wee 3.0 for *Mischocyttarus* major species groups. Absolute (above) and relative (below) Bremer supports are presented for ingroup branches, except when the value exceeded the upper limit considered (i.e. >100%).

Solving the problem of relationships of *Kappa* seems to be decisive to reconstructing phylogeny in *Mischocyttarus*. This subgenus appeared as more closely related to *Phi* in most of the weighted analyses, or to part of *Phi* in the unweighted analysis (figs 173, 176, 177, 178, 179, 180). Sets of character transformations supporting such hypotheses are large and similar among analyses, involving: character 5: 0 > 1 (hairs on posterior ventral part of the gena longer and more numerous; *weighted only*); character 12: 0>1 (ocelli moderately separated, positioned as the vertices of an equilateral triangle; *unweighted only*), character 20: 1 > 3 (central portion of the pronotal carina completely reduced at center); character 32: 2 > 1 (hind tarsal claws asymmetric, the internal one larger and presenting the apex sharp or narrowly pointed; *weighted only*); character 33: 1 > 2 (propodeum with lateral surface inflated and with lateral posterior concavity); character 34: 2 > 3 (propodeal median furrow wide and triangular); character 35: 1 > 2 (metanotum triangular and moderately convex); character 39: 0 > 2 (first metasomal segment with a shallow profile, ventrally with a poorly developed angle at a point positioned posteriorly to the spiracle); character 40: 0 > 1 (lateral margin of first metasomal sternum reduced for the most part, sharp only on its distal extremity character; *unweighted only*) 46: 2 > 1 (antenna strongly shortened, with a hook-like apex, apical articles cylindrical, distinctly narrower than basal ones; *weighted only*); character 52: 1 > 0 (digitus of the male genitalia very long, distally with a finger-like shape).

However long the above list of characters, the only transformation that is unique in all the trees is in character 34 referring to shape of the propodeal median furrow. The list reflects the great general similarity between species of *Kappa* and *Phi*. Suffice to say that all these species were considered members of a single subgenus by Richards (1945). Perhaps the most apparent of these similarities refers to the reduced pronotal carina (apomorphic and rather restricted in the genus *Mischocyttarus*). A hidden but not less important character is the elongated digitus of male genitalia (plesiomorphic in the genus). However, the male mandible in *Kappa* species has only three apical teeth, a derived feature shared with all species of *Haplometrobius*, *Megacanthopus* and *Omega*. This is the main reason for the different relations of *Kappa* obtained in weighted analysis with "k" equal to 1, where it appears as part of a clade including also species of the *M. heliconius* group. In respect of this character, it is interesting to note that in most analyses where *Kappa* and *Phi* result closely related, the primitive state "with four apical teeth" appears in *Phi* as a reversed synapomorphic character of this subgenus. The only exception to this particular instance of character optimization was in the analysis under equal weigths, where a radically different position of *Monogynoecus* makes the derived state in *Kappa* being treated as independent of that in other subgenera wich also present a male mandible "with three teeth".

While the hypothesis of a clade formed by the "afoveate" groups of *Mischocyttarus* (see figs. 174-180) was in some sense expected based on taxonomic tradition (see for example constitution of *Megacanthopus* sensu Richards, 1945), a monophyletic group formed by the subgenus *Omega* and the species-groups of *M. surinamensis* and *M. prominulus* (of *Haplometrobius*) verified in all kinds of analyses is a new result of this study. Support for this clade in weighted analysis (k = 1) comes mainly from three characters (see also Apendix 2): character 8: 0 > 4 (apex of female clypeus narrowly rounded); character 54: 0 > 5 (aedeagus from above with distal portion narrow, then suddenly expanding to form a well differentiated apex distinctly angular at sides); character 56: 2 > 1 (sclerotized portion of the base of the aedeagus as a linear elongate lobe developed anteriorly up to the paramere basal processes). In some trees, characters 52: 1>3 (shape of digitus) and 58: 3>2 (hairs of parameral spine) also appeared as synapomorphies. Only transformations in characters 52, 54, and 56 are unique within *Mischocyttarus*. However, state 3 of character 52 actually occurs only in part of the group of *M. surinamensis* and in the group of *M. prominulus*. States 5 and 1 of characters 54 and 56 respectively occur in the whole clade, but are changed in some elements of *Omega* (the first character in an undescribed species related to *M. buyssoni*, and the second in the group of *M. punctatus*). Other unique transformations supporting progressively less inclusive groups within the component are in character 6: 0>1 (frontal region of the head in female strongly protuberant; present in the *M. prominulus* and *M. punctatus* groups), and in character 41: 0>1 (first metasomal sternum without a dense cover of short hairs, tegument shining; present in part of the *M. prominulus* group and in subgenus *Omega*).

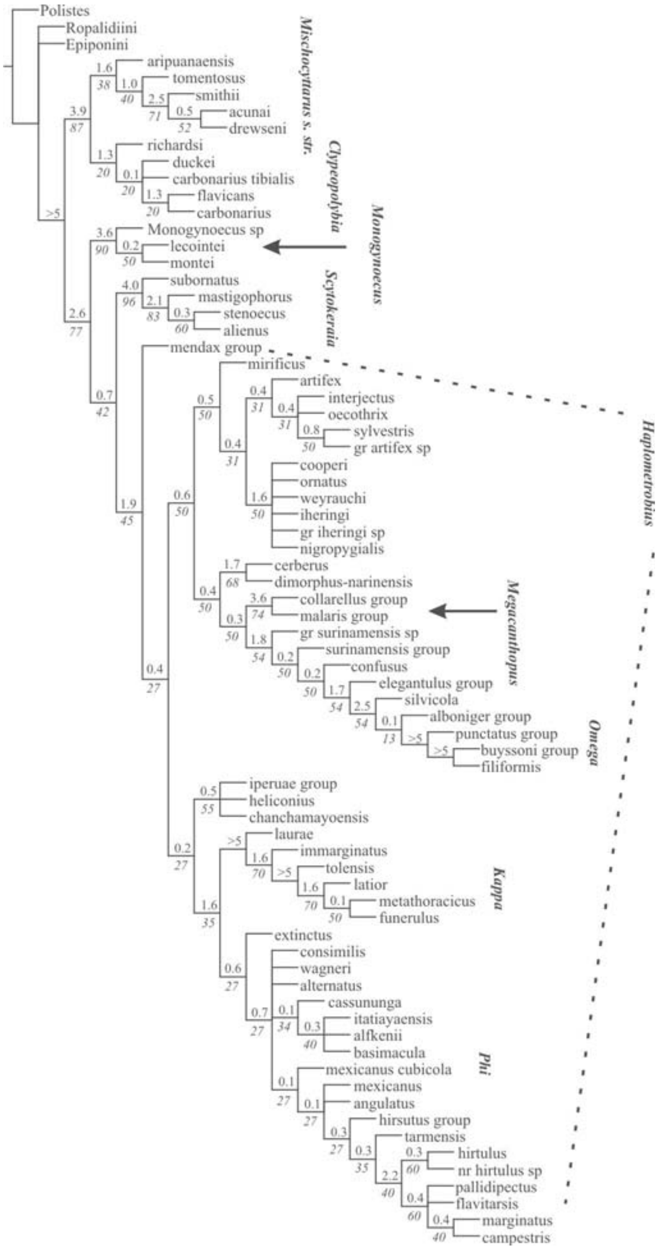


Fig. 177. Strict consensus of 9 trees (Fit= 388.2) found under implied weights (k=3) with Pee-Wee 3.0 for *Mischocyttarus* major species groups. Absolute (above) and relative (below) Bremer supports are presented for ingroup branches, except when the value exceeded the upper limit considered (i.e. >100%).

A close relationship between the species-groups of *M. iheringi* (in the present sense) and *M. artifex* was suggested in all weighted analyses. Some of the topologies presented *M.*

mirificus as an outer element sister to a clade formed by the *iheringi* group plus a major subset of the *artifex* group, i.e. making the latter paraphyletic. In certain number of trees found with k= 3, subgenus *Megacanthopus* appeared as part of this whole component, being sister to a monophyletic *artifex* group.

In the subgenus *Phi*, the only patterns repeated across weighted analyses are the sister-group relationship between *M. extinctus* and remaining species, and the clade formed by a small subset of the species of Richards´s 1978 group of *M. flavitarsis* (Figs. 174, 176-180).

Unseen forms

A considerable number of described species of *Mischocyttarus* could not be examined. As already stated, *M.* (*Monogynoecus*) *onorei* Cooper could possibly be important for inference of primitive states in the genus. Two other significant missing pieces of evidence are *M. minifoveatus* Cooper (1998a) and *M. tertius* Richards (1978). In both cases, the male is unknown, and female descriptions are incomplete to the point of making impractical the inclusion of these species as terminals in the study. *Mischocyttarus minifoveatus* seems to be similar to species of the *M. mendax* group, differing mainly by the shape of clypeus being wider than high, with the apex "pointed", and by the pronotal anterior margin being strongly raised. The posterior ocelli also seem to be more separated than in the *mendax* group. The species is here assigned to a new monospecific group of *M. minifoveatus*.

Mischocyttarus tertius was described only from the two female types, without information of nest. It has a set of pronotal features referable to some species of the *M. iheringi* group, i.e. with anterior margin raised and reflexed, secondary margin present, and with a "small but deep" fovea. The well separated posterior ocelli also indicate similarity with another species from Mato Grosso treated by Richards (1978) under the name *M. undulatus*. Richards´s emphasis on the clypeal apex of *M. tertius* being "not at all truncate" possibly relates to the author´s intention of discriminating the species among others of the *artifex* group to which it was originally assigned. The species is here tentatively assigned to the *M. iheringi* group.

Redefinition of limits and contents of several species-groups

As indicated in the works of Cooper (1996a, 1996b, 1997a), and Silveira (1998, 2002, 2004) who made extensive corrections to the limits of some of the subgenera and species-groups treated by Richards (1978), several of these groups are not properly defined, i.e. they lack an efficient diagnosis based on unique characters or combinations of characters. Most of Richards's species-groups are parts of *Phi* and *Haplometrobius*, the largest subgenera in species numbers. Here I present an annotated register of the species-groups along with a list of their constituent species (or probable species for those not actually examined, or cases in which males are unknown and critical for correct assigment), and respective diagnoses. The revised groups are largely based on results of

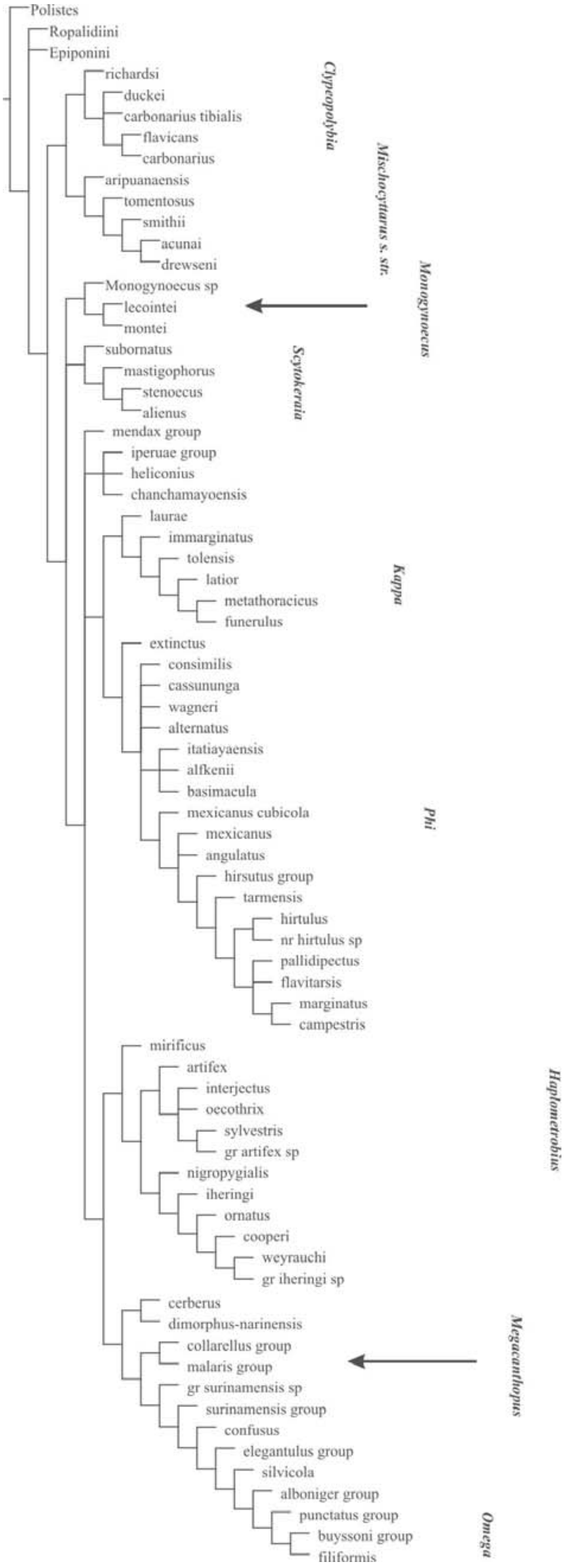


Fig. 178. Strict consensus of 18 trees (Fit= 413.9) found under implied weights (k=4) with Pee-Wee 3.0 for *Mischocyttarus* major species groups.

the present study, but monophyly is eventually relaxed as a critetion of validity of groups, since the main aim is to preliminarily describe morphological diversity in the genus and facilitate further studies.

Subgenus *Phi*

1) group of *M. flavitarsis*: *M. fisheri* Snelling, *M. bruneri* Bequaert & Salt, *M. campestris* Raw, *M. marginatus* (Fox), *M. chapadae* (Fox), *M. pallidipectus* (Smith), *M. hirtulus* Zikán, *M. inca* Zikán, *M. duidensis* Richards, *M. oreophilus* Zikán (?), *M. barbatulus* Richards (?), *M. rufipes* Zikán (?),

Pronotal secondary margin absent, anteromedian lamella narrow; female clypeal apex narrowly rounded; pronotal carina reduced; male mandible very robust, apical teeth very strong; male gena as wide as in female; metanotum distinctly convex; inner claw of hind tarsus very sharp.

2) group of *M. tarmensis* Richards.

Pronotal secondary margin absent, anteromedian lamella narrow; female clypeal apex round; pronotal carina reduced; male mandible and gena normal; apex of male antenna hook-like; propodeum less swollen and without pronounced posterior concavities at sides; body hairs long and conspicuous especially on head and propodeum.

3) group of *M. hirsutus* Richards: *M. commixtus* Richards, *M. mixtus* Richards, *M. ecuadorensis* Zikán, *M. barbatus* Richards, *M. peduncularius* Zikán, *M. transandinus* Richards, *M. rufomaculatus* Richards (?).

Pronotal secondary margin present, obtuse, not strongly projecting over anteromedian lamella; female clypeal apex narrowly truncate; male mandible and gena normal; apex of male antenna hook-like; body hairs long and conspicuous especially on head and mesosoma, erect hairs on frons and mesoscutum measuring nearly two occelar diameters; sculpture strong; black species commonly with diffuse reddish marks on mesosoma.

4) group of *M. mexicanus* (de Saussure): *M. angulatus* Richards, "*M. angulatus* morph *ictericus*" Richards, *M. costaricensis* Richards; *M. mexicanus cubicola* Richards, *M. phthisicus* (F.), *M. cubensis* (de Saussure).

Pronotal secondary margin obtuse or sharp; female clypeal apex narrowly truncate; male mandible and gena normal; apex of male antenna with articles very broad and short; metanotum rather convex; body hairs commonly long and conspicuous especially on head and propodeum (short in *M. phthisicus, M. mexicanus cubicola,* and probably *M. cubensis*).

5) group of *M. alfkenii* (Ducke) and *M. basimacula* (Cameron): *M. mamirauae* Raw, *M. flavicornis* Zikán, *M. paraguayensis* Zikán, *M. bahiae* Richards, *M. aracatubaensis* Zikán, *M. gilvus* Zikán;

Pronotal secondary margin sharp and projecting over anteromedian lamella; female clypeal apex narrowly truncate; male mandible and gena normal; apex of male antenna with articles very broad and short, 13 one and a half times as long as wide at base; male clypeus touching eyes; metanotum noticeably flattened; body hairs shorter and less conspicuous.

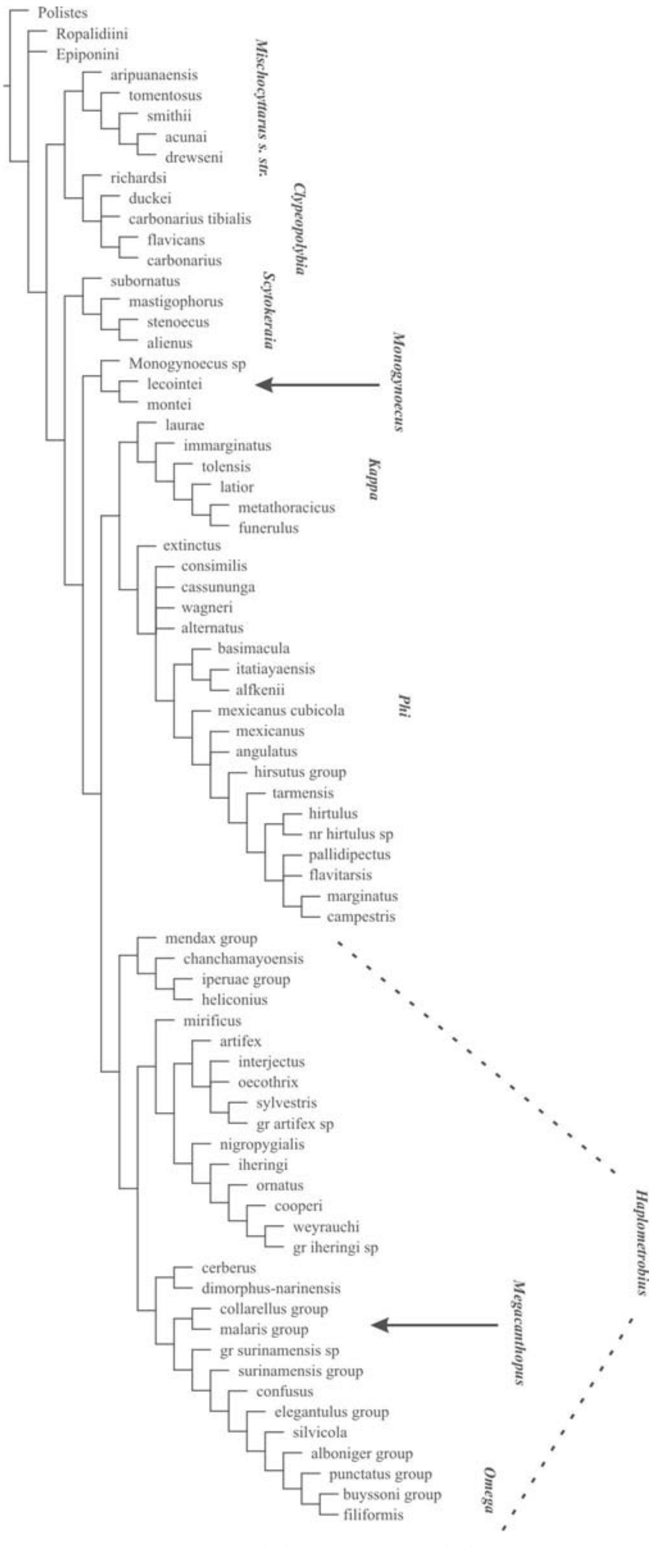


Fig. 179. Strict consensus of 6 trees (Fit= 433.6) found under implied weights (k=5) with Pee-Wee 3.0 for *Mischocyttarus* major species groups.

6) group of *M. itatiaeyensis* Zikán and *M. costalimai* Zikán: *M. riograndensis* Richards,

M. scitulus Zikán, *M. infrastrigatus* Zikán, *M. fluminensis* Zikán (?), *M. similatus* Zikán (?), *M. catharinaensis* Zikán (?), *M. mutator* Zikán (?), *M. rivulorum* (?), *M. lules* Willink (?).

Pronotal secondary margin sharp and projecting over anteromedian lamella; female clypeal apex narrowly truncate; male mandible and gena normal; apex of male antenna with articles broad and short, 13 two times as long as wide at base; male clypeus narrowly separated from eyes; metanotum noticeably flattened; body hairs shorter and less conspicuous.

7) group of *M. wagneri* (du Buysson) and *M. alternatus* Zikán: *M. imeldai* Zikán, *M. plaumanni* Zikán, *M. brackmanni* Zikán, *M. proximus* Zikán, *M. mourei* Zikán, *M. lanei* Zikán, *M. declaratus* Zikán, *M. cabauna* Zikán, *M. confirmatus* Zikán, *M. petiolatus* Richards (?);

Pronotal secondary margin sharp and projecting over anteromedian lamella; female clypeal apex narrowly truncate; male mandible and gena normal; apex of male antenna hook-like; male clypeus touching eyes, covered with very conspicuous dense silvery pubescence; pronotal carina centrally reduced; metanotum rather convex; metasomal first tergum as long or longer than hind femur + trochanter.

8) group of *M. cassununga* (von Ihering) and *M. consimilis* Zikán: *M. cearensis* Richards, *M. extinctus* Zikán: *M. crypticus* Zikán, *M. cryptobius* Zikán; *M. lilae* Willink; *M. mimicus* Zikán (?);

Pronotal secondary margin sharp and projecting over anteromedian lamella; female clypeus relatively narrow, apex narrowly truncate or rounded; male mandible and gena normal; apex of male antenna hook-like; hairs on posterior ventral part of gena short and inconspicuous; metanotum rather convex; male clypeus touching eyes, silvery pubescence not very conspicuous; pronotal carina centrally reduced.

(Former Subgenus *Haplometrobius*)

1) group of *Mischocyttarus minifoveatus* Cooper (1998a).

Anterior margin of proepisternum not reflexed; pronotal secondary margin absent, anteromedian lamella strongly raised, carina not projecting at sides, fovea present; clypeus a liitle wider than high, apex pointed; occipital region unmarginned.

2) group of *Mischocyttarus mendax* Richards (see Cooper, 1996b): *M. montivagus* Cooper, *M. moronae* Cooper, *M. tectus* Cooper, *M. occultus* Cooper, *M. reclusus* Cooper, *M. tunari* Cooper.

Anterior margin of proepisternum not reflexed; pronotal secondary margin absent, carina angularly slightly elevated at center, not projecting at sides, fovea present; female clypeal apex bidentate; occipital region narrow and unmarginned; male antenna elongate, without erect hairs; digitus short and round.

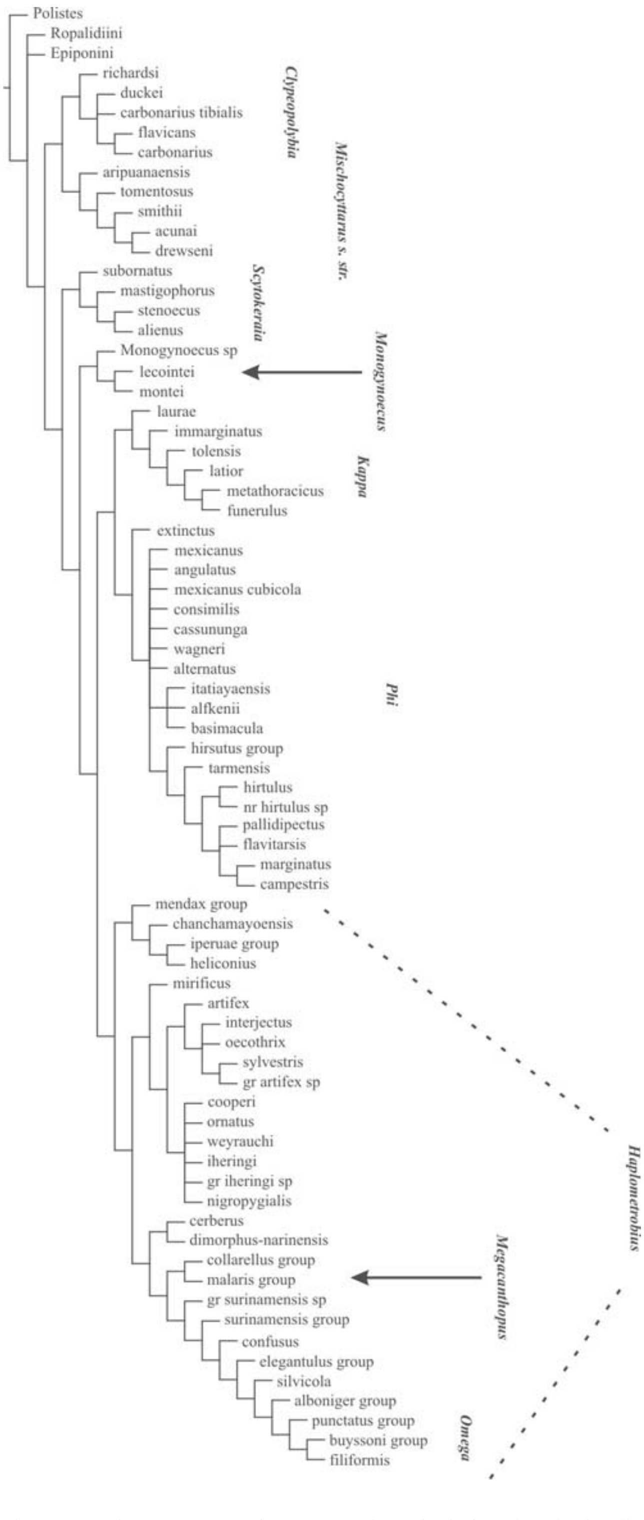


Fig. 180. Strict consensus of 72 trees (Fit= 450.5) found under implied weights (k=6) with Pee-Wee 3.0 for *Mischocyttarus* major species groups.

3) group of *Mischocyttarus heliconius* Richards: *Mischocyttarus heliconius iperuae* Richards, *M. chanchamayoensis* Richards, *M. sericeus* Richards, *M. piger* Richards, *M. undulatus* sensu Richards (1945).

Anterior margin of proepisternum not reflexed; pronotal secondary margin absent, anteromedian lamella reflexed; fovea present; female clypeal apex narrowly rounded; occipital region carinate; male antenna always elongate, without erect hairs, apical part narrow and spirally rolled.

4) group of *Mischocyttarus surinamensis* (de Saussure): *M. tricolor* Richards, *M. decimus* Richards, *M. bahiaensis* Zikán, *M. hoffmanni* Zikán, *M. ignotus* Zikán, *M. garbei* Zikán, *M. confusus* Zikán, *M. melanoxanthus* Richards, *M. xanthocerus* Richards, *M. cleomenes* Richards, *M. paulistanus* Zikán, *M. confusoides* Zikán, *M. souzalopesi* Zikán, *M. claretianus* Zikán; *M. bequaertii* Richards.

Anterior margin of proepisternum raised and reflexed; pronotal secondary margin absent, humeral region projecting laterally, fovea absent; clypeal apex narrowly rounded; occipital region just compressed dorsally, not really carinate; male antenna nearly always elongate, with erect hairs, apical part very narrow and spirally rolled (short with apex hook-like in only one undescribed species from Panamá).

5) group of *Mischocyttarus prominulus* Richards: *M. pallidus* Zikán, *M. silvicola* Zikán, *M. melanoleucus* Richards, *M. elegantulus* Zikán, *M. annulatus* Richards, *M. alboniger* Richards, *M.* tenuis Richards;

Anterior margin of proepisternum raised and reflexed; pronotal secondary margin absent, anteromedian lamella strongly reflexed, humeral region projecting laterally, fovea absent; female clypeal apex narrowly rounded; occipital region distinctly carinate; male antenna always with apex short and hook-like; posterior part of the head around occipital foramen produced into a shallow cavity with a smoothly rounded boundary, never sharply margined; hairs on posterior ventral part of gena short and inconspicuous.

6) group of *Mischocyttarus cerberus* (Ducke) (see also Silveira. 2004): *M. illusorius* Richards, *M. nomurae* Richards, *M. peruanus* Zikán, *M. dimorphus* Zikán, *M. narinensis* Cooper.

Anterior margin of proepisternum raised and reflexed; pronotal secondary margin sharp; fovea absent; inner claw of hind tarsus narrow, nerver spoon-shaped; male antenna always elongate, apical part very narrow and spirally rolled, no antennomere with erect hairs; male mandible with tooth 1 (posteriormost) much larger than the others; digitus very long but sac-like, not "digitiform"; paramere spine with moderately numerous elongate hairs.

7) group of *Mischocyttarus iheringi* Richards: *M. weyrauchi* Zikán, *M. saussurei* Zilán, *M. vredeni* Richards, *M. naumanni* Richards, *M. cooperi* Richards, *M. longicornis* Zikán, *M. nigropygialis* Zikán, *M. macarenae* Cooper, *M. ornatus* Zikán, *M. travassosi* Zikán, *M. curitybanus* Zikán, *M. undulatus* sensu Richards (1978, p. 413-414; in part, only specimens from Mato Grosso, Brazil).

Anterior margin of proepisternum not reflexed; pronotal secondary margin sharp; fovea absent in nearly all instances except for a residual one in *M. tertius* and *M. undulatus* s. Richards; female clypeal apex narrowly truncate; occipital region most often compressed or carinate; male antenna always elongate, with erect hairs, apical part very narrow and spirally rolled; male aedeagus short and absolutely straight in lateral view, ventral process as a rounded lobe contorted inwards,

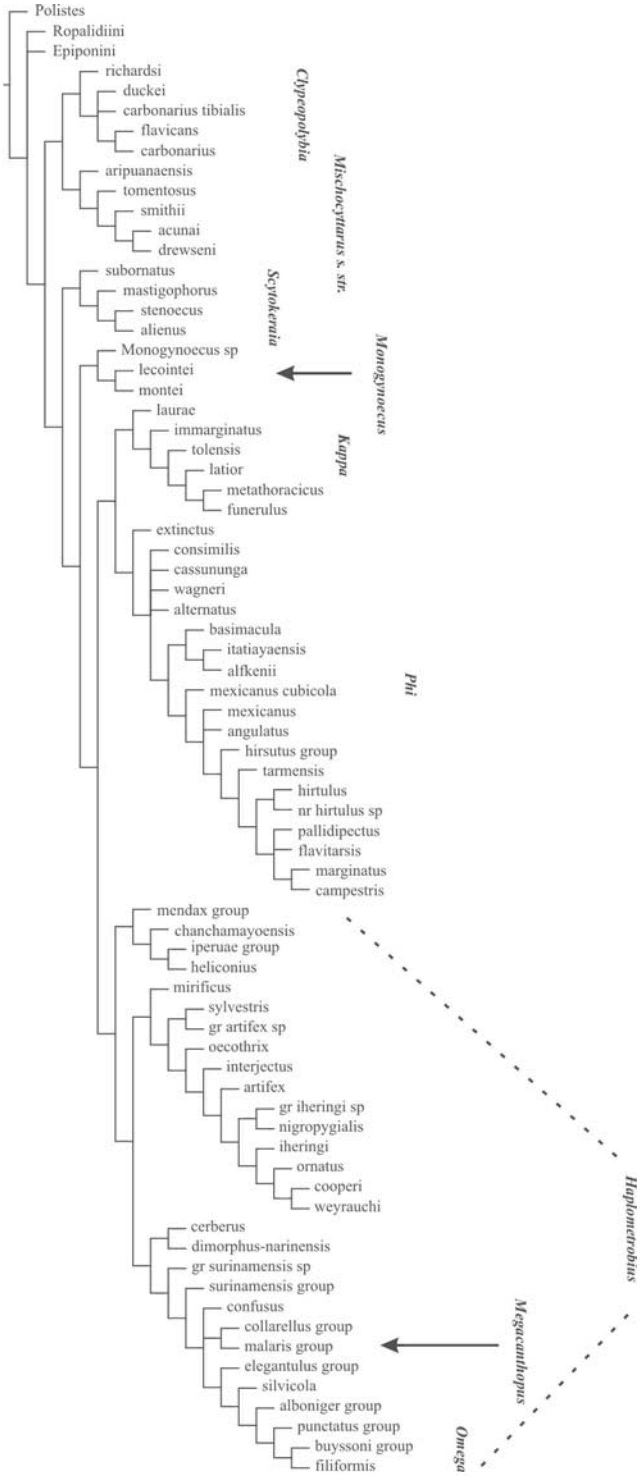


Fig. 181. Strict consensus of 3 trees found under implied weights (k=1) with TNT 1.0 for *Mischocyttarus* major species groups.

without teeth; digitus short, with a rounded shape, rarely triangular.

8) group of *Mischocyttarus artifex* (Ducke): *M. sylvestris* Richards, *M. lemoulti* (Buysson), *M. schadei* Zikán, *M. ypiranguensis* Fonseca, *M. mirificus* Zikán, *M. peruviensis* Richards, *M. thrypticus* Richards, *M. chloroecus* Cooper, *M. leucoecus* Cooper, *M. filipendulus* Cooper, *M. maculipennis* Cooper, *M. polymorphus* Cooper, *M. reflexicollis* Zikán, *M. capichaba* Zikán, *M. interjectus* Zikán, *M. giffordi* Raw, *M. oecothrix* Richards, *M. synoecus* Richards, *M. interruptus* Richards, *M. nigroclavatus* Zikán, *M. undulatus* (Ducke).

Anterior margin of proepisternum not reflexed; pronotal secondary margin sharp; fovea absent; clypeal apex bidentate; male antenna moderately elongate with distal articles often distinctly flattened below and not much longer than wide in dorsal view, in a few species with apex short and hook-like (*mirificus* and allies), frequently with conspicuous erect hairs; male aedeagus with ventral process as a large angular lobe; digitus triangular; paramere spine nearly glabrous, or with short hairs at the apex (*mirificus* and allies).

A new classification for *Mischocyttarus*

Haplometrobius Richards was the only subgenus of *Mischocyttarus* whose monophyly was consistently negated in this study. Acceptance of results obtained in the unweighted analysis would lead also to rejection of *Phi* (see Fig. 173). However, this latter result was contradicted by all analyses using weights, what seems to be sufficient reason for keeping such a otherwise well delimited group. The consensus tree of figure 174 (from weighted analysis, k= 1), together with relative branch support values are valuable guides to decide about which major clades and species-groups should possibly be reflected in a classification of the genus. If enlargement of the concept of *Omega* for inclusion of the *M. prominulus* and *M. surinamensis* species-groups seems unavoidable, doing the same for *Kappa* to include the *M. heliconius* group is probably not so straightforward given that character support is in this case weak, involving only two relatively variable features (occipital carina and clypeal apex). Equally weak is character support for the component linking elements of the *M. artifex* and *M. iheringi* groups, mainly based on shape of pronotal anterior margin and male antennal hairs, which vary broadly among *Haplometrobius* groups.

The classification proposed here preserves validity of all previous subgenera except *Haplometrobius* (sensu Richards, 1978). If the analyses have shown a good level of confidence in monophyly of some of the *Haplometrobius* less inclusive groups, relationships among them are largely uncertain. The solution adopted here for this problem is to use the name *Haplometrobius* narrowly for the *M. iheringi* group only, containing the type species *M. iheringi* Zikán, and raising to subgenus level other species-groups whose monophyly has been effectively tested, i.e. the *M. cerberus* group and the major part of the *M. artifex* group, with other former *Haplometrobius* groups being treated as *incertae sedis* (see

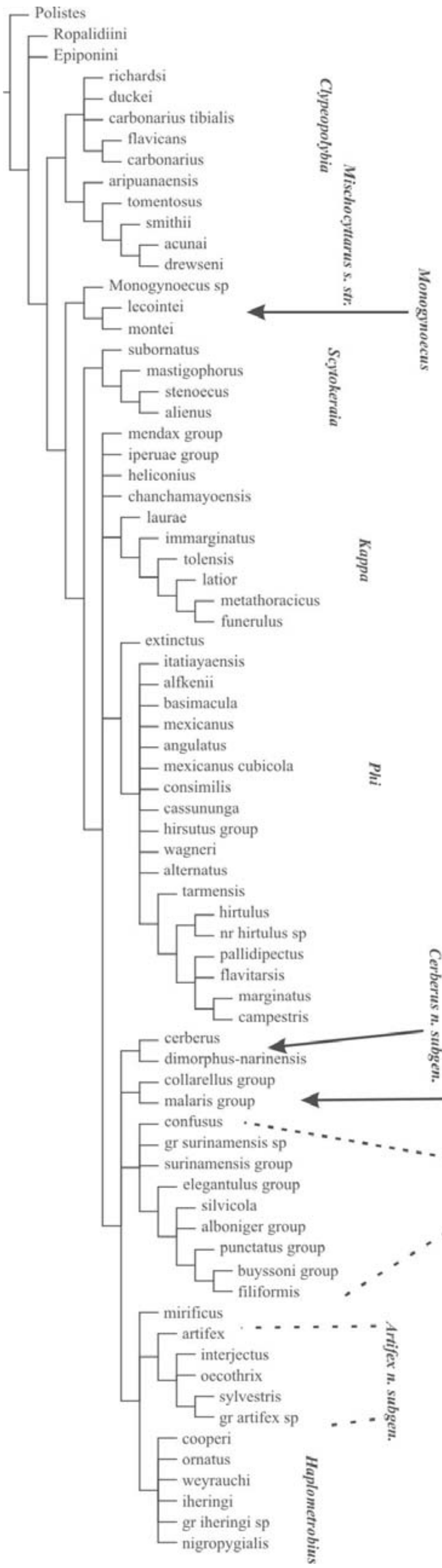


Fig. 182. Strict consensus of trees found under implied weights with Pee-Wee 3.0, values of the constant of concavity varying from 1 to 3. Subgenera with their limits and content as conceived in the classification presented in this work.

below). If *Mischocyttarus mirificus* Zikán and a few close allies (*M. ypiranguensis,* Fonseca; *M. schadei* Zikán; *M. thrypticus* Richards) must properly be considered uncertain within the new subgenus created for the *M. artifex* group (see below), it should be stressed that *M. mirificus* actually shows the large triangular ventral aedeagal process, a distinct unique feature of the *M. artifex* group, and also constructs the very elongate nests so typical in the group.

The classificatory decisions are in fairly agreement with the consensus between the trees obtained in weighted analyses with values of "k" equal to 1, 2 and 3 (Fig. 182). If the criticism could be made of excessive splitting regarding recognition of three relatively small species-groups (a reduced *Haplometrobius* and two new subgnera; see below), the alternative situation of a single very large subgenus containing a very heterogeneous array of (afoveate) species is probably worse. Furthermore, the name *Omega* de Saussure, the oldest available for such a group would have as synonym at least one very distinctive taxon, *Megacanthopus* which should then be treated as a species-group (in addition to *Omega* itself in its Richards´s 1978 "Monacanthocnemis" sense; a fact also occurring in the context of the alternative solution proposed here). However, knowledge of the relations among such large clades as *Phi* and *Kappa* (and the afoveate component) is certainly a prerequisite to making the best decisions at this level of inclusiveness. All that can be done now, and that would be probably useful is to name informally the two basalmost clades within the genus, for which I suggest the names "Saussurea" for *Mischocyttarus* s. str. + *Clypeopolybia*, and "Duckea" for the large component formed by the remaining groups.

Genus *Mischocyttarus* de Saussure, 1853.

Subgenus *Mischocyttarus* de Saussure, 1853: 19.
Type species: *Zethus labiatus* Fabricius, 1805, by designation of Ashmead, 1902.

Subgenus *Clypeopolybia* Brèthes, 1923: 16.
Type species: *Clypeopolybia duckei* Brèthes, 1923 (=*Polistes flavicans* Fabricius, 1804), by monotypy.

Subgenus *Monogynoecus* Richards, 1941: 126.
Type species: *Megacanthopus lecointei* Ducke, 1904, by original designation.

Subgenus *Scytokeraia* Cooper, 1997a: 117.
Type species: *Mischocyttarus mastigophorus* Richards, 1978, by original designation.

Subgenus *Phi* de Saussure, 1854: 183.
Type species: *Vespa phthisica* Fabricius, 1793, by designation of Bequaert, 1943.
Monocyttarus Richards, 1978: 307. Type species: *Polybia flavitarsis* de Saussure, 1854, by original designation; synonymy by Carpenter & Day, 1988.

Subgenus *Kappa* de Saussure, 1854: 200.
Type species: *Polybia injucunda* de Saussure, 1824, by designation of Bequaert, 1933.

Subgenus *Haplometrobius* Richards, 1978: 389. [= group of *M. iheringi* Richards]
Type species: *Mischocyttarus iheringi* Zikán, 1935, by original designation.

Subgenus Artifex subgen. n. [= group of *M. artifex* Ducke]
Type specie: *Mischocyttarus artifex* Ducke, 1914; absolute tautonymy.

Subgenus Cerberus subgen. n. [= group of *M. cerberus* Ducke]
Type species: *Mischocyttarus cerberus* Ducke, 1918; absolute tautonymy.

Subgenus *Omega* de Saussure, 1854: 206. (sensu this work)
Type species: *Polybia filiformis* de Saussure, 1854, by monotypy.

Subgenus *Megacanthopus* Ducke, 1904: 358.
Type species: *Megacanthopus collaris* Ducke, 1904, by designation of Bequaert, 1933.

Incertae sedis
group of *Mischocyttarus heliconius* Richards
group of *Mischocyttarus mendax* Richards
Mischocyttarus minifovetaus Cooper

Key to subgenera and species-groups of *Mischocyttarus*

1. Base of fore and mid femora with a ring-like sulcus; anterior two-thirds of mesoscutal margin adjacent to tegula reduced; first metasomal segment often strongly compressed, lateral profile very deep with a prominent ventral angle posterior to the spiracle, tergal margins closely approximated below at this point, sternum with a "strangled" appearance; male antenna linear not tapering distally; digitus of male genitalia distinctly pilose 2

Base of fore and mid femora without a ring-like sulcus; mesoscutal margin adjacent to tegula nearly always complete; first metasomal segement differently shaped; male antenna nearly always tapering distally; digitus of male genitalia approximately glabrous 3

2(1). Lateral symmetric indentations of the female clypeus rather shallow; female fore femur in section with a roughly round contour; propodeum with anterior medial surface rather strongly raised, median furrow deep and distinctly triangular; male aedeagus very wide from base to apex; nest comb circular with central peduncle .... Subgenus *Mischocyttarus* s. str. de Saussure.

Lateral symmetric indentations of the female clypeus very deep; female fore femur with posterior surface strongly flattened, with a sharp edge ventrally sometimes "lamellate"; propodeum with anterior medial surface oblique, median furrow deep or shallow, linear; male aedeagus narrowing distally; nest comb polygonal with eccentric peduncle .... Subgenus *Clypeopolybia* Brèthes.

3(1). Frons and interantennal area in female looking depressed, antennal sockets close to each other, separated by a distance no longer than their height, socket aperture facing forwards, with fairly circular contour, its marginal lamella high and "free"; pronotum humeral region nearly always without vestiges of angle, contour seen from above practically continuous with the anterior region of the pronotum, carina often strongly reduced, fovea very small or absent; male mandible with four apical teeth, antennal apex short hook-like; aedeagus very wide from base to apex, distal portion short and dorsally flattened, with parallel sides; aedeagal ventral process as a very long narrow lobe .... Subgenus *Monogynoecus* Richards.

Frons and upper portion of interantennal area in female more swollen and raised, socket aperture directed more laterally, contour not regularly circular, marginal lamella looking as if turned and compressed outwards; humeral region with noticeable angle (if round, then carina exceptionally developed), fovea variable; male mandible with four or three teeth, antenna variable; male aedeagus and ventral process differently shaped 4

4(3). Inner margin of fore coxa very low, not reflexed; female clypeus with apex widely truncate and bidentate; posterior dorsal part of the head narrow, strongly dipping backwards behind eyes and ocelli; anterior region of pronotum without a secondary margin, anteromedian lamella narrow, humeral region not forming lateral lobe, carina usually low; tooth 1 of male mandible with external surface convex, similar to female, its posterior border curved; male antenna elongated, article 13 slender, strongly compressed, often acuminate ...... Subgenus *Scytokeraia* Cooper.

Inner margin of fore coxa more often high and reflexed, if very low then the female clypeal apex not at all bidentate; posterior dorsal part of the head wider; pronotum variable; tooth 1 of male mandible planar, distal portion often with a linear aspect, unlike that of female; male antenna variable, article 13 differently shaped, rarely compressed 5

5(4). Pronotal carina total or partially reduced at center, not lamellate there; fovea present; first metasomal segment with a shallow lateral profile, without a prominent ventral angle posterior to the spiracle; male digitus quite long, digitiform; male antenna never with erect conspicuous hairs 6

Pronotal carina continuous from side to side (if interrupted centrally then the fovea is absent); first metasomal segment laterally more often with a noticeable ventral angle posterior to the spiracle; male digitus nearly always shorter, round or triangular, never digitiform; male antenna with or without erect hairs 14

6(5). Anterior margin of proepisternum elevated and strongly reflexed, forming a very wide and freely detached lateral collar; occipital region often carinate; posterior ocelli nearly always widely separated, positioned as basal vertices of a low triangle; male mandible with three teeth; male antenna with well developed tyloids; larvae with just one abdominal appendix-like process .... Subgenus *Kappa* de Saussure.

Anterior margin of the proepisternum low, not reflexed; occipital region unmargined, not carinate; posterior ocelli never so widely separate; male mandible with four teeth; male antenna nearly always with tyloids reduced; larvae with two abdominal appendix-like processes .... (Subgenus *Phi* de Saussure) 7

7(6). Pronotal secondary margin absent, anteromedian lamella narrow not raised; pronotal carina reduced 8

Pronotal secondary margin present, obtuse or sharp, anteromedian lamella wider; pronotal carina reduced or not 9

8(7). Female clypeus with apex narrowly rounded; male mandible very robust, apical teeth very strong; male gena as wide as in female; metanotum distinctly convex; inner claw of hind tarsus strictly sharp .... group of *M*. (*Phi*) *flavitarsis* (de Saussure).

Female clypeus with apex wider round; male mandible and gena normal; metanotum less convex; inner claw of hind tarsus less strictly sharp .... group of *M*. (*Phi*) *tarmensis* Richards.

9(7). Apex of male antenna pointed, hook-like 10

Apex of male antenna linear with articles broad and short 12

10(9). Pronotal secondary margin low, obtuse, not strongly projecting over anteromedian lamella; body hairs long and conspicuous especially on head and mesosoma, erect hairs on frons and mesoscutum measuring nearly two occelar diameters; sculpture strong; black species commonly with diffuse reddish marks on mesosoma ...... group of *M*. (*Phi*) *hirsutus* Richards.

Pronotal secondary margin sharp and strongly projecting over anteromedian lamella 11

11(10). Hairs on posterior ventral part of gena normally long and conspicuous; female clypeus with apex narrowly truncate; male clypeus covered with very conspicuous dense silvery pubescence; propodeal median furrow wide and shallow; metasomal first tergum as long or longer than hind femur + trochanter .... group of *M.* (*Phi*) *wagneri* (du Buysson) and *M.* (*Phi*) *alternatus* Zikán.

Hairs on posterior ventral part of gena short and inconspicuous; female clypeus with apex narrowly truncate or rounded; male clypeus with silvery pubescence not so conspicuous; propodeal median furrow longer and deeper; metasomal first tergum shorter .... group of *M.* (*Phi*) *cassununga* (von Ihering) and *M.* (*Phi*) *consimilis* Zikán.

12(9). Metanotum rather convex; body hairs commonly long and conspicuous especially on head and propodeum (short in *M. phthisicus, M. mexicanus cubicola,* and probably *M. cubensis*) .... group of *M.* (*Phi*) *mexicanus* (de Saussure).

Metanotum more flattened; body hairs shorter and less conspicuous 13

13(9). Male clypeus touching eyes; male antennal article 13 very short, one and a half times as long as wide at base .... group of *M.* (*Phi*) *alfkenii* (Ducke) and *M.* (*Phi*) *basimacula* (Cameron).

Male clypeus narrowly separated from eyes; male antennal article 13 slightly longer, two times as long as wide at base or a little more .... group of *M.* (*Phi*) *itatiaeyensis* Zikán and *M.* (*Phi*) *costalimai* Zikán.

14(5). Pronotum laterally with a fovea, pronotal anterior region without secondary margin, carina tending to be angularly raised at center; male antenna never with conspicuous erect hairs 15

Pronotum nearly always without a fovea, anterior region with or without secondary margin, carina differently shaped at center (rarely if pronotum with fovea, then anterior region with a sharp secondary margin, and male antenna with conspicuous erect hairs) 17

15(14). Occipital region carinate or with compressed edge; margin of hypostoma often with lamella elevated near articulation of mandible; pronotal anteromedian lamella always raised and reflexed; medium to large species .... group of *M. heliconius* Richards.

Occipital region unmargined; margin of hypostoma with lamella low; pronotal anteromedian lamella variable; small species 16

16(15). Female clypeus with apex truncate and weakly bidentate; pronotal anteromedian lamella narrow not noticeably raised .... group of *M. mendax* Richards.

Female clypeus with apex pointed; pronotal anteromedian lamella strongly raised .... group of *M. minifoveatus* Cooper.

17(14). Aanterior margin of proepisternum elevated and strongly reflexed, forming a very wide and freely detached lateral collar 18

Anterior margin of proepisternum not strongly reflexed 23

18(17). Anterior region of pronotum with a sharp secondary margin; inner claw of hind tarsus narrow, nerver spoon-shaped; male antenna always elongate, apical part very narrow and spirally rolled, no antennomere with erect hairs; male mandible with tooth 1 (posteriormost) much larger than the others; male digitus very long but sac-like, not “digitiform” .... subgenus *Cerberus* subgen. n.

Anterior region of pronotum never with secondary margin; inner claw of hind tarsus wider, often spoon-shaped; male antenna variable; male mandible with tooth 1 (posteriormost) normal, not enlarged; male digitus variable 19

19(18). Humeral region of pronotum with a distinct rounded contour; pronotal carina strongly convex, lamella very high, usually diminishing gradually at sides; pronotal anteromedian lamella nearly always strongly relfexed and ending laterally in a hook .... subgenus *Megacanthopus* Ducke.

Humeral region of pronotum angled laterally, never with rounded contour; pronotal carina straight or concave; pronotal anteromedian lamella not produced laterally into a hook; male aedeagus from above nearly always with distal portion suddenly expanded and distinctly angular laterally, base of the aedeagus a linear elongate lobe developed anteriorly up to the paramere basal processes .... (subgenus *Omega* de Saussure) 20

20(19). Posterior part of the head around occipital foramen produced into a deep cavity below, its ventral portion horizontal, sharply margined, like a shelf; paramere spine of male genitalia nearly glabrous 21

Posterior part of the head around occipital foramen produced into a shallow cavity with a smoothly rounded boundary; paramere spine of male genitalia with long conspicuous hairs 22

21(20). Proepisternum with a pre-marginal raised crest (double margined); male antenna short, apex hook-like; nest comb vertical with one to three elongated rows of cells .... group of *M.* (*Omega*) *punctatus* (Ducke).

Proepisternum without a pre-marginal raised crest (simple margined); male antenna elongated, spirally rolled; nest comb not elongated .... group of *M.* (*Omega*) *filiformis* (de Saussure).

22(20).Frontal region of female protuberant; occipital region carinate, usually blackened .... group of *M.* (*Omega*) *prominulus* Richards

Frontal region of female normal, not noticeably protuberant; occipital region at most with a dorsal compressed edge .... group of *M.* (*Omega*) *surinamensis* (de Saussure).

23(17).Female clypeus with apex bidentate; male mandible often with tooth 1 very elongated; male aedeagus curved in lateral view, ventral process as a large triangular lobe; nest often with elongated vertical comb .... subgenus *Artifex* subgen. n.

Female clypeus never bidentate; male mandible with tooth 1 normal, not very elongated; male aedeagus straight in lateral view, ventral process as a small rounded lobe contorted inwards; nest variable, rarely with elongated vertical comb .... subgenus *Haplometrobius* Richards.

Acknowledgments. This paper is part of a doctorate thesis presented at the “Museu de Zoologia da Universidade de São Paulo”. I am very grateful to Dr. Carlos Roberto Brandão, Dr. Sérvio T. Pires Amarante, Dr. Eliana Cancello, Dr. Sergio Vanin, and many other teachers and colleagues in S. Paulo and Belém for generous help in many aspects of the work. Dr. James M. Carpenter kindly revised the manuscript. I am also grateful to Dr. Junichi Kojima, Dr. Carlos Sarmiento and the curators of the various institutions for the material borrowed for this study.

REFERENCES

Arnett, R. H; G. A. Samuelson & G. M. Nishida. The Insect and Spider Collections of the World. Gainesville, Sandhill Crane Press, 310 p.

Arévalo, E.; Y. Zhu; J. M. Carpenter & J. Strassmann. 2004. The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. **BMC Evolutionary Biology 4**:1–16.

Bequaert, J. 1933. The neartic social wasps of the subfamily Polybiinae (Hymenoptera: Vespidae). **Entomologica Americana (n. ser.) 13**: 87–150.

Bequaert, J. 1937. Two Central American social wasps, accidentally introduced into the United States. **Bulletin of the Brooklyn Entomological Society 32**: 116.

Bequaert, J. 1943. New and imperfectly known neotropical Polybiinae (Hymenoptera, Vespidae). **Journal of the New York Entomological Society 50**: 295–308.

Bin, F.; F. Wäckers; R. Romani & N. Isidoro. 1999. Tyloids in *Pimpla turionellae* (L.) are release structures of male antennal glands involved in courtship behaviour (Hymenoptera: Ichneumonidae). **International Journal of Insect Morphology 28**: 61–68.

Bremer, K. 1994. Branch support and tree stability. **Cladistics 10**: 295–304.

Brèthes, J. 1923. Primera contribución para el conocimiento de los Strepsipteros argentinos. **Revista de la Facultad Nacional de Agronomía, Universidad de La Plata 15**: 18 pp.

Carpenter, J. M. 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). **Systematic Entomology 7**: 11–38.

Carpenter, J. M. 1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). **Systematic Entomology 12**: 413–431.

Carpenter, J. M. 1988a. The phylogenetic system of the Stenogastrinae (Hymenoptera: Vespidae). **Journal of the New York Entomological Society 96**: 140–175.

Carpenter, J. M. 1988b. Choosing among multiple equally parsimonious cladograms. **Cladistics 41**: 291–296.

Carpenter, J. M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae, p. 7–32. *In*: Ross, K. G. & Matthews, R. W. (eds.). **The Social Biology of Wasps,** Ithaca, Cornell University Press, 678 p.

Carpenter, J. M. 1993. Biogeographic patterns in the Vespidae (Hymenoptera): Two views of Africa and South America, p. 139–155. *In*: Goldblatt, P. (ed.). **Biological Relationships between Africa and South America**, New Haven, Yale University Press.

Carpenter, J. M. 1996. Phylogeny and biogeography of *Polistes*, p. 18–57. *In*: Turillazzi, S. & West-Eberhard, M. J. (eds.). **Natural History and Evolution of Paper-Wasps**, Oxford, Oxford University Press.

Carpenter, J. M. 1997. Phylogenetic relationships among european *Polistes* and the evolution of social parasitism (Hymenoptera: Vespidae, Polistinae). **Mémoires du Muséum National d'Histoire Naturelle 173**: 135–161.

Carpenter, J. M. 1999. Taxonomic Notes on Paper Wasps (Hymenoptera: Vespidae; Polistinae). **American Museum Novitates 3259**: 44 pp.

Carpenter, J. M. & M. C. Day. 1988. Nomenclatural notes on Polistinae (Hymenoptera: Vespidae). **Proceedings of the Entomological Society of Washington 90**: 323–328.

Carpenter, J. M.; J. E. Strasssmann; S. Turillazzi; C. R. Hughes; C. R. Solís & R. Cervo. 1993. Phylogenetic relationships among paper wasp social parasites and their hosts (Hymenoptera: Vespidae; Polistinae). **Cladistics 9**: 129–146.

Carpenter, J. M. & J. W. Wenzel. 1988. A new species and nest type of *Mischocyttarus* from Costa Rica (Hymenoptera: Vespidae; Polistinae), with descriptions of nests of three related species. **Psyche 95**: 89–99.

Charnley Jr., H. W. 1973. The value of the propodeal orifice and the phallic capsule in Vespid Taxonomy (Hymenoptera, Vespidae). **Bulletin of the Buffalo Society of Natural Sciences 26**: 1–76.

Cooper, M. 1996*a*. The subgenus *Monogynoecus* Richards of *Mischocyttarus* de Saussure (Hym., Vespidae, Polistinae) with descriptions of two new species. **Entomologist's Monthly Magazine 132**: 23–28.

Cooper, M. 1996*b*. The *mendax* group of *Mischocyttarus* (Hym., Vespidae, Polistinae) with descriptions of new species. **Entomologist's Monthly Magazine 132**: 273–280.

Cooper, M. 1997*a*. A new subgenus of *Mischocyttarus* de Saussure (Hym., Vespidae). **Entomologist's Monthly Magazine 133**: 117–129.

Cooper, M. 1997*b*. The subgenus *Megacanthopus* Ducke of *Mischocyttarus* de Saussure (Hym., Vespidae), with a key and three new species. **Entomologist's Monthly Magazine 133**: 217–223.

Cooper, M. 1998*a*. Two new species of *Mischocyttarus* (Hym., Vespidae) with notes on some members of the *iheringi* group. **Entomologist's Monthly Magazine 132**: 89–93.

Cooper, M. 1998*b*. New species of the *artifex* group of *Mischocyttarus* de Saussure (Hym., Vespidae) with a partial key. **Entomologist's Monthly Magazine 134**: 293–306.

Dias-Filho, M. M. 1975. Contribuição à morfologia de larvas de vespídeos sociais do Brasil. **Revista Brasileira de Entomologia 19**: 1–36.

Ducke, A. 1904. Sobre as vespidas sociaes do Pará. **Boletim do Museu Goeldi 4**: 317–374.

Ducke, A. 1905. Nouvelles contributions à la connaissance des vespides sociales de l'Amérique du Sud. **Revue d'Entomologie (Caen) 24**: 5–24.

Ducke, A. 1913. Zur Synonymie einiger Hymenopteren. **Deutsche Entomologische Zeitschrift 1913**: 330–333.

Ducke, A. 1914. Über Phylogenie und Klassifikation der socialen Vespiden. **Zoologische Jahrbuchen Abteilung fur Systematik, Geographie und Biologic der Tiere 36**: 303–330.

Ducke, A. 1918. Catalogo das vespas do Brazil. **Revista do Museu**

Paulista 10: 314–374.

Farris, J. S. 1983. The logical basis of phylogenetic analysis, p. 7–36. *In*: Platnick, N. I. & Funk, V. A. (eds.). **Advances in Cladistics**, 2**.** Proceedings of the second meeting of the Willi Hennig Society. New York, Columbia University Press, 218 p.

Fontal-Cazalla M. F.; M. L. Buffington; G. Nordlander; J. Liljeblad; P. R. Farré; J. L. N. Aldrey; J. P. Villar & F. Ronquist. 2002. Phylogeny of the Eucoilinae (Hymenoptera: Cynipoidea: Figitidae). **Cladistics 18**: 154–199.

Gadagkar, R. 1991. ***Belonogaster, Mischocyttarus, Parapolybia*, and Independent- founding *Ropalidia*,** p. 149-190. In: Ross, K. G. & Matthews, R. W. (eds.). The Social Biology of Wasps, Ithaca, Cornell University Press, 678 p.

Garcete-Barrett, B. R. 1999. **Guía ilustrada de las avispas sociales del Paraguay (Hymenoptera: Vespidae: Polistinae)**. London, The Natural History Museum, 44 p.

Giannotti, E. 1998. The colony cycle of the social wasp *Mischocyttarus cerberus styx* Richards, 1940 (Hymenoptera, Vespidae). **Revista Brasileira de Entomologia 41**: 217–224.

Giannotti, E. 1999. Social organization of the eusocial wasp *Mischocyttarus cerberus styx* (Hymenoptera, Vespidae). **Sociobiology 33**: 325–338.

Giannotti, E. & Fieri, S. R. 1991. On the brood of *Mischocyttarus* (*Monocyttarus*) *cassununga* (Iheringi, 1903) (Hymenoptera, Vespidae). **Revista Brasileira de Entomologia 35**: 263–267.

Giannotti, E. & Silva, C. V. 1993. *Mischocyttarus cassununga* (Hymenoptera, Vespidae): external morphology of the brood during the post-embrionic development. **Revista Brasileira de Entomologia 37**: 309–312.

Goloboff, P. A. 1993*a*. Estimating character weights during tree search. **Cladistics 9**: 83–91.

Goloboff, P. A. 1993*b*. **Nona: A tree searching program.** Program and documentation available at http://www.zmuc.dk/public/phylogeny.

Goloboff, P. A. 1997. Self-Weighted Optimization: Tree Searches and Character State Reconstructions under Implied Transformation Costs. **Cladistics 13**: 225–245.

Goloboff, P. A. & J. S. Farris. 2001. Methods for quick consensus estimation. **Cladistics 17**: 526–534.

Goloboff, P. A.; J. S. Farris & K. C. Nixon. 2005. **T.N.T. Tree Analysis Using New Technology**. Program and documentation, available at http://www.zmuc.dk/public/phylogeny.

Gorton, E. T. Jr. 1978. Observation on the nesting behavior of *Mischocyttarus immarginatus* (Rich.) (Vespidae: Hymenoptera) in a dry forest in Costa Rica. **Insectes Sociaux 25**: 197–204.

Goulet, H. & J. T. Huber. 1993. **Hymenoptera of the World: an identification guide to families**. Research Branch Agriculture Canada, 509 p.

Hunt, J. H. 1991. Nourishment and the evolution of the social Vespidae, p. 426–450. *In*: Ross, K. G. & Matthews, R. W. (eds.). **The Social Biology of Wasps**, Ithaca, Cornell University Press, 678 p.

Jeanne, R. L. 1970. Chemical defense of brood by a social wasp. **Science 168**: 1465–1466.

Jeanne, R. L. 1972. Social biology of the Neotropical wasp *Mischocyttarus drewseni*. **Bulletin of the Museum of Comparative Zoology of Harvard University 144**: 63–150.

Jeanne, R. L. 1980. Evolution of social behavior in the Vespidae**. Annual Review of Entomology 25**: 371–396.

Kojima, J. 1982. Taxonomic revision of the subgenus *Icarielia* of the genus *Ropalidia* (Vespidae) in the Philippines. **Kontyû 50**: 108–124.

Kojima, J. 1984. *Ropalidia* wasps in the Philippines (Hymenoptera, Vespidae). (I) Subgenus *Icariola*. **Kontyû 52**: 522–532.

Kojima, J. 1998. Larvae of social wasps (Insecta: Hymenoptera; Vespidae). **Natural History Bulletin of the Ibaraki University 2**: 7–227.

Kojima, J. & K. Kojima. 1988. Three new species of *Polistes* Latreille (Hymenoptera: Vespidae) from Papua New Guinea, with notes on the taxonomic status of the subgenus *Stenopolistes* van der Vecht. **Journal of the Australian Entomological Society 27**: 69–80.

Litte, M. 1977. Behavioral ecology of the social wasp, *Mischocyttarus mexicanus*. **Behavioral Ecology and Sociobiology 2**: 229–246.

Litte, M. 1979. *Mischocyttarus flavitarsis* in Arizona: social and nesting biology of a polistine wasp. **Zeitschrift fur Tierpsychologie 50**: 282–312.

Litte, M. 1981. Social biology of the polistine wasp *Mischocyttarus labiatus*: survival in a Colombian rain forest. **Smithsonian Contributions of Zoology 327**: 1–27.

London, K. B. & R. L. Jeanne. 1996. Alarm in a wasp-wasp nesting association: do members signal cross-specifically?. **Insectes Sociaux 43**: 211–215.

Machado, V. L. L. & F. M. Wiendl. 1976. Aspectos do comportamento de colônias de *Mischocyttarus cassununga* von Ihering, tratadas com alimento marcado por radiofósforo. **Anais da Sociedade Entomológica do Brasil 5**: 78–85.

Melo, G. A. R. 1999. Phylogenetic Relationships and Classification of the Major Lineages of Apoidea (Hymenoptera), with emphasis on the Crabronid Wasps. **Scientific Papers (Natural History Museum of the University of Kansas) 14**: 1–55.

Nixon, K. C. 2002. WinClada ver. 1.00.08 Published by the author, Ithaca, NY. Available at http://www.cladistics.com/about_winc.htm

Nixon, K. C. & Davis, J. I. 1991. Polymorphic taxa, missing values and cladistic analysis. **Cladistics 7**: 233–241.

O'Donnell, S. 1992. Gastral rubbing observed in *Mischocyttarus immarginatus* (Hymenoptera: Vespidae) in Costa Rica. **Sphecos 23**: 5.

O'Donnell, S. 1999. The function of male dominance in the eusocial wasp *Mischocyttarus mastigophorus* (Hymenoptera: Vespidae). **Ethology 105**: 273–282.

Queller, D. C.; J. E. Strassmann & C. R. Hughes. 1992. genetic relatedness and population structure in primitively eusocial wasps in the genus *Mischocyttarus* (Hymenoptera: Vespidae). **Journal of Hymenopterological Research 1**: 81–89.

Rapôso-Filho, J. R. 1987. Atividades dos machos de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Vespidae – Polistinae). **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 40**: 17–23.

Rapôso-Filho, J. R. 1989. Comportamento de defesa e agregação das colônias de *Mischocyttarus extinctus* Zikán, 1935 (Vespidae – Polistinae). **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 42**: 37–43.

Rapôso-Filho, J. R.; C. Calloni & G. Delfino. 1994. Structural and ultrastructural features of the glands in the VI and VII gastral sternites of female *Mischocyttarus* (*Kappa*) *atramentarius* Zikán 1949 (Hymenoptera Vespidae). **Ethology Ecology & Evolution, Special issue 3**: 47–52.

Rapôso-Filho, J. R. & V. M. Rodrigues. 1984*a*. Vespídeos sociais: condição dos ovaríolos durante o ciclo de desenvolvimento das colônias de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Vespidae, Polistinae, Polybiini). **Revista Brasileira de Entomologia 28**: 295–300.

Rapôso-Filho, J. R. & V. M. Rodrigues. 1984*b*. Habitat e local de nidificação de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Polistinae – Vespidae). **Anais da Sociedade Entomológica do Brasil 13**: 19–28.

Rapôso-Filho, J. R. & V. M. Rodrigues. 1986. O órgão de van der Vecht em *Mischocyttarus extinctus* Zikán (Polistinae, Vespidae). **Naturalia, São Paulo, 11/12**: 107–116.

Rapôso-Filho, J. R. & V. M. Rodrigues. 1987. O comportamento de "mouthing"de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Vespidae – Polistinae). **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 40**: 11–16.

Rapôso-Filho, J. R. & V. M. Rodrigues. 1988. Comportamento de corte da dominante pelas não-operárias de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Polistinae – Vespidae). **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 41**: 39–46.

Raw, A. 1985. Two new species of *Mischocyttarus* (Vespidae, Hymenoptera) from Brazil. **Revista Brasileira de Entomologia 29**: 107–112.

Raw, A. 1996. *Mischocyttarus* (*Monocyttarus*) *mamirauae*, a new species of social wasp (Hymenoptera, Vespidae) from flooded Amazon forest. **Boletim do Museu Paraense Emílio Goeldi (nova série), Zoologia 12**: 3–8.

Reid, J. A. 1942. On the classification of the larvae of the Vespidae. **Transactions of the Royal Entomological Society**, **London 93**: 285–331.

Richards, O. W. 1940. Preliminary diagnoses of some new species of *Mischocyttarus* Saussure (Hymenopt., Vespidae). **Annals and Magazine of Natural History 5**: 176–183.

Richards, O. W. 1941. The classification of the genus *Mischocyttarus* Saussure (Hymenopt., Vespidae). **Proceedings of the Royal Entomological Society**, **London** (**B**) 10: 124–130.

Richards, O. W. 1945. A revision of the genus *Mischocyttarus* de Saussure (Hymen., Vespidae). **Transactions of the Royal Entomological Society**, **London 95**: 295–462.

Richards, O. W. 1971. **The biology of the social wasps (Hymenoptera, Vespidae).** Biological Review (Cambridge) 46: 483–528.

Richards, O. W. 1973. The subgenera of *Polistes* Latreille (Hymenoptera, Vespidae). **Revista Brasileira de Entomologia 17**: 85–103.

Richards, O. W. 1978. **The social wasps of the Americas excluding the Vespinae**. London, British Museum (Natural History), 580 p.

Saussure, H. F. de. 1853–1858. **Études sur la familie des Vespides. 2. Monographie des guêpes sociales, ou de la tribu des Vespiens**. Paris: Masson, and Geneva: J. Cherbuliez.

Silva, M. N. 1988. Análises morfométricas em adultos de *Mischocyttarus* (*Kappa*) *atramentarius* Zikán, 1949 (Hymenoptera – Vespidae). **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 41**: 29–38.

Silva, M. N. & Oliveira, S. M. do C. 1989. Variação no tamanho do corpo e no desenvolvimento de *Mischocyttarus atramentarius* (Hymenoptera, Vespidae), durante o ciclo de desenvolvimento das colônias. **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 42**: 25–36.

Silva, M. N. & V. M. Rodrigues. 1987. Observações sobre a proximidade de nidificação de duas vespas sociais neotropicais. **Boletim do Instituto de Ciências Biológicas e Geociências, Juiz de Fora 40**: 25–34.

Silveira, O. T. 1998. *Mischocyttarus* (*Mischocyttarus*) *aripuanaensis*. A new social wasp from western-central Brazil, and redescription of *Mischocyttarus lindigi* Richards (Hym., Vespidae, Polistinae). **Papéis Avulsos de Zoologia, S. Paulo 40**: 359–367.

Silveira, O. T. 2002. *Mischocyttarus acunai* Alayo: A Caribbean member of the subgenus Mischocyttarus s. str. de Saussure (Hymenoptera: Vespidae; Polistinae). **Natural History Bulletin of Ibaraki University 6**: 7–10.

Silveira, O. T. 2004. The male of *Mischocyttarus nomurae* Richards, with a re-examination of the limits and contents of the *M. cerberus* species group (Hymenoptera, Vespidae, Polistinae, Mischocyttarini). **Revista Brasileira de Entomologia 48**: 335–338.

Silveira, O. T. 2006. Revision of the subgenus *Kappa* de Saussure of *Mischocyttarus* de Saussure (Hym.; Vespidae, Polistinae, Mischocyttarini). **Zootaxa 1321**: 1–108.

Starr, C. K. 1988. The nesting association of the social wasps *Mischocyttarus immarginatus* and *Polybia* spp. in Costa Rica. **Biotropica 20**: 171–173.

Strassmann, J. E.; D. C. Queller & C. R. Solis. 1995. Genetic relatedness and population structure in the social wasp, *Mischocyttarus mexicanus* (Hymenoptera: Vespidae). **Insectes Sociaux 42**: 379–383.

Wenzel, J. W. 1998. A generic key to the nest of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). **American Museum Novitates 3224**: l–39.

Wenzel, J.W. 1991. Evolution of nest architecture, p. 480–519. *In*: Ross, K. G. & Matthews, R. W. (eds.). **The Social Biology of Wasps,** Ithaca, Cornell University Press, 678p.

Wenzel, J. W. & J. M. Carpenter. 1994. Comparing methods: adaptive traits and tests of adaptation, p. 79–101. *In*: Eggleton, P. & Vane-Wright, R. I. (eds.). **Phylogenetics and Ecology**, London, Academic Press, 378 p.

Wilkinson M. 1995. A comparison of two methods of character construction. **Cladistics 11**: 297–308.

Windsor, D. M. 1972. Nesting association between two neotropical Polybiine wasps (Hymenoptera, Vespidae). **Biotropica 4**: 1–3.

Zikán, J. F. 1935. Die sozialen Wespen der Gattung *Mischocyttarus* Saussure, nebst Beschreibung 27 neuen Arten (Hym., Vespidae). **Arquivos do Instituto de Biologia Vegetal, Rio de Janeiro 1**: 143–203.

Zikán, J. F. 1949. O gênero *Mischocyttarus* Saussure (Hymenoptera, Vespidae), com a descrição de 82 espécies novas. **Boletim do Parque Nacional do Itatiaia 1**: 1–125.

Received 11/09/2007; accepted 23/06/2008