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**TORYMINAE**  
**(HYMENOPTERA: CHALCIDOIDEA: TORYMIDAE)**  
**A REDEFINITION, GENERIC CLASSIFICATION,**  
**AND ANNOTATED WORLD CATALOG OF SPECIES**

By

E. E. GRISSELL

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Monographic works on insects are published in the Memoirs series. Memoir 02 is on the phylogeny of the family Torymidae (Hymenoptera: Chalcidoidea) and includes a generic classification of the Toryminae and an annotated catalog of the world species. Several new generic and species synonymies are proposed. Keys are given to subfamilies and to the tribes and genera (except Torymini) of Toryminae.

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**ABSTRACT**

Within the family Torymidae two subfamilies are recognized: Megastigminae and Toryminae. The latter is redefined to include Monodontomerinae and Thaumatoryminae. Toryminae is revised and seven tribes are recognized of which two are new: Microdontomerini and Torymoidini. The types of nearly 100 generic names were examined and 54 genera are recognized. Eleven new generic synonymies are proposed: *Ameromicrus* Nikol'skaya 1954 and *Pondorymus* Bouček 1978 = *Torymoides* Walker 1871; *Senegalella* Risbec 1951 and *Thesia* Risbec 1951 = *Pseudotorymus* Masi 1921; *Exopristoides* Bouček 1982 = *Exopristus* Ruschka 1923; *Iridophagoides* Erdős 1964 and *Tarachodiphaga* Ferrière 1955 = *Podagrionella* Girault 1913/159; *Liodontomerus* Gahan 1914 [December] = *Idiomacromerus* Crawford 1914 [September]; *Lochitomorpha* Szelenyi 1957b = *Pseuderimerus* Gahan 1919a; *Mellitotorymus* Steffan 1964 = *Adontomerus* Nikol'skaya 1955; *Pachytomoides* Girault 1913/140 = *Palmon* Dalman 1825 (revised status). The following generic *nomina nuda* have been discovered and are placed under their respective valid names (in parentheses): *Eridontomeroidella* Ramakrishna Ayyar 1919 (*Pseudotorymus* Masi 1921); *Perissocentroides* Blanchard 1938 (*Zglyptonotus* Crawford 1914). The new genus *Gummilumpus* Grissell is described with *Neopalachia bouceki* Grissell, from Dominican Republic amber, as the type species. Ten species names are synonymized, and 82 new combinations are proposed. Lectotypes are selected for 25 species. Keys are given to subfamilies of Torymidae, and tribes and genera (except Torymini) of Toryminae. An annotated world catalog is presented for 53 genera and 497 nominal species names (426 valid, 71 synonyms); additionally, the single genus *Torymus* is treated as a checklist of 483 nominal names (317 valid, 166 synonyms). A review of biology is given with reference to phylogeny, and a host/parasitoid list is provided for all species (except *Torymus*). Appendices are given that treat genera removed from Torymidae, a summary of all nomenclatural changes, matrices of characters used for phylogenetic study, a complete summary of the numbers of taxa in Toryminae, and fossil species of the subfamily. Two alphabetical indexes are given, one to hosts and one to nominal names of all taxa. Nearly 700 cited references are listed in the literature section.

**INTRODUCTION**

Parasitic and phytophagous wasps of the family Torymidae are found throughout the world. Torymidae is represented by about 875 valid species names and 250 synonyms and, as a result of this study, is divided into two subfamilies: Megastigminae



and Toryminae. The concept of the latter subfamily is considerably altered from historical use and is the object of the remainder of this work.

Biologically the family is diverse, notwithstanding that host records exist for only about one-third of its species and detailed biological studies have been undertaken for only a fraction of this number. Based on known host records, approximately 85 percent of torymids are entomophagous and 15 percent are phytophagous. Both types of behavior occur in each subfamily, but Megastigminae is primarily phytophagous with a few entomophagous species, whereas Toryminae is primarily entomophagous. The entomophagous species of Toryminae are associated with 51 families of insects in 8 orders, with hosts predominantly gall-forming Hymenoptera and Diptera. Lepidoptera and Coleoptera form a considerably smaller group of hosts, and about 10% of known torymids are egg parasitoids with the majority of these attacking mantid egg cases. Many species act as facultative hyperparasites, and a few are known which consume both plant and animal tissue. Strictly phytophagous species of Toryminae (several species of *Torymus* Dalman) are seed-feeders in Rosaceae (e.g., apple and pear) and Aceraceae (e.g., maple). Phytophagous species of Megastigminae (about 90% of the subfamily) have been reared from at least 7 plant families and most are associated with seeds of coniferous trees and rosaceous plants. The entomophagous species of the subfamily are mostly associated with hymenopterous and dipterous gall-formers.

This study began as a review of the four known nearctic species of one subfamily (then called Erimerinae) that parasitize Eurytomidae (Chalcidoidea) in grass stems. Not long into the study it became questionable whether the single putative defining character distinguishing the Erimerinae from the Monodontomerinae (with well over 300 species) was valid. The character difference, involving hind-tibial spur number, occurred in apparently unrelated members of both subfamilies. It seemed necessary, therefore, to study the Monodontomerinae in order to better assess the placement of Erimerinae.

The only previous attempt to understand Monodontomerinae at the world level was undertaken by Szelenyi (1957b), who treated only 28 genera (of the then estimated 50+ valid names known), and who admitted that most of his generic concepts were based on the literature. After my own study and analyses of taxa placed as Monodontomerinae, however, it became apparent that the group was "defined" only by its lack of synapomorphies. That is, the group was what was left over after all the "good" (i.e., readily defined) taxa were removed. In the present work I examined more than three times as many generic names (valid and invalid) as Szelenyi and recognize double his number of genera. I base almost all of my decisions on the type specimens of these names.

Once the phylogenetic study of Monodontomerinae was well underway, it became apparent that some genera of the so-called subfamily were closely related to genera assigned to the subfamilies Toryminae and Thaumatoryminae. From the inception of my study it had never been my intent to revise (or catalog) the species-rich Toryminae (of authors). Toryminae historically has always represented an "easily defined" higher taxon based on the synapomorphy of a forward projecting lobe of the metapleuron. This state is autapomorphic within the Chalcidoidea, and there has never been doubt that Toryminae was a monophyletic group (even if not couched in this term). Its position implicitly has been derived, and most recently Bouček (1988:143) stated that

Toryminae was a “more specialized group” relative to the Monodontomerinae. Thus, my original hypothesis of phylogeny, based on all foregoing literature and thought, was that Monodontomerinae shared a sister group relation with Toryminae. After many repeated phylogenetic analyses, however, I could find no justification to support this hypothesis. It became apparent that “Toryminae” simply represented a monophyletic clade of the paraphyletic “Monodontomerinae.” This discovery created a considerable increase in the size of the project as originally conceived, and although the number of genera increased by only 11, the number of species names more than doubled from 448 names to 980 (including synonyms), 483 of which were represented by the single genus *Torymus*.

My attempt to understand the higher classification of Toryminae as it existed took many years of study. It then took nearly as many years to unlearn and to begin anew with some objectivity. Since its inception this project has had ever-changing boundaries (and titles) and has become more “interesting” at each turn of the data. Anyone who contemplates the nature of evolution and the inadequacies of human nature would expect nothing less. In spite of the hydra-headed nature of this research, I have reached a point where the study is complete enough to have evaluated many of the problems inherent in the family, to have created a set of hypotheses which form a basis for future work, and to initialize the next phase for those braver than I.

The body of this work is divided into two major parts. The first (pages 9 to 175) discusses the history of the family Torymidae, demonstrates its monophyly, discusses its putative subfamilies and tribes, presents a key to subfamilies, tribes, and genera of Toryminae (excluding Torymini), and explains the phylogenetic aspects and reclassification adopted in this study. Within this part the first phylogenetic study of world genera of what once was referred to as Monodontomerinae is presented. The analysis supports the hypothesis that within the paraphyletic group Monodontomerinae arose the taxa once referred to as Toryminae (of authors), Thaumatoryminae, and Erimerinae, and that these taxa cannot, therefore, all be regarded as subfamilies. As a result of my study, I hypothesize that all these groups form a single monophyletic taxon called Toryminae.

The second major part of this work (pages 176 to 291) is an annotated catalog to world genera and species of Toryminae in agreement with the classification established in the first part. Because a catalog is meant to be practical and easily used, the arrangement of genera and species is alphabetical so that no knowledge of phylogenetic hierarchy is required.

The work at hand is unique in combining a world reclassification and catalog into a single entity. The two would appear to be a logical combination, but to accomplish the goal required some duplication of effort which I tried to reduce to a minimum. For example the generic headings in the reclassification stress the names, type-specimens examined, and synonymies in relation to the final nomenclatural and phylogenetic decisions made in that section. The catalog, on the other hand, simply lists the generic names without additional comment. Similarly, I placed summaries of biology, distribution, and available keys with the reclassification to give an overview of the genus with all its information distilled in one place for comparative purposes. These sections are not then found in the catalog, which some might assume to be the logical place. In essence the reclassification is a complete overview of the genus, whereas the catalog is a complete species by species compilation of the data. Under the generic headings of

both sections, I refer the reader by page number to the complimentary sections that can be consulted for additional information.

Two aspects involving the taxon previously referred to as Toryminae (= Torymini of this study) are not treated as fully as others. First, I provide only a species checklist and synonymy for the genus *Torymus*. Although I do provide an annotated catalog and host-parasitoid list for the 10 other genera of the tribe (and of all the remaining Toryminae), the single genus *Torymus* is so large that it needs a rigorous revision before its nomenclature is cast in the form of a catalog. With a total of 483 nominal species names (317 valid, plus 166 synonyms) of the total 532 nominal names for Torymini, this research will not be done for some time to come. Second, the remaining taxa of Torymini, numbering 10 genera with 38 valid species (plus 11 synonyms), are treated only at the level of tribe in the key and taxonomic discussions. I have not attempted any revisionary work within Torymini because in order to understand these genera one would need a thorough understanding of *Torymus*. This genus is difficult to define succinctly, and many of the genera assigned to Torymini appear to be specialized forms of *Torymus*. Because Torymini is an easily recognized monophyletic group, and a numerically large one at that, I believe its study forms a nomenclaturally and taxonomically necessary study in its own right. This will be a daunting research project that will take many years of study. I provide a beginning, at least, to the nomenclature of Torymini as we currently understand it.

#### ACKNOWLEDGMENTS AND MUSEUMS

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The excellent habitus drawings were rendered by Mary Lou Cooley (Figs. 65-67, 69-70), Erik Denno (Figs. 62-64), Natalia Florenskaya (Fig. 68), and Linda Lawrence (Fig. 71). I thank these artists for their work. Additionally, I thank Terri Taylor for taking the scanning electron micrographs and for the preparation of their plates (Figs. 382-429), and Linda Lawrence and Mike Schauff for assistance in creating several of the computer generated, graphic illustrations.

For exceptional supervision and help far beyond the call of duty with respect to the phylogenetic analyses used in this paper I thank Mary Mickevich, for without her help and patient explanation I surely would have made a lot more mistakes than I have. I also thank the following: Marcus Graham for much scholarly input into my understanding of the bedeviling nomenclature associated with several species of *Monodontomerus*; Gerard Delvare for nomenclatural information about Podagrionini; Mike Schauff and George Venable for oft-needed assistance in solving computer-generated

disasters suspiciously common in my research. I am especially thankful to John Heraty, Gary Gibson, Bob Poole, and Dave Nickle for their strength and perseverance in reviewing and commenting on this manuscript. They discovered many inconsistencies and mistakes and suggested many constructive improvements.

In checking current nomenclature for the host list, I had the help of many co-workers, and I thank them all for their assistance. The following researchers are located in the U. S. National Museum of Natural History as part of the Systematic Entomology Laboratory or the Smithsonian Department of Entomology: Lepidoptera: R. W. Hodges, D. C. Ferguson, R. W. Poole, D. R. Davis, R. K. Robbins, M. A. Solis; Diptera: R. J. Gagne, A. L. Norrbom, N. E. Woodley; Hymenoptera: D. R. Smith, R. W. Carlson, A. S. Menke, P. M. Marsh, B. Danforth, B. Norden; Orthoptera: D. A. Nickle; Hemiptera: T. J. Henry. In addition, W. E. Steiner (SI, Department of Entomology) and D. C. Wasshausen and E. R. Farr (SI, Department of Botany) helped with the nomenclature of Madagascar plants. T. Griswold (USDA, Bee Biology and Systematics Laboratory) checked the bee listing. J. Kirkbride (USDA, Systematic Botany, Mycology, and Nematology Laboratory) provided some helpful information on plant nomenclature. Even though these workers have checked the list, I must assume full responsibility for any errors that found their way into the compilation.

A great number of curators and institutions loaned material during this study and I thank them all. The following is a list of museums and the abbreviations I've used throughout the text. I have borrowed material only from the museums where curators are listed in parentheses. Some museums are listed because that is where type material is deposited (or reportedly deposited).

### Abbreviations Used for Museums

AMNH	American Museum of Natural History, New York, USA
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia (Ian Naumann)
BMNH	The Natural History Museum, London, England (Z. Bouček, J. Noyes)
BPBM	Bernice P. Bishop Museum, Honolulu, USA
CA	California Academy of Sciences, San Francisco, USA (P. Arnaud)
CNC	Canadian National Collection, Ottawa, Canada (C.M. Yoshimoto, G.A.P. Gibson)
CDA	California Department of Agriculture, Sacramento, USA (M. S. Wasbauer)
FCNM	Facultad de Ciencias Naturales y Museo, La Plata, Argentina (L. De Santis, R. Ronderos)
FM	La Specola Museum, Florence, Italy
FSCA	Florida State Collection of Arthropods, Gainesville, USA (L. Stange, J. Wiley)
HNHM	Hungarian Natural History Museum, Budapest (J. Papp)
HU	Hokkaido University, Sapporo, Japan
IARI	Indian Agricultural Research Institute, New Delhi, India (S. I. Farooqi)
IEA	Instituto di Entomologia Agraria, Portici, Italy
IPAL	Institut für Pflanzenschutzforschung der Akademie der Landwirtschaftswissenschaften, Eberswalde, Germany
IZ	Instituto di Zoologia (Entomologia), Rome, Italy (A. V. Taglianti)

IZU	Institute of Zoology, Ukrainian Academy of Science, Kiev, Commonwealth of Independent States (M. D. Zerova)
LU	Laval University, Quebec, Canada
MBR	Museo Argentina de Ciencias Naturales "Bernadino Rivadavia," Buenos Aires, Argentina (J. M. Gallardo)
MCSN	Museo Civico di Storia Naturale "G. Doria," Genoa, Italy (R. Poggi)
MHNB	Musee d'Histoire Naturelle "Grigore Antipa," Bucharest, Romania
MHNG	Museum d'Histoire Naturelle, Geneva, Switzerland (C. Besuchet)
MND	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Museum National d'Histoire Naturelle, Paris, France (J.R. Steffan, M. Lachaise)
MRCB	Musee Royal du Congo Belge, Tervuren, Belgium
MZL	Museum of Zoology, Lund, Sweden
NCSU	North Carolina State University, Raleigh, USA (R. L. Blinn)
NIAS	National Institute of Agricultural Sciences, Tokyo, Japan
NMP	National Museum, Prague, Czechoslovakia
NMV	National Museum of Victoria, Melbourne, Australia
NMW	Naturhistorisches Museum, Vienna, Austria (M. Fischer)
OUM	Oxford University Museum, Oxford, England (C. O'Toole)
PPRI	Plant Protection Research Institute, Pretoria, South Africa
QM	Queensland Museum, Brisbane, Australia (T. C. Dahms)
SAM	South Australian Museum, Adelaide, Australia (E.G. Matthews)
SJC	Saint John's College, Agra, India
SMNH	Swedish Museum Natural History, Stockholm, Sweden (K.-J. Hedqvist, T. Kronstedt)
UC	University of Ceylon, Colombo, Sri Lanka
UCB	University of California, Berkeley, USA (L. Caltagirone)
UCD	University of California, Davis, USA (R.O. Schuster)
UCK	University of Calicut, Kerala, India (T. C. Narendran)
UN	University Degli Studi di Napoli, Napoli, Italy (G. Tomasetta)
UCR	University of California, Riverside, USA (S. I. Frommer).
USNM	National Museum Natural History, Washington, D.C., USA
USU	Utah State University, Logan, USA (F.D. Parker, V. Tepedino, P. Torchio)
WSU	Washington State University, Pullman, USA (R. Zack)
ZIAN	Zoological Institute, Leningrad, Commonwealth of Independent States (E.S. Sugonyayev)
ZMB	Zoologisches Museum, Berlin, Germany
ZMC	Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark (B. Petersen)

#### METHODS

Some methods are explained as needed in the text. For example, the introduction to the catalog (p. 176) explains how it was developed and how it is to be used. General information is summarized below.

## **General**

*Taxonomic procedures:* Author names for torymid species appear only in the catalog and the terminal index. For host species, author names appear only in the host-parasitoid list for Toryminae and its index. This avoids unnecessary repetition of author names and provides a single source where the data can readily be found. Citations for A. A. Girault are given as the date plus the sequential number assigned to each of Girault's papers by Dahms (1983), who made an exhaustive study of the works of Girault. Thus, I use, for example, 1915/243 rather than 1915a, because it is more direct, repeatable, and conveniently suits a bibliographic database. In the literature cited section, the dates for Girault are listed chronologically, then sequentially by Dahms' number.

*Morphology:* Terminology used in this paper is illustrated in Figs. 1-25. All character states (and their transformation series) are described in "Characters Analyzed for Relationships" (p. 31) and illustrated in Figs. 39-47. Measurements were made with a Wild M5 and ocular micrometer. Objects were measured in the flattest, longest view possible with both ends in focus.

*Illustrations:* Illustrations were prepared using a camera lucida with a Wild M5 dissecting microscope. In most cases drawings were enlarged or reduced with a photocopier to insure that all were the same size before inking. This makes direct comparison possible, and often the contrast is much more striking than if drawn to scale. SEM and slide material was cleaned in alcohol or a proprietary cleaner (e.g., Formula 409™) by hand agitation. Whole specimens (alcohol preserved or dried) were soaked for 24 to 72 hours in KOH and examined in temporary glycerine slide mounts. For SEM genitalic mounts, the genitalic capsule was removed from alcohol preserved specimens and soaked overnight in KOH, then washed in distilled water, transferred to 70% ethanol, 95% ethanol, absolute alcohol, and critical point dried. All parts were glued to gold wire using dilute, water-soluble glue. Material was examined and photographed using a Cambridge Stereoscan 100 set at 10<sup>5</sup> (coated) or 2 kv (uncoated).

## **Phylogenetic Analyses**

Analyses were performed using PHYSYS (© 1983, Farris and Mickevich) and run by M. F. Mickevich on the University of Maryland Univac mainframe computer under the auspices of the Maryland Center for Systematic Entomology (MCSE). The character matrices were entered as taxa by character, alpha-numeric data bases (Appendix III, IV). The DWAG.S tree estimation routine, which carries out global branch swapping for a user-determined number of trees, was used to calculate the maximum number of minimum-length trees. This technique searches for local optima of the most parsimonious branching patterns. Multistate characters were coded as a "best-guess" series of states ordered as transformations for the purpose of analysis (Mickevich 1982). These were then re-ordered, if necessary, using Transformation Series Analysis (TSA, Mickevich 1982) to fit successive tree estimates until the states and the trees stabilized. As an additional test of stability, a successive approximation character weighting procedure was used to assess the congruence of weighted and unweighted character data. When TSA on Wagner trees stabilized and successive-weighting trees agreed with them in topology, we considered the analytical process complete for the given set of data. On several occasions I added or deleted taxa or

added, deleted, or changed interpretations of character states, and after each change the procedure was repeated. In total, nearly 50 runs of these data were made, and the results are discussed further in the "Phylogenetic Analyses" section (p. 27) and for each taxon. (Some subsets of these procedures are detailed in Mickevich and Grisell, in preparation.)

The treatment of phylogeny for each taxon is somewhat different than is usually the case in monographs of this nature. I divided the entire study into two sections: 1) the working hypothesis, and 2) the ending hypothesis. The working hypothesis is the first finalized result (over 45 analyses) which included all taxa of questionable generic placement, that is, synonyms of described genera or undescribed taxa that differed in a character state from the valid name. The working hypothesis treated the most number of taxa (65, counting Torymini as a single taxon) that could be recognized by putative character state differences. This was essentially a "splitters" hypothesis. Using the working hypothesis, character states, and biological and geographical information, I made node by node comparisons of taxa in an attempt to determine what states and changes defined them. This is discussed for each taxon in the "Working Hypothesis" section. Using this procedure I created a new, or ending, hypothesis that recognized a reduced number of taxa (43, counting Torymini as a single taxon) and alternate character state definitions in some cases. This might be called a "lumpers" hypothesis. This hypothesis was again subjected to phylogenetic analysis as outlined above. The results of this analysis are discussed for each taxon under the "Ending Hypothesis" section. A discussion of both hypotheses is also given for character states in "Characters Analyzed for Relationships" (p. 31).

### **Generic Treatments**

The following subheadings are used in the generic discussions and the types of information provided are summarized.

*Generic Synonymy.* - List of synonymical generic names, the type species of each name, the depository (or depositories) of type series, and whether or not the type specimen was examined. In a few cases the type species of the genus may have been described from specimens that were distributed among several museums, and these depositories are listed. The single location of the type specimen for each species is listed in the catalog under the relevant species.

*Number of Species.* - The number of species currently recognized for the respective genus.

*Distribution.* - A summary of distribution by zoogeographic region and country.

*Hosts.* - A condensed summary of the known hosts of the genus (detailed host records are given in the catalog).

*Keys.* - Keys to species are listed along with regions that they cover.

*Recognition.* - Diagnostic characters that define the genus within the context of the tribal diagnosis; usually the least number of characters needed to correctly characterize the taxon.

*Phylogeny and Synonymy.* - This discussion is broken into two sections as needed: 1) Phylogeny, being a discussion of hypothesized relationships, including the Working Hypothesis and Ending Hypothesis, as explained above, and 2) Synonymy, a discussion of proposed nomenclatural changes. In most cases the two are interdependent and are discussed together. In some cases where nomenclatural problems are

complex or there are a long series of generic synonyms, synonymy is placed in its own section after phylogeny.

*Discussion.* - Additional generalized information is presented as needed. This section is meant to explain in narrative fashion some of the problems (and their solutions, if any) associated with the genus in question.

It may be noted that no generic redescriptions are given in the classic sense. Often such descriptions amount to endless pages of descriptive words in which the only real differences between taxa are confined to a single sentence. I have attempted to circumvent this by presenting a recognition section that diagnoses each genus within the context of the tribe, the finalized character matrix (Appendix IV), and an explanation and illustration of all characters and their states (Figs. 39-47). To repeat this information in descriptive form seems more than is absolutely necessary, especially when it is only the synapomorphies that define a taxon.

## TORYMIDAE

### Family Systematics

The definition of Torymidae has been an ongoing task since Walker first proposed the name in 1833. As can be seen from the short history presented below, there has never been a time when the family was uniquely characterized even on simple morphological grounds, let alone what we would now call synapomorphies. For that reason I first discuss the family concept from an historical perspective giving the placement of included and excluded taxa based on studies up to the inception of my own. This is presented as an “overview” of the classification without explanation. I then define the monophyly of Torymidae based on my work, discuss “historical” characters which do not define the family, outline methods of recognition, and discuss placement of the particularly intractable genus *Echthrodape* Burks which has caused problems since its description.

### *Historical Perspective*

Walker (1833) described “Torymidae” to include the following taxa (current subfamily placement in parentheses): *Megastigmus* Dalman (Megastigminae), *Priomerus* Walker (now *Podagrion* Spinola, Monodontomerinae), *Torymus* Dalman, and *Callimome* Spinola (both Toryminae). Walker also included in Torymidae genera that are now placed in the Ormyridae and Perilampidae. This “family” was not defined by any particular character, but rather by a descriptor of some 17 lines and a discussion of wing venation as it existed in genera now placed in Eurytomidae, Leucospidae, and Chalcididae.

Förster (1856) followed Walker (1833), adding a few genera to the family, namely *Cryptopristus* Förster, *Diomorus* Walker, *Glyphomerus* Förster, *Syntomaspus* Förster, and *Lochites* Förster but removing Ormyridae and Perilampidae as separate families.

In 1875 Walker proposed the new family “Sycophagoidae” which included *Idarnes* Walker among other taxa, but he did not define or characterize the family.

Thomson (1876) was the first to recognize the subtribes “Megastigmides” (now = Megastigminae) and “Torymides” (now = Toryminae + “Monodontomerinae” of authors). He also included the subtribe “Ormyrides” in a group that he called “Tribus



Torymina.” He did not place the podagrionine or the sycophagine genera in his scheme. Even though they were known in his time, they did not occur in Sweden, the focus of his work. His characterization of the tribe (= present-day Torymidae) was based on the reduced hind femur (i.e., not enlarged like the Chalcidinae), large collar, the mesosoma without large punctures, the metallic body, and the presence of an occipital carina.

Howard's classification (1885, 1886) was much like Thomson's, placing the present genera of the Toryminae, Megastigminae, Monodontomerinae, and Ormyridae in a single subfamily, the Toryminae, and placing this subfamily within the Chalcididae. He did not recognize tribes or subtribes. He placed the genus *Podagrion* in the subfamily Chalcidinae and did not treat the sycophagines at all. He defined the “Toryminae” by the reduced hind femur, the mesosoma “not greatly developed,” the large “collar,” and the metallic body. In essence he simply followed Thomson (1876).

Like Howard (1885, 1886), Dalla Torre (1898) placed all present-day families of Chalcidoidea in the single family Chalcididae, placed present-day Toryminae, Monodontomerinae, and Megastigminae in the subfamily Toryminae, and placed podagrionines in Chalcidinae. Unlike Thompson and Howard, however, Dalla Torre placed ormyrids as a separate subfamily, and he placed sycophagines in Agaoninae. As this was a catalog, no definitions were given for taxa.

Ashmead (1899a) created the superfamily Chalcidoidea and upgraded the subfamilies of previous workers to family level. He described in a key the new subfamilies Monodontomerinae (for torymids with an “entire” mesepisternum) and Idarninae (he did not designate these as new taxa). He included also Toryminae, Megastigminae, Monodontomerinae, Podagrioninae, (in part), and Ormyrinae as subfamilies of Torymidae. This classification was repeated by Ashmead in his 1904a monograph, in which he defined the family basically on the “very large” hind coxae. Schmiedeknecht (1909) followed Ashmead, simply changing the subfamilies to tribes of Toryminae of the family Chalcididae. Strand (1911a), following Schmiedeknecht, added the new tribe Pulvilligerini (now Megastigminae, see Bouček 1988).

Crawford (1914) recognized the following subfamilies in the Torymidae: Ormyrinae, Megastigminae (Pulvilligerinae and Eutanycomminae, also both recognized, are now regarded as Megastigminae), Idarninae, Toryminae, Monodontomerinae, Podagrioninae, and the new subfamily Erimerinae. The family was not characterized. Hoffmeyer (1931) followed the same classification as Crawford (1914) and also did not define the family concept.

Peck (1951) elevated both Ormyrinae and Podagrioninae to family level. Nikol'skaya (1952) did not recognize subfamilies of Torymidae, but retained *Podagrion* as a torymid and recognized Ormyridae as a family. Burks (1958b) placed Podagrionidae as a subfamily in the first supplement to Peck's work (1951).

In the 1960's two new subfamilies were placed in the Torymidae: Bouček (in Peck *et al.* 1964) proposed the new subfamily Thaumatoryminae and Hill and Riek (in Hill 1967a, 1967b) described the new subfamily Epichrysomallinae. Hill and Riek did not define the family Torymidae, but Bouček (in Peck *et al.* 1964) did, based on the following features: hind coxa usually at least 3 times larger than the fore coxa, large pronotum, complete parapsidal grooves (= notauli), and short stigmal vein. Bouček recognized Ormyridae as a distinct family (sharing the characters just mentioned) and separated it from Torymidae on such characters as body shape, shorter antennae,

coarsely pitted abdomen, and short ovipositor (among other features). Until the 1960's, Sycophaginae (or Sycophagini) was often placed as an Agaonidae, whereas Idarninae (or Idarnini) was placed as a Torymidae (e.g., Ashmead 1904a, Schmiedeknecht 1909). Wiebes (1961) proposed that the two groups should be placed together and Joseph (1964) formally did so, placing them as tribes in the subfamily Idarninae. Wiebes (1966) pointed out that Sycophagoidae (Walker 1875) was an earlier name than Idarninae (Ashmead 1899a) and that the group should be called Sycophaginae.

Riek (1970) placed the Podagrioninae, Toryminae, Sycophaginae, Megastigminae, and Monodontomerinae in the Torymidae and reduced Ormyridae to a subfamily of Pteromalidae. He characterized torymids by the emarginate first gastral tergum, 2 hind-tibial spurs (except in Podagrioninae), and the hind tibia not grooved above at apex for the reception of the basitarsus (except in Podagrioninae). Riek (1970) was the first to recognize and state that Monodontomerinae was "characterized mainly by the absence of diagnostic features."

Bouček (1976a) subdivided Podagrioninae into two tribes (Podagrionini and Palachiini, the latter new). In 1978 Bouček recognized the Sycophaginae, Toryminae, Thaumatoryminae, and Monodontomerinae as Torymidae. He reduced the subfamily Podagrioninae to the two tribes proposed in 1976a and placed them both in the Monodontomerinae, at the same time recognizing the tribes Monodontomerini and Chrysochalcissini. He also suggested (1978:125) that the "non-femorate" genera of Monodontomerinae might conceivably be united as a tribe. Nikol'skaya and Zerova (1978) essentially followed Bouček (1978).

Burks (1979) (based on unpublished hypotheses of chalcidoid evolution) believed that Agaonidae should be placed with Torymidae and did so in the newly issued catalog of Nearctic Hymenoptera. Following Riek (1970), Burks (1979) placed Ormyrinae with the Pteromalidae. In 1981 Bouček *et al.* removed Epichrysomallinae from the Torymidae and placed it in the Pteromalidae. They also suggested that Ormyridae might better be placed as a subfamily of Torymidae and listed it as such in a chart of classification.

In his monumental work on Australasian chalcidoids, Bouček (1988) made several important changes. He placed Epichrysomallinae and Sycophaginae in the Agaonidae, elevated Ormyrinae to family level, and recognized only Megastigminae, Monodontomerinae, Thaumatoryminae, and Toryminae as Torymidae. The family was defined by the presence of an occipital carina, the margins of the hypostoma medially constricted or fused below the occipital foramen, the elongate cerci placed on the membrane between gastral terga 7 (metasomal tergum 8 of this paper) and 8 (metasomal tergum 9 of this paper), and the flap-like 8th gastral tergum.

Mani (1989), with little comment, returned to the classification proposed by Ashmead (1904a), which included Idarninae and Ormyrinae as subfamilies of Torymidae. Although the work includes diagnoses and keys to taxa, families and genera are poorly defined, and the work appears to represent simply an oversight of 90 years' worth of literature.

Most recently, Gibson (1993) adopted Bouček's 1988 classification in his overview of world Chalcidoidea, as did Narendran (1994) in his monograph on Indian Torymidae.

### ***World and Regional Literature***

The literature contains many references to Torymidae, but comprehensive treatments at the family level are limited and generally regional in nature. Below I list some of the most important (and sometimes useful) literature for the family. References that profile species or genera of limited areas are cited under generic systematics or in the species catalog. Theoretically, coverage provided in the present work now renders most of these works obsolete.

Catalogs or check-lists: The most recent world catalogs are those of Dalla Torre (1898) and Schmiedeknecht (1909). The New World is relatively well cataloged because of the Nearctic works of Peck (1963) and Grissell (1979) and the Neotropical works of De Santis (1967, 1979, 1980, 1983, 1989) and De Santis and Fidalgo (1994). Regional, more or less comprehensive, listings for the Old World include (in alphabetical order by area): Australia: Bouček 1988; Central Europe: Wall 1984; India: Farooqi 1986 (which replaces Mani 1938), Narendran 1994 (which updates Farooqi); Philippines: Baltazar 1966. Some smaller, limited treatments include: Finland: Hellen 1934 (annotated list); Great Britain: Bouček and Graham 1978b; Korea: Paik 1978; Madagascar: Risbec 1956; Sri Lanka: Ramakrishna Aiyar 1925.

Keys that offer some degree of overview of the genera and/or species of Torymidae include: WORLD — Ashmead 1904a (genera); Schmiedeknecht 1909 (genera). AFROTROPICAL — Bouček 1978 (species). AUSTRALIAN — Bouček 1988 (genera); New Zealand: Noyes and Valentine 1989 (genera). NEOTROPICAL — Cuba: Alayo and Hernandez 1978 (genera). NEARCTIC — Crawford 1914 (genera). ORIENTAL — India: Farooqi 1985 (genera); Mani 1989 (species); Narendran 1994 (species). PALEARCTIC — Commonwealth of Independent States: Nikol'skaya 1952 (species); Nikol'skaya and Zerova 1978 (species); Europe — Mayr 1874 (genera, some species), Wall 1984 (genera); Czechoslovakia: Peck *et al.* 1964 (genera); Denmark: Hoffmeyer 1930d, 1931 (species); Hungary: Erdős 1960 (species).

### ***Monophyly of Family***

As may be deduced from the *Historical Perspective* above, the question of monophyly in the Torymidae has been long-standing, even if not couched entirely in the words of modern systematics. The elements that have been unstable for over a century generally revolve around the following taxa or groups of taxa: the fig wasps, including directly Sycophaginae (sometimes called Idarminae) and indirectly the Agaonidae (*sensu* Bouček 1988); Podagrioninae (placed variously as its own family, a subfamily of Torymidae, or a tribe of Monodontomerinae); and Ormyridae (placed as a subfamily of Torymidae, a subfamily of Pteromalidae, or its own family). Each of these taxa (except Agaonidae, *sensu* Bouček 1988) is generally considered to be a phylogenetic unit (= monophyletic), but they move about in hierarchical schemes because we know so little about the phylogeny of Chalcidoidea.

Alternatively, the presumed monophyletic units that have consistently been included in the family Torymidae for over a century are the Megastigminae, the Toryminae, and the Monodontomerinae. These 3 taxa and the podagrionines are the ones I have studied in greater detail.

In the discussion of monophyly which follows I detail 5 putative synapomorphies that have been used to define Torymidae, give my assessment of their credibility, and redefine or refine definitions to be more technically correct. Additionally, I point out

other chalcidoid taxa that share the particular structure and discuss them in relation to Torymidae. Of particular significance are the genera *Echthrodape* and *Chromeurytoma* Cameron, which are discussed with each character and then again separately at the end of the character discussion. Members of the genus *Echthrodape* have been placed in Perilampidae (Burks 1969b), Eucharitidae (Bouček 1988), and Torymidae (Darling 1988b, Gibson 1993; Heraty 1994 and Bouček 1994, both pers. comm.). *Chromeurytoma* is currently placed in Pteromalidae (Bouček 1988). I also discuss the family Ormyridae, which has been placed as a subfamily of Torymidae.

The 5 putative synapomorphies are: 1) construction of metasomal tergum 8 (Mt8) and position of cercus; 2) presence of flap-like Mt9; 3) elongation of cercus; 4) presence of occipital carina; and 5) construction of hypostomal carinae. In all candor I must admit that defining the monophyly of Torymidae based exclusively on a single synapomorphy, or even a group of synapomorphies, is not entirely certain for two reasons. The first is that I have not surveyed all non-torymids (i.e., other Chalcidoidea) for the presence or absence of the same features. However, my overall experience with Chalcidoidea is fairly extensive, and I have examined much non-torymid material in an effort to assess all taxa that approach Torymidae in structure as suggested in the literature. Second, although Torymidae appears to be monophyletic, all characters found within the family may be found singly or in some form (possibly parallel or convergent) in other chalcidoids.

For purposes of discussion in the ensuing section, the easiest way to count metasomal terga (Mt) is to look for the posterior paired spiracles, which are always on metasomal tergum 7 (Mt7) (Fig. 19). Mt8 is defined by setose cerci, either exerted or not. In most Chalcidoidea, Mt9 is fused with Mt8 (Figs. 23, 25, 33, 36), but in Torymidae Mt9 is a distinct, "flap-like," setose sclerite separated from Mt8 (Figs. 22, 24, 26-30). It is sometimes called the "epipygium," but according to Bouček (1988:16) this term should be reserved for cases where Mt8 and Mt9 are fused (= syntergum). Although previous workers have detailed abdominal morphology in Torymidae (e.g., Breland 1938b, Bucher 1948, Copland and King 1972) and Agaonidae (*sensu* Bouček 1988; e.g., Grandi 1929, 1930, Copland *et al.* 1973, Gordh 1975), the complexities associated with Mt8 and Mt9 do not seem either to have been observed or commented on by them. In the few cases where details of Mt8 and Mt9 were recognized by Domenichini (1953, Torymidae, Agaonidae) and Wiebes (1966, "sycophagine Torymidae" as then defined, now = Agaonidae, *sensu* Bouček 1988), no particular significance was attributed to their structure.

1. *Construction of Mt8 and position of cercus* (Figs. 22-36, 418-421): In female torymids, Mt8 is dorsally a transverse, parallel-sided band (at least across its apical portion) that may be subdivided posteriorly (Figs. 22, 24, 26-30, 420-421). The cercus is inserted into a translucent area on the posterolateral margin of Mt8. It is sometimes mistakenly stated that the cercus is inserted in the membrane between Mt8 and Mt9, but this is incorrect. The area at the base of the cercus is translucent and extends to the inner edge of the tergum, which gradually changes to membrane. Because of this the cercus appears to arise from membranous tissue that surrounds Mt8 and Mt9 and forms the anal tube. [Note that in scanning electron microphotographs, Figs. 420-421, the membranous area appears solid due to its coating.] In almost all torymids the cercus sits on a flattened, inwardly deflected surface of the tergum that is delimited along its outer margin by a distinct, semicircular carina (Figs. 26-29). In

some taxa of the presumptively advanced Podagrionini this carina is reduced or absent. In some torymids (especially Torymini) Mt8 is split transversely along the dorsum of this carina and is thus divided into anterior and posterior halves (Figs. 24, 26, 28, 420). Additionally, the posterior half can be split longitudinally in the middle (Figs. 24, 27B, 28B). In some taxa (e.g., *Megastigmus*) the entire dorsum of Mt8 may appear longitudinally split but this is due to the tergum being translucent (less sclerotized) medially, not to an actual physical separation. Apparently identical construction of Mt8 is found only in the Afro-Australian genus *Echthrodape* and the Australian genus *Chromeurytoma*, which are discussed in detail at the end of the character section (below).

In Agaonidae (*sensu* Bouček 1988) a similar but apparently modified construction is found only in the subfamily Sycophaginae. In this group Mt8 (Fig. 34) appears to be divided into two parts separated by a large triangular membranous area: 1) an anterior part with its hind margin deeply invaginated dorsomedially (Fig. 34B) (even appearing to be formed of two separate, lateral arms folding over and meeting at the center as in Fig. 9 of Wiebes 1966), and 2) a posterior part with cerci. In this case, the cercus actually appears to be inserted on a narrow membranous region between Mt9 and the lateral surface of the posterior part of Mt8 (based on slide mounted material). The structure of Mt8 in sycophagine wasps appears unique based on the complete transverse division of Mt8 (only partial in Torymidae), the movement of the posterior half of Mt8 (with cerci) some distance from the anterior half, and the anterior half with its hind margin deeply dorsomedially invaginated.

In non-sycophagine agaonids, Mt8 is a simple transverse band with no secondary transverse folds or splits. The cerci appear to arise either from the surface of the tergum (e.g., *Philotrypesis* Förster, Fig. 36) as in Pteromalidae, or are inserted on transparent areas at the posterolateral corners of Mt8 (e.g., *Blastophaga* Gravenhorst, Fig. 35) as in Torymidae.

In Ormyridae Mt8 (Fig. 418) is a simple transverse band with no secondary transverse folds or splits and is fused with Mt9 so that only a single tergum is apparent (some apparent lines of fusion may be seen with difficulty). The cercus arises from the surface of its tergum and there is no transparent base. In this respect, Ormyridae is pteromalid-like (Figs. 33, 419) and resembles the majority of Chalcidoidea.

2. *Articulated Mt9* (Figs. 22-36, 418-421): In female Torymidae, Mt9 is a freely articulated, flap-like appendage attached only at its base to the posterior margin of Mt8 (Figs. 22, 24, 26, 30). In male torymids, Mt9 either is not delimited or it is demarked by slight creases or lines along its lateral borders, similar to most non-torymid chalcidoids.

There is some question regarding the actual derivation of Mt9, i.e., whether it is a true 9th tergum that is fused with Mt8 in most non-torymid Chalcidoidea (Domenichini 1953, Ulenberg 1983, 1985) or a secondary division of Mt8 with the loss of Mt9 entirely (Gibson, pers. comm.). Because of this possible dichotomy, the question arises as to whether torymids retain a separate Mt9 as a symplesiomorphy in common with primitive Hymenoptera (e.g., Symphyta), whether this might be the groundplan condition in Chalcidoidea (and, thus, of no significance in establishing phylogeny), or whether a separate Mt9 is a secondarily derived synapomorphy for the family?

To address the question of Mt9, it can be stated that in chalcidoids that have Mt8 +

Mt9 fused (Fig. 33A) but still retain a slight suture or line of fusion between the two (e.g., cleonymine pteromalids), the cercus arises at the posterior margin of Mt8 (Domenichini 1953, Gibson 1986) so that the segment posterior to this suture is interpreted as a true Mt9. In torymids (Figs. 26-30) there is a distinct sclerotized "flap" immediately posterior to Mt8, and this flap appears in the position that is homologous with a true Mt9. Without contradictory information, it is most parsimonious to presume that this flap is Mt9.

Gibson (1989) stated that females of "Symphyta and various apocritans have Mt9 separate from Mt8," and he considered this the plesiomorphic state for "Hymenoptera and Apocrita." He stated that the "groundplan state for Chalcidoidea is unknown." In examining cleonymine pteromalids and all eupelmid genera, Gibson hypothesized that the fusion of Mt8 and Mt9 as a syntergum (with at most an indication of a suture between the two) should be the *plesiomorphic* state. Separate Mt8 and Mt9, found in only two non-related genera of Eupelmidae (*Eusandalum* Ratzeburg and *Metapelma* Westwood), indicated the *apomorphic* state. In Gibson's (1989) opinion, separate Mt8 and Mt9 were independently derived, secondary reversals in these two genera of Eupelmidae.

In almost all non-torymid Chalcidoidea, fused Mt8 + Mt9 appear to be present (Domenichini 1953). Certainly in Pteromalidae this is the case, and pteromalids are often considered to be the sister group to Torymidae. In Mymaridae, considered by some (but not all, see Gibson 1986, 1993) to be the sister group to Chalcidoidea, Domenichini (1953) showed that Mt8 + Mt9 are fused. It seems likely that the state of fused Mt8 + Mt9 is apomorphic with respect to Symphyta but plesiomorphic with respect to non-torymid Chalcidoidea. If this is true, then fused Mt8 + Mt9 would be the groundplan for Chalcidoidea, and all taxa of Torymidae are united by the synapomorphy of independent Mt8 and Mt9, which arose as a secondary reversal from the fused state found in putatively primitive Chalcidoidea. This is the hypothesis that I presently use, if for no other reason than it is not generally contradicted by the information we now have about Chalcidoidea.

Although an articulated Mt9 is found in all Torymidae, similar states are rarely found in other families of Chalcidoidea. The few known taxa include *Chromeurytoma* (Fig. 31), *Ditropinotella* Girault (Fig. 32), Ceinae (all Pteromalidae), and Sycophaginae (Fig. 34; Agaonidae *sensu* Bouček 1988). *Chromeurytoma* (Fig. 31) has a large, well-developed Mt9 that articulates with Mt8 (in this character it differs little in construction from members of the Podagrionini: Figs. 29, 421; *Echthrodape* also would be included here: Fig. 30); however, in *Asaphoideus* Girault, the only other genus of Chromeurytominae, Mt9 is as found in the genus *Cea* Walker where it is clearly demarcated but is fused basally and laterally for its entire margin with Mt8. *Cea* is a rare group, and I have examined only a few specimens. In *Ditropinotella* there is an exceptionally long apparent "Mt9," but as best I can determine this is merely a posterior extension of Mt8 (Fig. 32) and not separated at all from it. In these taxa, the structure of Mt9 does not appear to be homologous to that found in Torymidae and no relationships can be implied.

Within Agaonidae (*sensu* Bouček 1988) an articulated Mt9 (Fig. 34) is found only in Sycophaginae (e.g., *Apocryptophagus* Ashmead, *Sycophaga* Westwood, *Idarnes*, *Eukoebelae* Ashmead) and in no other subfamilies. Placement of Mt9 far posterad of the anterior half of Mt8, however, is unlike Torymidae (Figs. 26-30) and suggests

either an independent derivation of the character or perhaps a derived state with respect to Torymidae.

In Ormyridae (Fig. 418) there is no apparent Mt9 because it is fused with Mt8 as found in most Chalcidoidea.

Gibson (1989) pointed out that in *Metapelma* and *Eusandalum* (both Eupelmidae) Mt9 is separated from Mt8, but the characters were considered independent, secondary reversals within differing clades of Eupelmidae. This information is reported simply for the sake of completeness. Torymidae would seem to have no relationship with Eupelmidae in any phylogenetic analysis.

3. *Exserted Cerci on Mt8* (Figs. 22-36, 418-421): Exserted cerci are always cited as a distinguishing characteristic of Torymidae. All female torymids have obviously elongated cerci (Figs. 22, 24, 26-29), but this is not true of males in which cerci may be only slightly elongate. Elongate cerci may be found in *Echthrodape* (Fig. 30) and rarely in some members of the family Pteromalidae (e.g., *Cea*, *Chromeurytoma*: Fig. 31), Eulophidae (e.g., *Entia* Hedqvist), and Eupelmidae (*Archaeopelma* Gibson, Gibson, pers. comm.) but I do not consider some of these taxa to be a serious contradiction to the monophyly of Torymidae. More difficult to assess, however, is the occurrence of the cerci in at least some agaonids (*sensu* Bouček 1988).

To dispense with the pteromalid/eulophid/eupelmid groups first, it must be stated that the occurrence of exserted cerci in these groups is rare. In the cases of *Entia* and *Archaeopelma*, which have no known relationship to Torymidae, the elongation of the cerci certainly must be the result of convergent evolution. The same may be said for its occurrence in *Cea*, but in this case the relationship of Torymidae to Pteromalidae is not as distant as that with Eulophidae. In *Chromeurytoma* (Fig. 31, currently placed in Pteromalidae, Bouček 1988), however, where there is some indication of possible relationship based on the structure of Mt8 and Mt9, there is no reason to rule out a close relationship with Torymidae. Unfortunately we know very little about morphology or phylogeny in these groups. Both *Cea* and *Chromeurytoma* have Mt8 and Mt9 modified and different from other pteromalids, but, as explained above, this structure in *Cea* is also different from torymids while that of *Chromeurytoma* is the same. The latter genus is discussed in more detail at the end of this section.

Within Agaonidae (*sensu* Bouček 1988) exserted cerci may be found in some (but not all) Epichrysomallinae (e.g., *Odontofroggattia* Ishii), Sycoryctinae (e.g., *Apocrypta* Coquerel), Sycoecinae (*Diaziella* Grandi), Agaoninae (e.g., *Blastophaga*, Fig. 35), and Sycophaginae (all genera, Fig. 34). The sporadic occurrence of elongated cerci within genera of Agaonidae as well as within totally unrelated lineages such as *Entia* (Eulophidae) and *Cea* (Pteromalidae) suggest that the cercus is prone to independent development and that emphasis should be placed on other characters for establishing monophyly.

In Ormyridae the cerci are bump-like and non-exserted.

4) *Presence of occipital carina* (Figs. 3, 405-406, 408, 410): Bouček (1988) suggested that the presence of an occipital carina was the groundplan state for Torymidae (both females and males), and I agree, based on research presented later in this work (see p. 32). By way of summary, however, I would say that the character is homoplasious, having been lost in some Torymidae while appearing sporadically in Pteromalidae (*Chromeurytoma*, *Ditropinotella*, some species of Asaphinae, some Diparinae, some Pteromalinae), some Agaonidae (Epichrysomallinae), all Ormyridae, and

*Echthrodape*. Although an occipital carina defines the groundplan for Torymidae, it cannot be relied on to define unambiguously the monophyly of the family. It is possible in time that the presence or absence of an occipital carina may help establish the sister relationship of Torymidae to one of the few branches of the Pteromalidae or Agaonidae that has the carina. I discuss this further below.

5) *Construction of hypostomal carinae* (Figs. 3, 406, 408, 410): Bouček (1988) suggested that Torymidae + Agaonidae could be defined based on the presence of medially constricted or fused hypostomal carinae which meet some distance below the occipital foramen and the postgenae which are expanded to the median line, thus forming a "bridge" above the hypostomal carinae. Although this appears to be a valid groundplan feature for the two groups, the condition may be found in *Ditropinotella* and *Chromeurytoma* (putative Pteromalidae) and Ormyridae, thus again questioning its use for establishing monophyly. It is also found in *Echthrodape* as discussed below.

*Characters of potential use in establishing monophyly*: Towards the end of my study, a colleague, Steve Heydon, pointed out to me that the stipes of torymids are swollen or enlarged dorsally (Figs. 399, 401-405) whereas in pteromalids they tend to be more parallel-sided (Figs. 398, 400) (females only examined of each). This holds true for taxa examined in both subfamilies and all tribes of Torymidae, but I have not yet examined many pteromalids. This might be a worthwhile avenue for future exploration.

*Characters that do not provide evidence of monophyly*:

Having discussed characters that offer some evidence of monophyly in the Torymidae, I next discuss the characters used in previous "classifications" that do not provide evidence for monophyly. The enlarged hind coxae, for example, are not a synapomorphy that defines Torymidae. Not only are normal-sized hind coxae found in the Megastigminae and many of the primitive species of Toryminae (e.g., *Liodontomerus* Gahan = *Idiomacromerus* Crawford, *Microdontomerus* Crawford), but enlarged coxae are found at least in Chalcididae, Ormyridae, Leucospidae, and some Pteromalidae. Wing venation, although characteristic for many torymids, is quite variable and cannot define the family because relatively similar venation is found in many pteromalids and ormyrids. A lengthened ovipositor, long held to be an indication of relationship in the Torymidae, is found in some species of almost all families of Chalcidoidea, and so cannot be used to establish monophyly.

*Summary of monophyly and recognition*: Torymidae can be defined as monophyletic based solely on the structure of metasomal tergum 8 of females, the tergum being dorsally transverse (parallel sided), broadly posteriorly emarginate, and with the cercus inserted on a translucent, inwardly deflexed posterolateral subdivision of the tergum (most often delimited by an outer carina except for some Podagrionini). This synapomorphy separates Torymidae from all putatively closely related taxa, including Agaonidae (*sensu* Bouček 1988), but the structure appears to have arisen independently in the genus *Chromeurytoma* (which is questionably placed as a Pteromalidae, as discussed below). Additional synapomorphies that define the clade, but are not exclusively torymid, are a flap-like, articulated metasomal tergum 9 in females, and in both sexes, exerted cerci (though these may be reduced in some males) and the presence of an occipital carina and a hypostomal bridge created by the fusion of the hypostomal carina some distance ventrad of the occipital foramen. (See discussion of subfamilies,



below.)

Having defined Torymidae does not assure its easy recognition. For one thing, characters that elucidate the phylogeny of a taxon are not necessarily those that are readily visible. The terminal parts of the metasoma are tiny and may be contorted, withdrawn, or covered with exudates. Characters associated with the back of the head are not convenient for recognizing and sorting large numbers of taxa. Then, too, male Torymidae do not have all the requisite character states. Most torymids (both sexes) may be recognized by the following set of features: occipital carina usually present (as seen from dorsum of head); stigmal vein shortened, marginal vein at least twice as long as, and usually 4 to 10 times longer than, stigmal vein; hind coxa 1.5 to 3 times longer than forecoxa. In addition, in females the ovipositor is almost always exerted. In relatively few genera (e.g., *Microdontomerus*) there is no occipital carina and in others (e.g., *Ditropinotus* Crawford, *Idiomacromerus*) the carina is indistinct or weak enough to be overlooked except under certain angles of light. Also in these genera, the hind coxa tends to be nearly subequal in length to the forecoxa. In these genera the relatively short stigmal vein (0.2 to 0.3 times marginal, in both sexes) and the long ovipositor sheaths in females, distinguish individuals from Pteromalidae which they superficially might resemble. In Megastigminae, there is a well developed occipital carina and the hind coxa is scarcely longer than the forecoxa, but the stigmal vein is short and the stigma is posteriorly lengthened.

*Position of problem genera:*

***Echthrodape*:** This peculiar genus was described by Burks (1969b) based on the single species *E. africana* Burks reared from the bee genus *Braunsapis* Michener (Hymenoptera: Anthophoridae) from Kenya. (Burks mistakenly listed the genus *Allodapula* Cockerell as host, but the name *Braunsapis* appears on the specimen labels; see also Michener 1969.) He placed *Echthrodape* in Perilampidae with the caveat that "it might ... have been assigned to the Torymidae, Pteromalidae, or Perilampidae." Darling (1988b), who works primarily with Perilampidae, regarded *Echthrodape* "as most closely related to the Torymidae (Monodontomerinae)" based on the structure of the labrum, host associations, and enlarged hind coxae. Bouček (1988) assigned *Echthrodape* to Eucharitidae as the subfamily Echthrodapinae and added one species, *E. papuana* Bouček. Heraty (1994, pers. comm. and unpub. data), who has worked with the world eucharitid fauna and has examined the 2 described species of *Echthrodape* as well as 3 undescribed ones, maintains that *Echthrodape* does not belong in the family Eucharitidae. Recently Bouček (1994, in *litt.*) came to the same conclusion.

The inclusion of *Echthrodape* in Eucharitidae is suspect for 3 reasons: 1) it is an ectoparasite of solitary bees, a habit commonly found in the Torymidae but never in the Eucharitidae, which are all highly specialized ant parasites; Philomidinae, another taxonomically troublesome group that is parasitic on bees, is placed in Eucharitidae by Bouček (1988), excluded from Eucharitidae by Heraty (1994, pers. comm.), and suggested as the sister group to Perilampidae + Eucharitidae by Darling (1992); 2) it has a toothed hind femur which is commonly found in Torymidae but not in Eucharitidae; and 3) it has Mt8 and Mt9 structured as in Torymidae but not as in Eucharitidae.

In my earlier listing of characters that define monophyly in Torymidae, I included the structures as determined for *Echthrodape africana*, the type of the genus. (According to Heraty (1994, pers. comm.) the other described and undescribed species placed

in this genus are like the type.) In each case *Echthrodape* fits the definition given for the character, i.e., the structure of Mt8 and Mt9, the presence of an occipital carina, and the structure of the hypostomal carinae and bridge. The host association with bees lends additional credence to placement of *Echthrodape* with torymids, of which several clades share the biological habit. Because I can find no reason to exclude *Echthrodape* from Torymidae, and every reason to include it, I do so. This decision was made late in my work and after much discussion with John Heraty. For this reason it was not included in the phylogenetic analyses for the family. I include a further discussion of the genus under *Incertae Sedis* (p. 165).

***Chromeurytoma*:** There are at least 14 species included in this endemic Australian genus, and all are believed to be associated with galls on *Eucalyptus* and *Acacia* (Bouček 1988). Originally placed in Eurytomidae by Cameron (1912), Bouček recently (1988) stated that *Chromeurytoma* and the genus *Asaphoideus* (1 species) might be placed as either Torymidae or Pteromalidae, but he chose the latter. In my outline of torymid synapomorphies given above, *Chromeurytoma* (as exemplified by *viridis* Girault) fits the definition given for each character, i.e., the structure of Mt8 and Mt9, the presence of an occipital carina, and the structure of the hypostomal carinae and bridge. Based on this assessment alone, the genus would appropriately be placed as a torymid. I hesitate to do so, however, based on the following reasons. All Torymidae (including *Echthrodape*) have 8 flagellomeres between the pedicel and club, but *Chromeurytoma* has only 6. Antennae are variable throughout the Chalcidoidea, and even within Torymidae a number of segments may be reduced, but the total number remains consistent. This provides some pause for thought concerning the recognition of *Chromeurytoma* (and Chromeurytominae) as a torymid. Secondly, the only other known genus of Chromeurytominae, *Asaphoideus*, has the cerci of Mt8 arising from the sclerotized surface and Mt9, although apparent, fused basally and laterally for its entire margin with Mt8. This construction is unlike any found in Torymidae. If *Asaphoideus* is derived with respect to *Chromeurytoma*, then the abdominal states are reversals to a plesiomorphic condition, but if *Chromeurytoma* is derived with respect to *Asaphoideus*, then the abdominal states are homoplasious, either convergent or parallel developments with respect to Torymidae. The relative uncertainty associated with *Chromeurytoma* (and Chromeurytominae) leads me to believe that it is best not recognized as a torymid without further study.

### Subfamily Systematics

In this section I present a synopsis of the subfamily classification used in Torymidae up to Bouček (1988). In some cases I cannot add any information to the classification and accept it as stated along with the author(s) of the most recent assessment. In some cases I state the changes that I propose to make to the existing classification. This is simply a summary, *not an explanation*, of the changes that I am making as a result of my study. In essence it is a table of contents to help trace the movement of subfamily names. Some of these names are discussed here and no further if they have been removed from the family. In others the concept of the subfamily has changed since the inception of my study or because of it, and the reader is referred to the section (as indicated), which explains the reasons for my actions. These subfamilies are listed alphabetically.

### ***Recent and Present Classifications***

**Epichrysofallinae** (removed to Agaonidae, see Bouček (1988)):

Hill and Riek (in Hill 1967a, 1967b) described this subfamily, placed 11 genera in it, and included it in Torymidae. Bouček *et al.* (1981) placed it in Pteromalidae and later Bouček (1988) placed it in Agaonidae. I can add little to its present placement, but I discuss the subfamily further under the section on Sycophaginae (see below).

**Erimerinae** (now Microdontomerini, p. 72):

This subfamily was described by Crawford (1914) based on the hind tibia having only a single spur (as opposed to 2 for other members of the family). It was last recognized as a subfamily by Grissell (1979). Bouček (1988) referred to it as a tribe "... hardly separable from Monodontomerini." Since its description, other torymids have been recognized that have only one spur (e.g., Podagrionini), and some genera such as *Liodontomerus* (now = *Idiomacromerus*) have a second spur so short as to be easily overlooked. Spur number alone does not appear to be a basis for distinguishing subfamily limits (see also "Characters Analyzed for Relationships," p.31). In spite of the spur, the genera previously placed in Erimerinae appear to represent a monophyletic group based on the reduction of the eyes in males. Erimerinae is no longer recognized as a subfamily but is included as a clade in the tribe Microdontomerini.

**Megastigminae** (see p. 25):

There has never been much doubt about the monophyly of this subfamily and Bouček (1988:122) stated that "... the group has been regarded as a subfamily by all authors recognizing Torymidae as a family." I agree with this assessment.

**Monodontomerinae** (of authors) (see "Monophyly of Subfamilies, Toryminae," p. 26, and Monodontomerini, p. 117):

Ashmead (1899a:247) characterized this subfamily based on "the posterior margin of mesepisternum entire," and the "posterior femora beneath serrate or armed with 1 or 2 teeth." Later, additional taxa were placed in the group in which the hind femur was simple. Eventually the only defining character for the subfamily became the structure of the mesepisternum, but as this is the primitive condition found in all Chalcidoidea, its use to delimit a taxonomic group is unfounded. As a result of my study, I conclude that the subfamily Monodontomerinae (of authors) is a paraphyletic assemblage of taxa. It is discussed in more detail as cited above.

**Ormyrinae** (now placed in its own family):

In the overview of the history of torymids outlined above, it may be noted that about half the authors quoted (Walker 1833, Thompson 1876, Howard 1885, 1886, Ashmead 1904a, Crawford 1914, Bouček *et al.* 1981) placed the ormyrids within Torymidae and the other half (Förster 1856, Dalla Torre 1898, Peck 1951, Riek 1970, Peck *et al.* 1964, Burks 1979, Bouček 1988, Gibson 1993) placed them outside the family. Ormyrids share with torymids the construction of the back of the head, including an occipital carina and postgenal bridge with the hypostomal carinae meeting below the postgenal bridge. They also share similar wing venation and enlarged hind coxa, but these characters are homoplasious. Ormyrids, however, do not have the synapomorphy that defines Torymidae: Mt8 and Mt9 are totally fused, and the cercus

is not elongated but arises as a swelling on the surface of Mt8. These are pteromalid-like in construction. As the frequent inclusion of ormyrids with Torymidae suggests, the two outwardly appear to be related, and the most recent treatments of Ormyridae echo this opinion (e.g., Zerova 1978, Bouček 1988). DiGiulio (reported in Hanson 1992) suggested that *Ormyrus* Westwood shared genitalic characters with Megastigminae, but Hanson (1992) also reported that the genus shared its stout, curved hind-tibial spurs (possible synapomorphy) with “pteromalid-like specimens” presumably of unknown placement. Although Ormyridae is unquestionably monophyletic, its phylogenetic placement remains a puzzle. For now it is best recognized as a monophyletic group of uncertain relationship, and is discussed further under Sycophaginae.

**Sycophaginae** (and, indirectly, Agaonidae *sensu* Bouček 1988):

At the inception of my study this subfamily was considered a monophyletic clade of Torymidae (Hill 1967a, 1967b). It was an enigmatic group of fig-associated wasps consisting of 6 tribes and 34 genera (10 of which were unplaced as to tribe). This group was not part of my original study for two reasons: 1) although purportedly monophyletic, its synapomorphies had never been defined. Hill's classification was completely unsupported by evidence and no definitions of taxa were given (except for the new subfamily Epichrysomallinae and the new tribe Sycoecini); 2) whether or not monophyletic, the “subfamily” appeared to be a highly derived group of taxa, irrelevant to my study of the presumably more basal forms of “Monodontomerinae.” Of course this was a subjective assessment. I reasoned that if I could resolve the more basal groups, I would be able to later include the apomorphic groups without difficulty. My study of these basal groups has proven extremely difficult in itself and has become such a large project that I have not been able to study the Sycophaginae in a systematic manner.

Since Hill's classification, 4 of the 6 tribes themselves have been elevated to subfamilies, the remaining 2 placed as tribes within these subfamilies, and *all* have been transferred to the family Agaonidae (Bouček 1988). Thus, theoretically, Sycophaginae should be of no further concern to my study. But this classification raises the much larger question of the monophyly of both Torymidae and Agaonidae (*sensu* Bouček 1988). According to Bouček the limits of these two families “can now be settled by the presence [Torymidae] or absence [Agaonidae] of the horseshoe-like occipital carina” at least in the groundplan of the families. Other research, however, indicates that the situation is perhaps more complicated than is apparent. Somewhat in agreement, Copland *et al.* (1973) stated that Agaonidae (Agaoninae *sensu* Bouček 1988) was a distinctive group, based on overall ovipositor structure, but had several features in common with Sycophaginae and Epichrysomallinae, and that none of these had much in common with Torymidae. Quicke *et al.* (1994), in discussing ovipositor cross-section morphology and its implication for phylogeny, showed considerable variation between structures in Sycophaginae and Agaoninae (both placed in Agaonidae) as well as Epichrysomallinae (placed in Torymidae). Again, none of these taxa appeared similar to Torymidae (*sensu* this study).

In the following paragraphs I discuss several characters of possible importance to the eventual resolution of the placement of the taxa just mentioned.

*Occipital carina, hypostomal carina, and postgenal bridge:* In almost all Torymidae (as defined by this study) the occipital carina is present and in almost all Agaonidae

(except some *Epichrysomallinae*) it is absent. In both groups the hypostomal carinae meet below the occipital foramen and a postgenal bridge is formed. This construction is found in only a few other chalcidoids, including *Ormyridae* and a few scattered genera of *Pteromalidae*. Thus, the construction of the bridge could be viewed as a synapomorphy that unites *Torymidae* and *Agaonidae* + *Ormyridae* as sister groups, while the occipital carina suggests a subsequently divergent path. As I demonstrate later ("Characters Analyzed for Relationships," p. 31), the presence of an occipital carina appears to be the groundplan state for *Torymidae*. Bouček (1988:157) agrees with this viewpoint. Within *torymids* a loss of the carina is hypothesized to be a reversal. Based on the occipital carina alone, then, one could hypothesize that *Agaonidae* represents a derived clade within *Torymidae*. This is the simplest interpretation of data taken from the occipital carina and would also support the hypothesis that fig wasps are highly derived. Bouček (1988) placed the *Epichrysomallinae*, the only *agaonid* group with an occipital carina, as the most primitive group of *Agaonidae*, which suggests its potential position as intermediary between the basal *Torymidae* and remaining, presumably derived, subfamilies of *Agaonidae*.

If, on the other hand, one accepts the absence of the occipital carina as the plesiomorphic state (shared with *Pteromalidae*), then the hypotheses needed to explain putative relationships of any kind become more complicated. Two possibilities would exist:

Hypothesis 1: *Agaonidae* is a plesiomorphic group of *Torymidae*: This hypothesis agrees with Bouček's suggestion (1988:157) that *agaonids* arose from a seed-feeding ancestor because it places them near the plesiomorphic *Megastigminae*, a *torymid* group nearly exclusively seed-feeding in habit. But all *megastigminae* have the occipital carina and the only hypothesis that would fit the statement being made — that the absence of a carina is plesiomorphic rather than derived — is that *agaonids* retain the primitive state (no carina) with respect to the *megastigminae* and thus are their sister group. Based on biology this might seem unlikely because *megastigminae* feed phytophagously on relatively more primitive plants (e.g., conifers, rosaceous plants) whereas *agaonids* are all confined to the more derived types of figs. However, this may be more an indication of adaptive radiation within a new host niche than indication of wasp phylogeny.

Hypothesis 2: *Agaonidae* is derived from some group other than *Torymidae*: Although this hypothesis is worthy of much further study, it is problematical in that there seems to be little evidence to derive the lineage from any other group except possibly the *Pteromalidae*. Bouček (1988) pointed out that both *Torymidae* and *Agaonidae* share the presence of a postgenal bridge (shared with *Ormyridae* as well), which tentatively unites them and separates them from *Pteromalidae*, which does not have the bridge. While this statement is generally true, a few putative *pteromalids* such as *Ditropinotella*, *Chromeurytoma*, and *Cea* also share the postgenal bridge. The ramifications of this hypothesis will remain unclear without further phylogenetic analyses of all *pteromalids*.

*Construction of Mt8 and Mt9*: In all *Torymidae* (Figs. 26-30), *Mt8* is dorsally transversely continuous across its basal portion, with the cercus inserted on a translucent area of the posterolateral margin (always somewhat bent inwardly, and with an outer surrounding carina in all but the most derived taxa) and *Mt9* is an articulated, flap-like appendage. In *Agaonidae* (Fig. 34) only the subfamily *Sycophaginae*

approaches this construction, while in all other non-sycophagine agaonids (Figs. 35, 36) Mt8 and Mt9 are fused, usually with the cercus arising from its surface (although in some genera — e.g., *Blastophaga*, Fig. 35 — it may arise on a transparent area near the posterior border). The condition of a fused Mt8 and Mt9 (Fig. 33) is found in most chalcidoids, and is most likely the plesiomorphic state. Based on this structure, non-sycophagine agaonids would appear to be plesiomorphic with respect to Torymidae, while in Sycophaginae the construction of Mt8 and Mt9 is not entirely homologous with that found in Torymidae and is apparently autapomorphic for the subfamily Sycophaginae. Placement of Sycophaginae in either Torymidae or Agaonidae (*sensu* Bouček 1988), based on this character, is problematic, but the invaginated hind margin of Mt8 (Fig. 34) and Mt9 placed some distance from it, appear to be a more developed (or extreme) expression of the structure found in Torymidae than that found in Agaonidae. If this is true, then Agaonidae as now recognized is paraphyletic. The structure of Mt8 and Mt9 in Sycophaginae suggests that its placement in Agaonidae (*sensu* Bouček 1988) should be reconsidered.

*Exserted Cerci:* In all Torymidae the cerci are exserted (Figs. 26-30). In Agaonidae the character is variable with some agaonid subfamilies having the cerci exserted (e.g., Sycophaginae: Fig. 34, Sycoecinae, Agaoninae: Fig. 35), while in others it is not (e.g., Otitesellinae), and in some subfamilies genera may show both states (e.g., Epichrysomallinae, Sycoryctinae). As the condition is also variable in Pteromalidae (i.e., exserted in *Chromeurytoma*: Fig. 31, and *Cea*), it provides little evidence to support phylogenetic placement of any taxon at this time.

*Summary of Sycophaginae:* As Gibson (1993) pointed out, we do not yet know what attributes of the above taxa are plesiomorphic or apomorphic, nor which attributes are shared because of inheritance from a common ancestor or convergence from the shared fig-gall niche. Therefore, a discussion of their phylogeny is only an academic challenge at this point. Based on the above characters the following statements can be made concerning the relationships of Sycophaginae, non-sycophagine agaonids, torymids, ormyrids, and pteromalids: 1) the presence of a postgenal bridge implies a possible relationship among Torymidae, Ormyridae, and Agaonidae (including Sycophaginae), and its absence in Pteromalidae (except in a few genera) suggests that Pteromalidae is a plesiomorphic sister group of the former taxa; 2) the absence (groundplan) of an occipital carina in most Pteromalidae, its presence in Torymidae (groundplan) and Ormyridae, and its absence in Sycophaginae and most non-sycophagine Agaonidae, again argues for a plesiomorphic placement of Pteromalidae, with Ormyridae and Torymidae derived relative to it. In this character, agaonids would appear to be most directly derived from some branch of pteromalids (a single loss of carina) rather than from torymids which would require either a secondary loss or a retention of the primitive state; and 3) the condition of Mt8 and Mt9 in Sycophaginae and Torymidae argue for a derived placement of these two taxa with respect to the fused Mt8 and Mt9 found in all non-sycophagine Agaonidae, all Ormyridae, and nearly all Pteromalidae. Pteromalidae and Ormyridae do not differ in this structure, and it could be argued that in Sycophaginae Mt8 and Mt9 appear to be more derived than in Torymidae. In non-sycophagine agaonids the metasomal structure does not appear to be homologous with that found in Pteromalidae or Ormyridae, and its exact interpretation is problematic.

From the above summary it seems apparent that 1) Pteromalidae is the most

plesiomorphic taxon; 2) Torymidae and Agaonidae are likely sister taxa; 3) non-sycophagine agaonids (i.e., Epicrysomallinae, Sycoryctinae, Agaoninae, Sycoeciinae, and Otitesellinae) are basal with respect to Sycophaginae and Torymidae; 4) a sister relationship between Sycophaginae and Torymidae cannot be eliminated based on the data; 5) Sycophaginae appears more derived than either non-sycophagine agaonines or Torymidae, but, based on its metasomal construction, appears more likely derived from Torymidae than non-sycophagine agaonids; and 6) Ormyridae shares some pteromalid and some torymid features and its placement is still questionable.

In past work some of the above subfamilies (e.g., Epicrysomallinae, Otitesellinae) were placed in Pteromalidae (Bouček *et al.* 1981) and more recently, when placed in the Agaonidae, Bouček (1988) alludes to the fact that these subfamilies may indicate a "convergence or indication of broader relationship" presumably to the Pteromalidae. I agree with this and suggest further that the resolution of problems concerning the phylogenetic relationships of torymids with agaonids will require that each subfamily be treated as a monophyletic unit independent of the other, that Sycophaginae in particular be reassessed because of its autapomorphic tergal construction relative to all other taxa, and that all taxa plus Pteromalidae be reassessed for construction of the hypostomal and metasomal areas.

#### **Thaumatoryminae** (= *Incertae sedis*, see p. 172):

The genus *Thaumatorymus* was described from a single species provisionally placed in the Monodontomerinae by Ferrière and Novicky (1954). Later, Bouček (in Peck *et al.* 1964:16) placed it in the monotypic subfamily Thaumatoryminae. The subfamily definition is based on characters derived from the only known species *T. notanisoides*. The characters which defined the subfamily were given as: "abdomen with long petiole; propodeum horizontal, spiracles broadly elevated; wing maculate; marginal vein rather short; head strongly convex, occipital carina dorsal; male antenna with whorled long hairs." Not discussed was the modified posterior margin of the mesepimeron (Fig. 368) which is slightly sinuate and distinctly raised above the surface of the metapleuron (which itself does not project forward but is slightly overlapped by the mesepimeron). This condition is unique in Torymidae and is found only in a somewhat similar form in *Propachytomoides* Girault (Podagrionini, Fig. 280B). This condition is not comparable to what occurs in Toryminae (of authors) where the metapleuron is sinuate to fit into the posterior mesepimeral emargination (Figs. 10, 425).

The majority of characters defining *Thaumatorymus* may be seen as homoplasious. For example, the elongate metasomal petiole is found in Torymini (*Ecdamua* Walker, *Odopoa* Walker) and in some Podagrionini (*Propachytomoides*, *Pachytomoides* Girault). The horizontal propodeum, which is a rather dubious state at best, is found in Torymini (*Mesodiomorus* Strand, some male *Physothorax* Mayr), some Monodontomerini (*Perissocentrus* Crawford), and Podagrionini in general. The maculate wing is found in examples throughout the Toryminae (*sensu* Grissell), including Torymini (some species of *Torymus*, *Odopoa*), some Microdontomerini (*Idiomacromerus*), and some Podagrionini (*Propachytomoides*).

Of the remaining characters, the wing venation (with marginal vein about 3X length of stigmal), the spiracles broadly elevated, the occipital carina present only on the upper half of the head, and the male antennae with whorled hairs are the only

potentially defining states for Thaumatoryminae.

The marginal venation of *Thaumatorymus* (Fig. 360) is unique among torymids. It differs from typical Torymini-Torymoidini clade venation (e.g., Fig. 60), in which the marginal vein is thin, elongate, and many times the length of the reduced stigmal vein. Although the marginal vein is structured somewhat as found in Monodontomerini (Fig. 59), being relatively thick and short (3-6X the length of the stigmal vein), in *Thaumatorymus* the entire complex of venation is markedly reduced to a relatively small, median section of the forewing (Fig. 360). Thus it may be considered autapomorphic and of little immediate use in establishing relationship with other taxa.

The spiracles certainly are distinctly structured in this species, and to my knowledge their equivalent is found in only one species of Torymidae, *Adontomerus eriogasteris* Nikol'skaya, which has the spiracles elevated comparably to *Thaumatorymus*. As other species of the genus *Adontomerus* are typical in propodeal structure, this demonstrates the possibility that the character is homoplasious and not of generic rank.

The setal condition of the male antenna is used to define genera of Megastigminae (e.g., *Paramegastigmus* Girault, *Malostigmus* Bouček, *Bootania* Dalla Torre, see Bouček 1988) and exists in states from absent to various patterns of whorled setae. It is interesting to note that the subfamily Pulvilligerinae was recognized based on the male antenna having whorled setae, but the subfamily was eventually synonymized under Megastigminae. The use of this character to help define a subfamily known from but a single species seems unwarranted.

I did not include *Thaumatorymus* in my analysis because I considered the genus (= subfamily of authors) to be a member of Toryminae (of authors) and not a valid subfamily. I placed it in Toryminae because of the slightly sinuate mesepimeron. In examining the species repeatedly (based, unfortunately, on only 2 specimens), I now consider the structure of the mesepimeron to be unique as described above (Fig. 368). I cannot place *Thaumatorymus* in the phylogeny proposed herein and for now treat it as an *incertae sedis* supported only by autapomorphies.

### **Toryminae** (of authors) (= Torymini, see p. 98):

There is little doubt that this group is monophyletic and that it is closely related to some taxa in what has been called the "Monodontomerinae." Bouček (1988:143) stated that "some more ordinary forms of this subfamily [Toryminae] greatly resemble some less specialized Monodontomerinae, but the pleural character seems to indicate Toryminae as a more specialized group (synapomorphy)." Again there is little doubt that Toryminae is a more specialized group. My original hypothesis was that Monodontomerinae + Toryminae were sister groups, with Toryminae more derived. Toryminae has been so easily defined, and is such a large group, that its monophyly has never been questioned. I still do not question its monophyly; I simply suggest that Toryminae shares a common ancestor with a member in the "Monodontomerinae" and thus both are part of a single, monophyletic lineage. The historical concept of "Toryminae" is now restricted to the tribal level Torymini, while all so-called "Monodontomerinae" become members of the Toryminae.

### **Monophyly of Subfamilies**

**Megastigminae:** Within Torymidae, the monophyly of Megastigminae is



hypothesized based on synapomorphies found in the wing venation and possibly the clypeus. In megastigmine torymids the stigma is enlarged in some manner (Figs. 8, 55) so that its anterior to posterior height is generally greater than its width and this height is also subequal to or greater than that of the costal cell. In other torymids the stigma is not enlarged (see Toryminae, below). In the majority of Megastigminae the clypeus is bilobed (Fig. 382) (the hypothesized groundplan state from which but few genera deviate, e.g., *Xenostigmus* Riek, *Bootanellus* Girault). The bilobed condition is not found in any other torymid (although emarginate clypeal margins occur rarely), and it differs from the condition found in some Pteromalidae (p. 39).

I made no attempt to study the genera of this subfamily other than to establish character state information as the hypothetical sister-group to the "Monodontomerinae" which formed the original basis for my study. As the monophyly of this group has never been challenged (see Bouček 1988), and as it is a relatively large group, its study is left for other times and/or other researchers.

**Toryminae:** As defined by this study the subfamilies Toryminae, Thaumatomyrinae, and Monodontomerinae (of authors) are now combined into a single, presumably monophyletic subfamily. My analysis returns us to the concept of Torymidae as propounded by Thomson (1876) in which all non-megastigmine torymids (= Toryminae + Monodontomerinae of authors) were simply members of the same category, "Torymides." Toryminae of authors has long been recognized based on the autapomorphy of the sinuate metapleural margin. This readily apparent structural anomaly makes Toryminae of authors one of the most easily defined of all groups of Chalcidoidea. But this character, as excellent as it may be for defining monophyly of the group, does not tell us anything about relationships between it and other taxa. Other than this single autapomorphy, Toryminae of authors does not differ markedly from genera such as *Torymoides* Walker or *Pseudotorymus* Masi which are referred to Monodontomerinae of authors. This latter group was defined only by the absence of apomorphic features, i.e., by symplesiomorphies. It has thus always been "defined" as what is left over once the Megastigminae and Toryminae (of authors) are removed. It is much easier to define two groups by taking out the apomorphic members and "defining" the left over group by the absence of the apomorphy. My work creates a new problem because it is scarcely easier to define the new concept of "Toryminae" than the old concept of "Monodontomerinae."

Based on my analyses, the only character that can now possibly define Toryminae *sensu* Grissell is wing venation (see p. 40 for discussion of wing vein states and polarities). Although the synapomorphy of wing venation is used to define monophyly in Megastigminae, its use in Toryminae is problematic. Within Torymidae, Toryminae is defined as having an unmodified stigma that is at most quadrate (Fig. 7) but often wider than high (Fig. 59), and shorter in height than the height of the costal cell (Figs. 56-61). This is clearly the plesiomorphic state as found in most chalcidoids. Based on other aspects of wing venation, however, especially the reduced post-marginal and stigmal veins found in most species of Toryminae, it is possible to hypothesize that although the stigma itself retains the plesiomorphic state, the wing veins as a unit are derived with respect to the outgroup Pteromalidae.

### PHYLOGENETIC ANALYSES

As Gibson previously pointed out (1989:10), our knowledge of the evolution and distribution of character states in the Chalcidoidea is at a primitive level. This lack of basic, essential knowledge, in turn, is confounded by preexisting, totally intuitive hypotheses of phylogeny. Which comes first, the character or the phylogeny? It is difficult to assess character polarity when the outgroup is unknown or highly questionable, when the ancestral or derived members of the outgroup are unknown, or when the monophyly of the outgroup is in question. In Chalcidoidea it is not even readily apparent that the taxa being analyzed — be they species, genera, tribes, or subfamilies — belong in the group in which they are placed. In a superfamily where the latest major revision (Bouček 1988) of 14 families of Australasian Chalcidoidea produced over 1000 generic transfers, where 550 valid generic names include over 300 newly proposed synonymies and nearly 150 new generic names, and where 28 new tribe and subfamily names are proposed, it is not unexpected that phylogenetic analyses prove intransigent. So it has proven with my studies of the “Monodontomerinae.”

At the inception of this study, the Monodontomerinae could not be defined by any single synapomorphy. Instead, the group represented the leftover taxa remaining once the Erimerinae, Megastigminae and Toryminae were defined by autapomorphies in the tibial spur, wing, and mesosoma, respectively. Worldwide, Monodontomerinae was represented by about 55 “valid” genera. The most recent world revision by Szelenyi (1957b) treated only 28 names and admitted that most of the generic concepts were based on the literature.

After assembling the literature, cataloging all known Monodontomerinae species, and examining nearly all the type specimens of the 55 genera (plus additional synonyms), it became apparent that much confusion existed about generic limits. Of the 55 genera, 24 were known from only the type-species, and often only the type-specimen, i.e., nearly 50% of all genera were monotypic. Another 7 genera (13%) were known from 2 species each. In these 31 genera, few specimens, other than the single types, were available for study. Under these circumstances, an “exemplar” approach to study had to suffice for a large number of generic taxa rather than a more rigorous “population” approach.

As a result of the status of the group, some information for characters was based entirely on the type-specimen of the type-species of each genus because at least *that* specimen represented the genus (for nomenclatural purposes). If discrete states of any defining character (old or new) could be found for those specimens, then at least there was a chance that the states would prove useful in a phylogenetic analysis. On the other hand, if discrete states could not be found, then the chances of the character having any phylogenetic value were lessened. After examining types of genera, I examined other species assigned to the genus. If species were found to differ in a state of presumed generic rank from the type of the genus, these species were coded as new terminal taxa.

During the course of this study, the number of taxa varied considerably from 64 at the maximum to 43 in the final analysis. Accounting for this larger initial value and the reason for variability was fourfold: 1) the number of representatives from the outgroup was increased from 1 genus to 4; 2) in several cases a species previously coded in one genus was found to have a conflicting character state and was placed as a new

unknown terminal taxon; 3) because a newly discovered, undescribed species differed in one character state (or sometimes two) from a known terminal taxon and was added as a single taxonomic unit of unknown stature; and 4) some terminal taxa were eventually synonymized with other taxa as a result of analysis, thus resulting in their loss.

In factor 1, above, the increase of outgroup genera was undertaken to include more putative primitive examples of the outgroup rather than using the single, relatively advanced genus (*Pteromalus* Swederus) by itself as originally proposed. In cases 2 and 3 the object was to find the most parsimonious placement for newly discovered taxa that differed from all other taxa by one or two character states. In these cases the states themselves were not intermediate, but were already recognized among states in the data matrix. Their presence in a taxon created a unique *set of states* that was not already found in one nomenclatural unit (i.e., terminal taxon) in the analysis.

Thus, the resultant assemblage of terminal taxa, as recognized during the various analyses of this study, ranged from the single species of monobasic genera, to single species of unknown genera which were unplaceable by recognized character states, to putative genera with hundreds of species, to putative subfamilies, to putative families. In each case the only *a priori* assumption made was that the unit as defined by its presumptive synapomorphies was monophyletic. I made every attempt to determine all character states used in the literature, to standardize and quantify these states, to examine all available taxa (except Toryminae of authors, discussed next), and to derive new characters and states from the specimens.

The putative subfamily Toryminae (of authors) was accepted as monophyletic based on the sinuate anterior margin of the metapleuron. Although composed of 12 genera, I used my sampling of over 100 species of *Torymus* (nearly one-third of all known species of the subfamily) to derive information for the data matrix. In retrospect each genus of Toryminae should have been included in my analysis as a separate taxon, but this group as a whole has always been accepted as monophyletic and is one of the few groups of Chalcidoidea that can be defined by a single, unambiguous synapomorphy. It therefore seemed appropriate to analyze the group as a unit relative to other taxa, rather than as separate, autonomous parts.

My phylogenetic study was initially based on an investigation of 36 characters coded for 54 genera (plus the outgroup, *Pteromalus*). Three presumptive subfamilies of Torymidae (Erimerinae, Toryminae, Megastigminae) were recognized and the genus *Pteromalus* was selected from the putative outgroup Pteromalidae. As the study progressed to nearly 50 computer-generated analyses, the number of characters dropped to between 24 or 25 and the number of taxa increased to 61 (plus 4 pteromalid genera representing the outgroup). The analyses concluded with 24 characters and 43 taxa. A discussion of the sequence of events follows next and then a discussion of the characters and their analyses follows after that (p.31).

Procedures. — The basic methodology for deriving the phylogenetic analysis was discussed under the methods section. Here I present the iterative procedure in terms of stages of analysis. Many analyses were undertaken merely to stabilize sets of transformation series, and these are more a matter of routine than of special interest. A total of 49 analyses were performed and the stages that occurred were as follows:

*STAGE 1*, 1 analysis (35 characters x 55 taxa): All data was analyzed including ratio data. *Pteromalus* was used as the outgroup. Minimum length Wagner trees consisted of 554 steps with a consistency index (CI) of 23 whereas successive approxi-

mation weigher trees (SW) surprisingly had a lower CI of 18. The anomaly of poorer weighted trees lead to a reexamination of all data, but especially the ratio data which were converted to descriptive data. As a result, some multiple characters were combined into a single character or were dropped with a subsequent loss or conversion of 10 of the original 35 characters (discussed below, see p. 54; see also Mickevich and Grissell, in prep.).

**STAGE 2**, 31 analyses (25 characters x 58 taxa): During this part of the analysis several factors were studied: character states were refined based on analyses of transformation series and the number of outgroup taxa (i.e., genera of Pteromalidae) was increased from 1 to 4. The increase occurred because *Pteromalus* was first used to represent the subfamily Pteromalinae of the Pteromalidae. The genus could not readily be coded as it proved to be too variable for the character states, and, as a result, much of the coding could only be entered as questionable data. Also, the phylogenetic position of the Pteromalinae within Pteromalidae is questionable, but it is presumed to be relatively advanced. Therefore, I added the genus *Janssoniella* Kerrich, which is a putative primitive member of the subfamily Pteromalinae and also the more primitive, and less variable, genera *Hemadas* Crawford (Ormocerinae) and *Lamprotatus* Westwood (Miscogasterinae) (all based on the work and suggestions of Steve Heydon, pers. comm.). Stabilization was reached at minimum length Wagner trees of 128 steps with a CI of 58 and successive weigher trees of CI 58.

**STAGE 3**, 5 analyses (25 characters x 64 taxa). Six unplaced taxa were added to the data. These were newly discovered taxa that differed from previously studied taxa by one or two character states. Stabilization was reached at minimum length Wagner trees of 146 steps with a CI of 51 and successive weigher trees of CI 65.

**STAGE 4**, 8 analyses (24 characters x 64 taxa: Appendix III). During this stage two characters were examined for their effect on the tree. One of the most unstable characters, the number of anelli, is a character on which great weight has been placed in the past. It is discussed more fully below under the character discussions. The character states for anelli were excluded from the analyses to see what effect this would have on the resultant trees (note, however, that the states are still included in the data matrix, Appendix III). Stabilization was reached at minimum length Wagner trees of 113 steps with a CI of 55 and successive weigher trees of CI 68. The trees produced with and without the anelli were essentially identical except that some of the taxa in the lower part of the tree (= Microdontomerini) moved about relative to each other. With anelli the Wagner tree had less structure basally than the successive weigher trees, but without the anelli, this was reversed. The second character, the occipital carina, was read into the data, but the state *No* (i.e., the absence of the carina) was coded as a question mark. The reason and results of doing this are discussed under the occipital carina character below.

**STAGE 4A** (the "Working Hypothesis," Fig. 37). During the year after STAGE 4 was completed, the character states of all taxa were reexamined using the Wagner trees from that stage as hypotheses of potential phylogeny. There were 3 basic tree structures that differed principally in the placement of *Torymus* (= exemplar for Torymini of authors, Torymini of this study), but otherwise were rather unstructured branching patterns of ill-defined polytomies. Fig. 37 shows one of the 3 Wagner trees from STAGE 4. This tree was selected by comparing the branching pattern of each Wagner tree with that of each successive weigher tree. The Wagner tree that most closely

matched a successive weigher tree was then chosen as my "Working Hypothesis" for additional analysis. During STAGE 4A I attempted to interpret the branching patterns in terms of *nomenclatural units*, i.e., given the hypothetical phylogeny, how would one interpret the largely unresolved tree into a meaningful method of classification? My approach was several-fold. Beginning at the bottom of the tree (the least resolved topology) I studied taxa in groups: first looking at a taxon as defined by the tree, then comparing taxa next to each other, then comparing groups of taxa to other groups, and so forth. I used presumptive synapomorphies as a first-level basis for comparison, then geographic distribution, and finally biological information. Where synapomorphies were poor (i.e., homoplastic characters) and geographic limits and/or biology overlapped, I placed the taxa as synonyms. Where synapomorphies were poor but taxa were widely allopatric, I made no changes in the current nomenclatural standing. This rather operational approach was used to study the entire complex of taxa. In so doing I discovered that my original coding of character states was not always correct, and I was forced to redefine 3 characters (occipital carina, wing venation, and tergal emarginations). In reviewing the taxa based on the tree, I derived a number of synonyms and hypothetically definable groups which I arranged as tribes or unplaced taxa (*incertae sedis*). Under the discussions of tribes and genera which follow I explain my reasons for these actions in sections referred to as "Working Hypothesis." On completion of this year-long restudy of all taxa I ran my "best-estimate" analysis of the data and nomenclatural decisions. This result is discussed next under STAGE 5.

STAGE 5 (the "Ending Hypothesis," Fig. 38), 4 analyses (24 characters x 43 taxa: Appendix IV). Stabilization was reached at 11 minimum length Wagner trees of 132 steps with a CI of 57 and 16 successive weigher trees of CI 57. These analyses are the direct result of the work performed in STAGE 4A. The reduced number of taxa reflect the synonymies produced in that analysis, but two new taxa were added: *Torymoidellus* Bouček (described after STAGE 4A) and *Thaumatorymus*. The latter, which has been placed as a subfamily of its own, was erroneously placed by me as a member of the *Torymus*-group of genera (= Toryminae of authors), but on further study I decided that it should be placed as a separate taxon in the data. (In the revisional section, another genus is added which was not included in my analyses at all. This is *Ophiopinotus* Husain and Kudesia and was omitted on purpose as explained under the generic section, p. 97.) The outgroup, 4 genera of Pteromalidae, was dropped, and *Megastigmus* was used instead. This was done for two reasons: 1) because of the lack of certainty concerning relationships of genera within Pteromalidae and between this group and Torymidae; and 2) because in the working hypothesis (end of STAGE 4A) *Megastigmus* (representing the Megastigminae) was placed as the basal group of torymids, and it was presumed that a known primitive outgroup would lead to a more informative result than would outgroups of unknown or questionable status. The reanalyzed anelli were read back into the data for the sake of completeness. The occipital carina was reassessed and the *No* state was reinstated as a valid state and not coded as questionable. The result of this series of analyses is shown in Fig. 38 and is discussed under each genus in the systematic sections as the "Ending Hypothesis." I use the term "ending" because I believe I can achieve no better results than this, but I accept them without a firm belief that they reflect the ultimate reality of evolution in the Torymidae. I would have used the term "Final Tree" but this would be presumptuous. No tree will ever be final.

### Characters Analyzed for Relationships

Identifying and defining characters that have been used to infer higher taxonomic categories in the putative subfamily Monodontomerinae has not been straightforward. The literature discussing the characterization and separation of the higher taxa (discussed under "Historical Perspective," p. 9) contains problems of character assessment that fall into 3 general categories:

1) Character states defined by relative comparisons: In these cases character states were "defined" (actually "characterized" would be a better term) by comparison to each other (with or without benefit of illustration). For example, in characterizing genera, the relatively simple shape of the hind femur has been described as more slender, slender, thickened, notably thick, less broadened, broadened slightly, weakly or hardly broadened, only moderately broadened, broad, very broad, conspicuously broadened, almost regularly broadened, broadly triangular, stouter, and very large (Szelenyi 1957b, Bouček 1978, Nikol'skaya and Zerova 1987).

2) Character states defined by absolute, yet inconsistent descriptors: Sometimes a character was presented in an absolute way so that it could be understood within the context of one paper (or by one author), but it was not comparable to other papers discussing the same structure. For example, the marginal vein was described by different authors as "longer than half of costal cell" (Bouček 1978), "about as long as the submarginal [vein]" (Szelenyi 1957b), or "at most 3 times as long as stigmal" (Bouček 1988). In such cases, the comparison may be of diagnostic importance to distinguish a pair (or more) of taxa, but the overall variation of the character and its states was never described.

3) Character states defined by "tentative" uniqueness: A "striking" or "unique" character state may be noted for one taxon, but later proves to be merely one point of a continuum that cannot be divided. For example, I described a fossil genus (Grissell 1980) that had the "metanotum ... 0.7X the length of the propodeum (generally much less than 0.5X in most genera)." After assessing all other genera, I found that, although 0.7X was the extreme for the subfamily, measurements of other genera were as high as 0.6X and it was not all that easy to measure the character accurately in the first place.

These sorts of problems are found in many systematic revisions but are especially common when trying to synthesize temporally and geographically widespread data at a world level. Essentially one must organize all data, both past and newly gathered, into a cohesive and consistent format. That is what I have attempted to do for this study. In the two sections that follow I first outline the characters on which this study is based and then discuss the characters that I tried to use but eventually abandoned. In a few cases (e.g., wing venation) the discussion overlaps both sections because I found different ways to look at the same character.

#### *Characters Used in Phylogenetic Analysis of Torymidae*

For characters below there may be two sets of discussions. The first is for the "Working Hypothesis," i.e., the phylogeny I used to establish nomenclatural groupings as described above; the second is for the "Ending Hypothesis." This is the final character data and transformation series used in this work. For each of these, I give the transformation series for the states, the consistency index (CI), and an analysis of

my penultimate and final hypotheses for the character. In some cases both agree. I illustrate each character and its transformation series as determined for the "Ending Hypothesis." A complete data matrix for both analyses is found in Appendices III (p. 324) and IV (p. 333).

### OCCIPITAL CARINA

#### Character 1 (Fig. 39)

#### STATES DESCRIPTION:

**Working Hypothesis:** *Weak* — an indefinite ridge seen only at certain angles of view and/or under certain lighting. *No* — no carina or indefinite ridge present. *Yes* — carina present as a sharp, obvious ridge. *Side* — carina clearly present laterally but absent dorsally. *Above* — carina clearly present dorsally but absent laterally.

**Transformation Series:** *No* — *Weak*, *Yes* — *Side*, *Above*. CI = 50.

**Ending Hypothesis:** *No* — carina absent, or if present: an indefinite ridge seen only at certain angles of view and/or under certain lighting with ventrolateral edges not extending below imaginary line drawn horizontally across *dorsum of occipital foramen*, dorsum arched, nearer hind ocelli than occipital foramen. *1* — developed, with ventrolateral edges extending nearly to imaginary line drawn horizontally across *venter of occipital foramen*, dorsum arched, nearer hind ocelli than occipital foramen or midway between both. *2* — developed, with ventrolateral edges extending below imaginary line drawn across *dorsum of hypostoma* or rarely touching hypostomal carina above base of mandible (and then ventrolaterally narrowed), dorsum arched, nearer to hind ocelli than to occipital foramen or midway between both. *3* — developed, *joining hypostomal carina* slightly above base of mandible, ventrolaterally expanded, dorsum arched, nearer to hind ocelli than to occipital foramen. *3A* — developed, nearly appearing to join hypostomal carina in upper half but abruptly turned downward towards base of mandible where it joins, ventrolaterally expanded, dorsum arched, nearer to hind ocelli than to occipital foramen. *4* — developed, *joining* (or nearly) hypostomal carina near median point, dorsum flat, nearer to occipital foramen than to hind ocelli.

**Transformation Series:** *1* — *NO*, *2*, *4*, *3A*, *3*. CI = 57.

**DISCUSSION:** The primary differences between the working and ending hypotheses lie in an expanded and more descriptive analysis of states as well as a recognition of more stable differences. I discovered that the position of the carina relative to the hind ocelli and occipital foramen as well as its relationship to the hypostomal carina were relatively stable expressions of the carina. Because the ending hypothesis is much more detailed, I do not discuss (or figure) the working hypothesis.

In both primitive (Symphyta) and advanced (Aculeata) Hymenoptera, the occipital carina is variably present or absent (D. R. Smith, A. S. Menke, pers. comm.). Gordh (1975:396) stated that for Chalcidoidea "... it is doubtful that the [occipital] carina is homologous with the occipital suture of more primitive insects." Therefore an assessment of polarity for this character must come from within the superfamily itself or from putative sister taxa. Even within the superfamily there is no assurance that the occipital carina is homologous among taxa. For example, Bouček (1988:13) stated

that in some groups of *Eurytoma* "... a probably analogous carina is developed," and he also stated (1988:118) that the occipital carina in some pteromalids "... should not be confused with a secondary transverse fold." Unfortunately it is all too simple to confuse such things. Schauff (1984) stated that the presence of an "occipital suture" was apomorphic in Mymaridae, but again there is no data to suggest that this suture is necessarily homologous with the occipital carina found in Torymidae. No worker has studied the occipital carina throughout the Chalcidoidea, nor has it been studied in depth in any phylogenetic study.

In investigating the phylogenetic implications of the occipital carina, I examined material within the Pteromalidae, the putative sister group to Torymidae. In Clenomyminae, one of the most plesiomorphic groups of the family (Heqvist 1961:91, Bouček 1974:129, Bouček 1988:243), the carina is absent in taxa examined (*Epistenia* Westwood, *Solenura* Westwood, *Lycisca* Spinola, *Heydenia* Förster, *Amotura* Cameron). In the Leptofoeninae, "... a specialized branch of a cleonymine outgroup" (Bouček 1988:268), the carina is present. Within the presumably most advanced subfamily Pteromalinae the apparently primitive genera (e.g., bark beetle parasites such as *Rhopalicus* Förster, *Dinotiscus* Ghesquière, *Cheiropachus* Westwood) have no occipital carina, whereas in presumably more advanced genera the carina may be absent (e.g., *Pteromalus*: Fig. 398; *Roprocercus* Ratzeburg: Fig. 400) or present (e.g., *Trichomalopsis* Crawford). This evidence indicates that the groundplan in Pteromalidae is the absence of an occipital carina and that its presence is apomorphic.

Within Megastigminae + Toryminae the pattern is reversed. All Megastigminae (Fig. 402) and almost all Toryminae have an occipital carina. Few species (I estimate less than 5% based on the New World fauna) are without the carina entirely, and they occur frequently among the basal groups (e.g., *Ditropinotus*, *Microdontomerus*, *Liodontomerus*). Rarely is the absence of a carina found beyond the basal group (e.g., *Oopristus* Steffan, *Stenotorymus* Masi). As currently accepted in the literature, several genera include species in which the carina is present or absent. For example, *Microdontomerus crassipes* Bouček (with carina) was included in the otherwise non-carinate genus *Microdontomerus*. *Lochites papaveris* Förster, the type species of *Lochites* Förster (with carina) has long been placed as a synonym of the non-carinate genus *Liodontomerus*. In my working analysis, I coded such contradictory units as separate terminal taxa (e.g., *Liodontomerus* and *Lochites*), rather than as single taxa, to see what their fit on the tree might be.

Some sets of analyses, including the final working hypothesis (but not the ending hypothesis) were run with the *No* state coded as a question mark. This was done because it is not known if the absence of a carina is a loss (i.e., present then lost — a reversal) or the retention of the primitive condition (i.e., occipital carina never present). Thus, in this instance, the absence might be either or both of two states. Philosophically absences could be considered informative because they might demonstrate a serial loss or gain, or they could be considered uninformative because the absence of knowledge cannot provide information about knowledge. By using a question mark the expectation was that I might determine the answer to this question based on the "known" (or positively expressed) states of the character. When coded as a question mark, the *No* state showed 8 reversals on the tree, whereas in previous analyses where the *No* state was used without reservation there were 5 reversals. It might be argued that under either circumstance the state seems to be a reversal (rather than a



loss), but the point is moot since under either approach the *No* state is uninformative.

Under the ending hypothesis (Fig. 38) all occipital states (Fig. 39, Character 1) are considered derived from state 1, which appears to be intermediate between the complete absence (e.g., Pteromalidae) and the complete presence (e.g., Podagronini) of a carina. If the absence of a carina is accepted as primitive, then state 1 would be considered an intermediate, primitive state of the carina for Megastigminae as well as *Glyphomerus* Förster and *Zaglyptonotus* Crawford. In Microdontomerini (node 3) the character is almost entirely poorly expressed (through presumptive reversal) and unstable even within genera. At nodes 9 and 11 the carina is well-expressed. The carina is most completely developed in the Podagronini (node 25) and Palachiini (node 21) which are putatively the most derived taxa.

Based on the foregoing discussion, I hypothesize that the absence of an occipital carina is the groundplan state of the Pteromalidae and that a few derived taxa within this family have the carina. I also hypothesize that the presence of an occipital carina is the groundplan state for Megastigminae + Toryminae. In this case an absence in some Toryminae indicates a reversal to the primitive groundplan state of the Pteromalidae. In the basal sister group Megastigminae all members have the carina, whereas in the basal Microdontomerini the carina is weakly expressed or absent, then above this group almost all taxa again have an obvious, strong carina with the rare exception of a few putatively derived taxa (e.g., *Oopristus*, *Stenotorymus*).

#### ANELLI

#### Character 2 (Figs. 40, 41)

#### STATES DESCRIPTION:

Working Hypothesis: 1 — having 1 anellus. 2 — having 2 anelli. 3 — having 3 anelli. 4 — having 4 anelli. 5 — having 5 anelli.

**Transformation Series:** 2 — [1 — 4], 3, 5. CI = variable, see below.

Ending Hypothesis: 1 — as above. 2 — as above. 2\* — single terminal taxon having 2, 3, or 5 anelli (or reduced basal flagellomeres) within the taxon. 4 — single terminal taxon having 4 or 5 anelli (or reduced basal flagellomeres) within the taxon.

**Transformation Series:** 2 — 1, 2\*, 4. CI = 33.

#### DISCUSSION:

**WORKING HYPOTHESIS:** Technically an anellus appears to be a greatly reduced (i.e., “ring-like”) flagellomere without ridge-like, multiporous plate sensilla (MPS). This must be considered an operational definition. All torymids have 8 flagellomeres of which at least the basal one is reduced to an anellus by this definition. Historically, anelli have been used to construct identification keys (e.g., Szelenyi 1957b) and to help define genera. Unfortunately, the “operational definition” has not been consistently applied, nor is it, in all cases, without its own set of problems.

In slide preparations of the type species of *Pseuderimerus* Gahan, for example, only the first flagellomere (= anellus) is “different” from the others: it has no setae or sensilla. Flagellomeres 2, 3, 4, and 5 are ring-like and have setae but no sensilla (and are thus “anelli” by operational definition), and flagellomeres 6, 7, and 8 have setae and sensilla. Properly we would say that *Pseuderimerus* has 5 anelli, but Gahan

(1933) stated that only the first was a “true ring joint,” and thus the genus has only one anellus. It is difficult enough to know what is technically (or even questionably) correct even when slides are made, but when viewed without benefit of slide preparation (Fig. 118) the distinction between anelli and reduced flagellomeres is nearly impossible to characterize. In *Erimerus* Crawford (sister taxon to *Pseuderimerus*) the first flagellomere is also “different” from the others, it has no sensilla but it does have setae, and the flagellomere is much elongated (i.e., not “ring-like”), being twice as long as wide. If diagnosed by the absence of setae, then *Pseuderimerus* has 1 anellus and *Erimerus* has none. If diagnosed by the absence of sensilla, *Pseuderimerus* has 5 anelli and *Erimerus* 1. If diagnosed by the criterion of “reduction” to a “ring-like” segment, then *Pseuderimerus* has 5 anelli and *Erimerus* has 0. Clearly there is a problem in interpretation and communication. Confounding the problem even further, however, is the fact that there are a half-dozen undescribed species of *Pseuderimerus* (as defined by several autapomorphies) in which the number of sensilla-less flagellomeres ranges from 2 to 5 depending on the species. All of these flagellomeres are “ring-like” in appearance.

In addition to problems apparent in counting anelli of different species, there are even problems within species. In series of *Pseudotorymus*, for example, a genus which is defined in part by its single anellus, I have seen a tendency in small specimens towards the reduction of flagellomere 2 into a sensilla-less “anellus” (Figs. 167-171, 175-176). Bouček (1978) also points out this same feature for an undescribed species of *Antistrophophlex* Crawford (now = *Microdontomerus*), and I have seen it in *Microdontomerus anthonomi* Crawford (Figs. 130-131) and *M. annulata* (Spinola) (Figs. 131-134). In small specimens of *Torymus obscurus* Breland, although flagellomere 2 became anellus-like in appearance, it did not lose its sensilla (Grissell 1976). Thus some specimens of a single species appear to have either 1 or 2 anelli, but the only “operational” distinction would be whether these flagellomeres lost their sensilla. This is not always readily apparent. I have even seen a single case where a paratype specimen of *Microdontomerus impolitus* Askew and Nieves (now = *Adontomerus*) had its left antenna (Fig. 129) with 2 anelli (by absence of sensilla) while its right antenna (Fig. 128) had only 1 anellus (by presence of sensilla). Clearly the use of this character in phylogenetic analyses must be considered with some reservation.

Just as the phylogenetic implications of the anelli have proven somewhat elusive in my study, similar unresolved results have been shown in the Eulophidae (Schauff 1991) or have been implied by reasoned avoidance (e.g., Eupelmidae, Gibson 1989). Even if a simple operational definition of anellus is used, that is, having no multiporous plate sensilla, it is not always easy to determine if a funicular is, in fact, an anellus or is merely a reduced funicular with obscure sensilla. To overcome this problem, I coded the states in three different ways during the working hypothesis stage. The first method was to ascertain all technically correct combinations of anelli, as defined by absence of MPS, and reduced funiculars and to code them accordingly. Thus, for example, an antenna with one anellus and one reduced flagellomere was coded as 1 + 1 but an antenna with two anelli was coded as 2. By this method I ended up with 8 states (Fig. 40, Character 2, left column). The second method was to code any reduction simply as a reduction and not to distinguish between anelli and funiculars. Thus, in the previous example, there would be only one state, namely 2, and it did not matter whether the two reduced funiculars were both anelli or one anellus and

one reduced funicular, or two reduced funiculars. By this method I ended up with 5 states (Fig. 40, Character 2, right column). The third method was simply to code all taxa as having only 1 or 2 anelli (by operational definition), with the hypothesis that any additional reductions in funiculars, regardless of what they were called, were uninformative.

In the first method after 21 analyses of the data, the condition of 2 true anelli was hypothesized to be the plesiomorphic condition for the outgroup. This immediately changed to 1 being primitive in *Megastigmus* and *Glyphomerus* at the base of the tree. Hypothetically, then, 2 anelli within Toryminae is a reversal to the primitive state of the outgroup. The second method with 20 analyses also resulted in the same hypothesis. The third method, after 3 analyses, was abandoned as uninformative based on a fourfold decrease in CI.

One additional experiment was conducted to attempt to resolve a problem that arose as a result of the second method of analysis discussed above. In this analysis (Stage 4) I compared the Wagner trees with the successive weigher trees to determine the difference in effect of weighted and unweighted data. The differences were significant in that the unweighted data placed the Megastigminae as a sister group to Toryminae, but the weighted data placed the Megastigminae in the middle of the tree thus creating even more paraphyly than already existed. Intuitively this latter placement is difficult to accept. By comparing states for each tree I determined that the anelli character was being weighted heavily and was producing the results found in the weighted trees. I ran the entire data matrix without reading the anelli character. The results after running both Wagner and weighted trees were similar, placing Megastigminae as the basal sister group to Toryminae. This also increased the CI of the Wagner trees from 51 (anelli read) to 55 (anelli unread) for the analyses. Eliminating the character of anelli increased the Wagner CI only by about 3%. The final tree for the working hypothesis (Fig. 37) is based on the absence of the anellar character.

In the transformation series developed from the last trees, states 1, 3, and 5 are each hypothesized as derived from state 2 with state 4 hypothesized to arise directly from 1. This hypothesis suggests that reductions in flagellar length occur in a non-linear fashion. That is, both 3 and 5 reduced flagellomeres are derived from the plesiomorphic state of 2 (outgroup), but 4 reduced flagellomeres arise from state 1, which requires first the enlargement of a flagellomere (from 2 reductions), then the subsequent reduction of 4 flagellomeres. In trying to establish some phylogenetic (as opposed to identification) value with the anelli, this data indicates that it may be too homoplasious a character on which to place much resolution of degree of relatedness.

ENDING HYPOTHESIS (Fig. 41, Character 2, cont'd.): In the ending analyses I adapted a convention of coding as follows. If a terminal taxon had species with 1 reduced basal flagellomere it was coded as state 1. If a terminal taxon had species with 2 reduced basal flagellomeres it was coded as state 2. If a single terminal taxon had species with differing numbers of reduced basal flagellomeres, I treated the reduction as a single character state for that group. For example, *Idiomacromerus* (= *Liodontomerus* of authors) had species with 2, 3, or 5 "anelli," as did *Eridontomerus* Crawford and *Torymoides* (no "4" was found in any of these taxa, but there is little reason to believe that it could not eventually be found). These taxa were coded as having state 2\* (this code is merely a convention and could have been called 2-4 to more accurately indicate the number of segments involved). The single terminal taxon

*Pseuderimerus* was found to have 4 or 5 "anelli" among its species and it was coded as a different state, 4. It could as well have been placed with 2\*, but at this point I was trying to establish the maximum number of potential categories of variation within a single terminal taxon. Because *Pseuderimerus* was defined by apparently reliable synapomorphies and appeared to represent a distinct lineage, it was characterized as state 4 for purposes of further study.

Based on the final transformation series, when considering pteromalids as the outgroup, state 2 was considered the primitive state, with states 1, 2\*, and 4 each derived independently from it. Within Torymidae, 1 reduced flagellomere was hypothesized as the primitive state with independent reductions (secondary reversals) considered as derived states.

In effect, neither the working hypothesis nor the ending hypothesis has provided much information for elucidating phylogeny. Anelli would not appear to be the first character of choice for establishing a phylogeny, and so I have adopted several purely practical approaches for using anelli in my generic analyses. If two terminal taxa agree *in all characters* except the anelli, I base my decision to either synonymize them or to recognize them as valid taxa on the following criteria:

**Geographic range:** Taxa that are widely allopatric (e.g., Nearctic, Australasian) are treated as distinct genera until demonstrated otherwise.

**Numerical size of taxon:** If two taxa each have a large number of species, I retain the generic name for both based on the philosophy that a complete study of the species is required to determine monophyly or paraphyly. This is obviously an operational decision, but to unite all taxa simply because I have not solved the problem of character state evolution would simply serve to create nomenclatural instability. By acknowledging that two groups are separated only by a difference in number of reductions in funiculars, I am attempting to maintain the most informative approximations of phylogeny.

## ANTENNAL CLUB

### Character 3 (Fig. 41)

#### STATES DESCRIPTION:

**Working and Ending Hypothesis:** *3Seg* — club formed of 3 flagellomeres indicated by distinct annulations that completely encircle club, no ventral micropilosity. *3Seg\** — club formed of 3 flagellomeres indicated by indistinct or poorly delimited annulations confined to dorsum of club, an area of micropilosity present ventrally. *1Seg* — club apparently formed of one segment, no annulations visible (probably 3 flagellomeres fused together, but possibly 2 are lost entirely), an area of micropilosity present ventrally.

**Transformation Series:** *3Seg* — *3Seg\**, *1Seg*. CI = 67 (working), 50 (ending).

**DISCUSSION:** With either Pteromalidae or *Megastigmus* as the outgroup there seems little doubt that a club formed of 3 distinct flagellomeres is plesiomorphic and a club formed by the fusion of 3 flagellomeres (or possibly the loss of 2, the structural morphology has yet to be studied) is apomorphic. Three flagellomeres were hypothesized by Gibson (1986) as the groundplan state for Chalcidoidea, but he pointed out that exceptions do occur in some cleonymine pteromalids. In Mymaridae a single club is

considered to be plesiomorphic (Schauff 1984), but this group is so phylogenetically removed from Torymidae that the evidence is of little direct consequence. A fused club (*1Seg*) arises in the palachine clade (nodes 22 and 23; Fig. 38), where it is hypothesized to be derived directly from the *3Seg* state. In the podagrionine clade (node 25; Fig. 38) the *3Seg\** state is also derived directly from the *3Seg* state. The presence of micropilosity on the ventral surface of the club appears to be correlated with the fusion (or loss) process. With the exception of a single taxon (*Mantiphaga* Ferrière: Podagrionini), micropilosity is associated only with the *3Seg\** and *1Seg* states.

#### MALE EYE

##### Character 4 (Fig. 39)

###### STATES DESCRIPTION :

Working and Ending Hypothesis: *Norm* — eye of “normal” size, postgenal area much narrower than width of eye. *Reduced* — Eye “reduced” in size, postgenal area as wide or wider than eye width.

**Transformation Series:** *Norm* — *Reduced*. CI (for both) = 100.

DISCUSSION : This character was not used at the generic level in previous revisionary work. The relatively long distance behind the eye of males of one species of *Pseuderimerus* was noted by its describer (Gahan, 1919a), but no mention has been made of this character for any taxa by subsequent workers. When I noted the same character in the only species of a presumed closely related genus, I attempted to quantify it. However, measurement of the width of the gena was not easy because of its curvature and the absence of a discrete posterior edge. The enlarged genal area is created by a reduced eye size, and this can be shown in illustrations and expressed qualitatively as two discrete character states. Females show no such development. Based on out-group comparison with Pteromalidae and *Megastigmus*, a narrow genal area (created by a “normal” sized eye) is plesiomorphic, whereas a wide genal area (created by a reduced eye) is apomorphic.

#### DORSAL SHAPE OF HEAD

##### Character 5 (Fig. 39)

###### STATES DESCRIPTION :

Working and Ending Hypothesis: *Trans* — head in dorsal view transverse, much wider than long. *Square* — head in dorsal view almost as long as wide. *Square\** — head in dorsal view intermediate between other states.

**Transformation Series:** *Trans* — *Square\**, *Square*. CI = 67 (working), 50 (ending).

DISCUSSION : This character was first used because the genus *Stenotorymus* was characterized as having a “subcubital” head (Bouček 1978). I subsequently discovered that “squarish” heads were evident in some palachines, some podagrionines, and in megastigmines. Previously I had seen the head shape used only at the species level in the genus *Torymus* (Grissell 1976). It seemed, however, that some attempt should be made to survey the character at the generic level. It was by no means easy to assay “squareness” even with specimens at hand. It is difficult to measure curved objects, and so I relied on subjective observation. The truly “square” head is found only in *Stenotorymus*, thus this state is autapomorphic. A somewhat intermediate state

(*Square\**) is found in the palachines and several podagrionines (*Pachytomoides* now = *Palmon* Dalman, *Podagrion* Spinola). The megastigmines are not consistent for this character, varying from transverse to *Square\**. From evidence provided by the tree, the transverse state is plesiomorphic with regard to Pteromalidae, but the *Square\** state, arising as it does at both the bottom of the tree (some megastigmines) and the top (several clades), seems too homoplasious to be of any phylogenetic value.

CLYPEAL APEX  
Character 6 (Fig. 41)

STATES DESCRIPTION :

Working and Ending Hypothesis: *Bilobed* — clypeus medially deeply emarginate with lateral edges lobed. *Emarg* — clypeus with slight median emargination but lateral edges barely evident. *Straight* — clypeus essentially straight and about at same level as ventral margin of head. *Toothed* — clypeus medially with tooth-like projection and lateral edges angulate. *Convex* — clypeus slightly convex and projecting but not much beyond ventral margin of head. *Enlarged* — clypeus greatly convex and projecting well beyond the ventral margin of the head. *Concave* — clypeus concave and with lateral margins somewhat angulate. *Recessed* — clypeus concave and with lateral margins produced into tooth-like structures.

**Transformation Series:** *Bilobed* — *Straight* — [*Convex* — *Recessed*, *Emarg*], *Toothed*, *Enlarged*, *Concave*. CI = 70 (working), 100 (ending).

DISCUSSION: The shape of the clypeal apex has been little-used in chalcidoid systematics except in the miscogasterine Pteromalidae. Heydon (1989) used the number, arrangement, and shape of denticles on the clypeal margin. In his analysis *Lamprotatus* was used as the most primitive of the five outgroup taxa selected to determine polarity for the states. I also used this genus as well as three other pteromalids for outgroup comparison. In my analysis the state *Bilobed* is considered provisionally plesiomorphic. Although I coded the taxa *Lamprotatus* and Megastigminae as *Bilobed*, this coding turns out to be too simple. *Lamprotatus* has a bilobed clypeus, but there is an auxiliary denticle on one of the lateral lobes and this creates the "... three asymmetrically arranged denticles" that Heydon described (1989) for the genus. This is obviously different than the bilobed condition found in *Megastigmus*. In spite of this error, the effect on the tree is of little consequence, because nearly all the states are autapomorphic. With the exception of the *Bilobed* state, none of the states of torymid clypeal structure are homologous to those described by Heydon (1989). The bilobed state is hypothesized to have arisen from the *Straight* state as are 3 additional states each of which is autapomorphic: *Concave*, *Enlarged*, *Toothed*. *Recessed* and *Emarg*, each autapomorphic, are derived secondarily through the *Convex* state which, itself, is derived from the *Straight* state.

MALAR KEEL  
Character 7 (Fig. 39)

STATES DESCRIPTION :

Working and Ending Hypothesis: *No* — no malar keel present. *Yes* — malar keel present (often accented by depressions on either side).

**Transformation Series:** *No* — *Yes*. CI (for both) = 100.

DISCUSSION: This is a simple 2 state character and the presence of the keel is a synapomorphy for *Rhynchotocida* Bouček + *Anneckeida* Bouček (Figs. 37E-node 27, 38E-node 19). The keel is not present in the outgroup nor any other member of the Megastigminae + Toryminae. It would appear to be derived from a modification of the malar sulcus.

#### WING VENATION

Character 8 (Fig. 42)

#### STATES DESCRIPTION:

Working Hypothesis: *Ptero* — marginal vein 1 to 2 times longer than stigmal vein, 0.8 to 2 times longer than postmarginal, stigma not enlarged, much shorter than stigmal vein. *Mega* — marginal vein 4 to 5 times longer than stigmal vein (not counting stigma), 0.8 to subequal in length to postmarginal vein, stigma enlarged, longer than wide, much longer than stigmal vein. *Mono* — marginal vein 2 to 6 (rarely slightly longer) times longer than stigmal vein, 1 to 3 times longer than postmarginal, stigma not enlarged, equal to or shorter than the stigmal vein (see also discussion below concerning this state). *Tory* — marginal vein 6 (rarely slightly less) to 12 or more times longer than stigmal vein, 3 to 7 times longer than postmarginal, stigma not enlarged, equal to or longer than the stigmal vein.

**Transformation Series:** *Ptero* — *Mega*, *Mono* — *Tory*. CI = 27.

Ending Hypothesis: *Ptero*, *Mega*, *Mono*, *Tory* as above. *Thaumat* — marginal vein about 3 times longer than stigmal vein, about 2 times longer than postmarginal, stigma not enlarged, subequal to stigmal vein, venation far removed from apex of wing (unique to this state). *Neopal* — marginal vein 3 to 5 times longer than stigmal vein, 1 to 3 times longer than postmarginal vein, stigma not enlarged, much shorter than stigmal vein, submarginal vein with coarse, elongated black setae, longer than tegula (unique to this state).

**Transformation Series:** *Mega* — *Ptero* — [*Mono* — *Thaumat*], *Tory* — *Neopal*. CI = 38.

#### DISCUSSION:

WORKING HYPOTHESIS: Wing venation has been used to some extent in delimiting genera, though no effort has been made previously to standardize comparisons across the literature. Numerous relative comparisons occur in the literature such as “stigmal vein short, but still developed” (Bouček 1978) or “marginal vein much shorter than submarginal” (Kamijo 1963). At first I attempted to organize the four wing vein parts into 3 quantitative characters based on ratios of veins with reference to the marginal vein. These ratios were: the length of the marginal vein divided by the length of the costal cell ( $MV/Cost$ ; the costal cell length is also a measure of the length of the submarginal vein), the length of the marginal vein divided by that of the stigmal vein ( $MV/Stig$ ), and the length of the marginal vein divided by the length of the postmarginal vein ( $MV/Pm$ ). After one analysis it appeared as if a study of wing venation based on subparts of the whole was of little practical application. First, there were no discontinuities in the data obtained for  $MV/Cost$  and  $MV/Pm$  and only two for

*MV/Stig*. Second, it was impossible to take consistent measurements even from the same specimen that did not overlap neighboring ratios. Essentially no discrete states could be detected by quantitative measures of separate parts. To reanalyze this problem qualitatively I drew the wing venations of all taxa (to the same size), overlaid these drawings (or actual specimens on the drawings through a drawing tube), and divided the taxa into 8 basic categories or types of venation. As the analysis progressed these states were finally reduced to 4 as indicated above under "STATES DESCRIPTION : Working Hypothesis." Although a few taxa did not fit these categories exactly, almost all could be placed to one of the four basic categories on the basis of the relationship of the stigmal vein to the marginal (exceptions are discussed under the taxa discussions).

Based on outgroup comparison, the state *Ptero* is considered primitive. The marginal and stigmal veins are generally about equal in length as is the postmarginal as well (exceptions occur, but the general appearance is similar to Fig. 54). Heydon (1989:195) hypothesized that in primitive pteromalids the marginal vein is shorter than the postmarginal and that in more advanced pteromalids the marginal vein is longer than the postmarginal. This agrees with the polarity as hypothesized above for states *Mono* and *Tory*. Darling (1988a:79) discussed the venation in the more derived Perilampidae and stated that a longer marginal vein than postmarginal occurs in the primitive genus *Perilampus*, and that a shorter marginal vein occurs in a more apomorphic genus such as *Krombeinius*. Darling's findings were tempered with caution (i.e., "both *Krombeinius* and *Perilampus* may be shown to have the plesiomorphic configuration"), so I do not consider this a serious contradiction to the hypothesis of Heydon's or my own.

Based on outgroup comparison with the pteromalids, an enlarged stigma is the apomorphic state. This is an autapomorphy for the Megastigminae, but otherwise lends little information to the study. The fact that in Megastigminae the marginal vein is somewhat shorter than the long postmarginal vein indicates a generally plesiomorphic wing by outgroup comparison. LaSalle (1987:7) hypothesized that an enlarged stigma was apomorphic within the Tanaostigmatidae. This may be taken as additional indication of the phylogenetic interpretation of this state, but the Tanaostigmatidae have no direct link to the torymids. The hypothesis that a short (to sessile) stigmal vein is apomorphic is indicated by the tree, but the states of *Mono* and *Tory* are sufficiently homoplasious as to suggest difficulty in using the character for phylogenetic purposes.

ENDING HYPOTHESIS (Fig. 38): After additional work on the above character states, it was necessary to add 2 new ones as discussed above. I also discovered that several taxa were coded incorrectly in the working hypothesis. The additional work increased the CI considerably. According to transformation series of both the working and ending hypotheses, the *Ptero* state is a retention at node 2, while the *Mega* state arises as an autapomorphy. In the ending hypothesis, *Tory* was derived from *Ptero* as was *Mono*. This disagrees with the working hypothesis in which *Tory* was derived from *Mono*. Again, however, the states are sufficiently homoplasious as to question their phylogenetic use. It is entirely possible that the states of *Mono* found in Microdantomerini (node 3) and Monodontomerini (node 14) are not truly homologous and that the states of *Tory* found in Torymini/Torymoidini (node 9), Podagroniini (node 25), *Palachia* Bouček (node 22), and *Chrysochalcissa* Girault (node 18) are



also not homologous. In the case of *Mono* this may be so, because in *Microdon-tomerini* the marginal vein is 2 to 4.5 times the postmarginal vein and in *Monodontomerini* it is 4 to 6.5. There is overlap, however, and I could not justify recognizing two states that overlapped in some taxa. In the case of *Tory* I could find no way to recognize discrete states for the taxa listed above.

### HIND FEMUR

#### Character 9 (Fig. 43)

##### STATES DESCRIPTION :

**Working Hypothesis:** *Simple* — hind femur with dorsal and ventral edges essentially parallel. *Angle* — ventral margin of hind femur with subapical angle. *Serrate* — ventral margin of hind femur with irregular, saw-like teeth, femur slightly enlarged in apical half. *Tooth* — ventral margin of hind femur with well-defined, subapical tooth, femur not noticeably enlarged. *Swollen* — ventral margin of hind femur with single, asymmetrically enlarged lobe that is slightly crenulate along ventral edge, femur enlarged. *Lobed* — ventral margin of hind femur with asymmetrically enlarged lobes, femur enlarged. *Bigteeth* — entire femur roundly enlarged, ventrally with one row of teeth on outside margin (teeth may be saw-like and numerous or enlarged and few. *2Rows\** — as for *Bigteeth*, but an inner row of bumps parallels outer row of teeth or an array of bumps is found. *2Rows* — as for *2Rows\** but an inner row of teeth (instead of bumps) parallels outer row of teeth. *Toothout* — ventral margin of hind femur enlarged medially with large, irregular teeth from middle to apex. *Neo* — as for *Toothout* except teeth saw-like and regular to apex. *2Teeth* — ventral margin of hind femur with 2 long, slender teeth near apex (smaller teeth may be present).

**Transformation Series:** *Simple* — *Serrate*, *Angle* — *Tooth* — [*Lobed* — *2Rows* — *2Rows\**], [*Bigteeth* — *Toothout* — *Swollen* — *Neo* — *2Teeth*]. CI = 79.

**Ending Hypothesis:** The only character state change was to combine states *Simple*, *Swollen*, and *Angle* into *Simple* (as defined below).

**Transformation Series:** *Simple* — *Serrate*, *Tooth* — *Lobed*, *Toothout*, [*2Rows* — *2Rows\**], [*Bigteeth* — *2Teeth* — *Neo*]. CI = 100.

##### DISCUSSION :

**WORKING HYPOTHESIS:** It might be deduced from the list of states and an examination of the figures that this character is a complex one. As with any structurally obvious and malleable character, a great deal of emphasis historically has been placed on the shape of the hind femur as an indication of generic (and even family) limits. In spite of this reliance, it is not always easy to assign a taxon to a group based solely on the structure of the hind femur. The distinction, for example, between *Simple* and *Angle* is not always apparent. The genera *Dimeromicrus* Crawford and *Torymoides* (synonymized by Bouček in 1988) differ only in that the former has a simple ventral margin and the latter has an angled margin. The same is true, in my opinion, for the genera *Pseudotorymus* and *Senegalella* Risbec, in which the former genus has a slight tooth-like angle while the latter is simple. Several genera (e.g., *Glyphomerus*, *Zophodetus* Grissell) have the ventral edge slightly protuberant apically and “nearly”

angulate and thus appear intermediate between *Simple* and *Angle*. There also may be some confusion between *Angle* and *Tooth*. I had difficulty placing several undescribed neotropical species that shared all the synapomorphies of *Zaglyptonotus* but in which the hind femur varied from *Simple* to *Angle* to *Tooth*.

Based on outgroup comparison the simple (unmodified) femur is undoubtedly plesiomorphic. As hypothesized by the most parsimonious transformation series, *Simple* gives rise independently to the conditions of *Serrate* and *Angle*. *Angle* then gives rise to *Tooth* which gives rise to *Bigteeth*. This transformation is evolutionarily sensible, that is, a simple femur evolves an angulation that becomes a tooth; the femur enlarges and more teeth are added. In this case the *Tooth* lineage also gives rise to the states of *Lobed*, *2Rows*, and *2Rows\**. The latter two states appear to be convergent with the *Bigteeth* state; however, they differ by having an additional, inner row of teeth or an array of raised bumps in addition to the outer row of distinct teeth. It would seem intuitively more direct for the *2Rows/2Rows\** states to be derived from the single row state (*Bigteeth*), but that is not supported by the tree. Also, the *Toothout* state is hypothesized to have arisen from a *Bigteeth* ancestor, but morphologically *Toothout* is somewhat intermediate between *Tooth* and *Bigteeth*. It seems just as likely that it arose independently from the *Tooth* state, but again this possibility it not supported by the tree.

ENDING HYPOTHESIS: In this set of analyses, the states of *Angle* and *Swollen* were combined with *Simple*. Considering the evidence given above for *Torymoides/ Dimeromicrus*, *Zaglyptonotus*, and *Glyphomerus* these states were not easily differentiated. Recoding and rerunning the data increased the CI of the character substantially. The transformation series, however, was not altered substantially. The state of *Toothout* (i.e., *Exopristus* Ruschka) is derived from *Tooth* (not *Bigteeth*), the states *2Rows* and *2Rows\** are derived directly from *Tooth* (not though *Lobed*), and the polarity of *2Teeth* and *Neo* is reversed. The change in position of *Toothout* is noteworthy, especially as discussed in the last paragraph.

#### HIND-TIBIAL SHAPE

##### Character 10 (Fig. 44)

##### STATES DESCRIPTION:

Working and Ending Hypothesis: *Straight* — hind tibia essentially straight from base to apex. *Curved\** — hind tibia slightly bent basally, but apical half straight. *Curved* — hind tibia curved from base to apex.

**Transformation Series:** *Straight* — *Curved*, *Curved\**. CI = 50 (working), 33 (ending).

DISCUSSION: A *Straight* hind tibia is considered plesiomorphic by outgroup comparison. The *Curved* state is hypothesized to have arisen directly from the *Straight* state in two independent lineages (Fig. 38): once in the monodontomerine-clade (node 16) and once at node 24. It is also hypothesized to have arisen in *Neopalachia* Bouček from the putatively intermediate state *Curved\** (node 21). This latter state arises twice from the *Straight* state, once in *Exopristus* and again at node 21. The character is homoplastic and is perhaps too subjective in its intermediate state (i.e., *Curved\**) to be correctly interpreted. It seems intuitively correct to assume that the curvature of the hind tibia is directly correlated to the enlargement of the hind femur, i.e., as the femur

increases in size and becomes more rounded, the tibia must curve to fit around it. It might have been possible to treat the hind femur and hind tibia as a single functional complex but I did not attempt this because evaluation of the curvature of the tibia is somewhat subjective. By combining this character with femur shape I would have compromised the interpretation of both.

#### HIND-TIBIAL APEX

Character 11 (Fig. 44)

##### STATES DESCRIPTION :

Working and Ending Hypothesis: *Trun* — apex of hind tibia truncate at right angles, equal in diameter to tibia, spur(s) placed at ventral corner. *Diagonal* — apex of hind tibia diagonally truncate, ventral corner an acute angle but not noticeable produced and truncation subequal to width of tibia, spurs placed at ventral corner. *Subpoint* — apex of hind tibia diagonally truncate, ventrally produced into acute angle, length of truncation subequal to cross section of narrow part of tibia, spur placed at apex of truncation. *Pointed* — apex of hind tibia diagonally truncate, ventrally produced into greatly acute angle, length of truncation longer than 2 or 3 times cross section of tibia, spur placed at base of truncation near basitarsus.

**Transformation Series** *Trun* — *Diagonal*, [*Subpoint* — *Pointed*]. CI (both) = 75.

DISCUSSION : The condition of the apex of the hind tibia varies independently from the shape of the hind tibia. Thus one can find a curved hind tibia that is truncate (e.g., *Rhynchotricida*) as well as pointed (e.g., *Podagrion*). For this reason the shape of the apex was treated as a character distinct from the overall shape of the hind tibia. The state *Trun* is hypothesized as ancestral by outgroup comparison. It is hypothesized to have given rise to the state *Diagonal* (autapomorphic for *Neopalachia*), and to *Subpoint* (node 24; Fig. 38) which arose independently in the monodontomerine and podagrionine clades. This follows also the pattern of the hind-tibial curvature. The *Pointed* state is hypothesized to have arisen once directly from the *Subpointed* state.

#### HIND-TIBIAL SPUR INSERTION

Character 12 (Fig. 44)

##### STATES DESCRIPTION :

Working and Ending Hypothesis: *Apex* — hind-tibial spurs arise at the apex. *Preapex* — hind-tibial spurs arise some distance from the apex.

**Transformation Series:** *Apex* — *Preapex*. CI = 100 (working), 50 (ending).

DISCUSSION : In chalcidoids the hind-tibial spurs normally arise at the apex of the tibia. This is certainly the plesiomorphic condition based on outgroup comparison and is the typical state found in a vast majority of Chalcidoidea. In *Perissocentrus* (node 15; Fig. 38) and *Aloomba* Girault (node 10; Fig. 38) the spurs are some distance removed from the apex (the exact distance is a species level character). In the working hypothesis (Fig. 37) these 2 taxa were placed in the same clade based on this character and the length of the spurs (next character). According to the ending hypothesis, these characters are considered homoplastic, and the taxa are placed in separate clades. So

far I have found no intermediate states for this character. Interestingly, this condition occurs in species found only in Australia (*Aloomba*) and the Neotropics (*Perissocentrus*). It should be noted that in Podagrionini the hind-tibial spur always arises at the apical truncation of the tibia although it may be found proximal to the basitarsus or some distance distad of it (see previous character). This was coded as part of the hind-tibial apex character because in that case the spur placement was always associated with the tibial apex and its shape (i.e., only found in the subpointed/pointed states).

### HIND-TIBIAL SPUR LENGTH

Character 13 (Fig. 44)

#### STATES DESCRIPTION :

Working Hypothesis: *Norm* — 2 spurs subequal in length or shorter than apical width of hind tibia, fine or bristle-like. *Thick* — 2 spurs subequal in length to hind tibia, noticeably thickened. *Long* — 2 spurs much longer than length of apical width of hind tibia, bristle-like.

*Transformation Series: Norm — Thick, Long. CI = 50.*

Ending Hypothesis: Same states as above plus: *Spine* — 2 spurs slightly longer than apical width of hind tibia, spine-like (wiry). *Wide* — 1 spur (or possibly 2 fused) subequal in length to apical width of hind tibia, thick and chisel-like.

**Transformation Series:** *Norm — Long, Spine, Thick, Wide. CI = 67.*

DISCUSSION: By outgroup comparison the *Norm* state is plesiomorphic among toymids. The *Thick* state is autapomorphic for *Rhynchotocida*. The *Long* state independently arises in 3 taxa *Perissocentrus*, *Aloomba*, and *Zaglyptonotus*. In the working hypothesis (Fig. 37) *Platykula* Huber + *Platykula*(A) was defined by the state *Long* but this was in error. The hind-tibial spurs in this clade are long, but they are not homologous to the state *Long* found in the taxa just mentioned. That is, the spurs are somewhat longer than the apex of the tibia, but they are constructed like wiry, black spines rather than the greatly elongate, pale colored spurs of the other taxa. The new state *Spine* is autapomorphic for *Platykula*. Possibly *Thick* should not be considered as a state analogous with length, but it is an expression of the condition of the spur and is autapomorphic as well, so that its inclusion here seems to pose little problem. The state *Wide* is autapomorphic for *Chalcimerus*, and the thick, chisel-shaped spur might conceivably be the result of the fusion of 2 spurs, but this is unknown. Certainly the spur of this genus is unlike the single spur found in the next clade up the tree (node 25; Fig. 38). All variations of the spur are considered to be derived from the *Norm* state. The spurs were analyzed separately from the shape of the hind tibia, the insertion on the hind tibia, or the numbers of spurs because they appear to vary independently of the hind tibia itself. For example, long spurs may be found inserted at the apex or preapically.

### HIND-TIBIAL SPUR NUMBER

Character 14 (Fig. 44)

#### STATES DESCRIPTION :

Working and Ending Hypothesis: *One* — hind tibia with one apical spur. *Two* — hind-tibia with two spurs, one of which may be slender and difficult to see.

**Transformation Series:** *Two — One. CI (both) = 50.*

DISCUSSION: Two apical spurs is considered the groundplan for torymids based on outgroup comparison. The loss of one spur is hypothesized to have occurred twice (Fig. 38): once at node 6 and once at node 24. In several cases it was not easy to ascertain the correct number of spurs. This is because one of the spurs occasionally may be extremely small and difficult to see (e.g., *Idiomacromerus*). In the working hypothesis, I first coded state *Two* as two states, with *TwoA* being 2 obvious spurs and *TwoB* being 1 obvious and 1 reduced spur. This, however, is an artificial approach, because there are still two spurs present. In some cases, for example extremely tiny specimens of *Liodontomerus* (now = *Idiomacromerus*), the second spur is merely relatively small because everything is small. In others, however, such as Palachiini (node 21), the second spur is tiny in spite of the fact that the adults are fairly large. I found in trying to code the states qualitatively that I could not be consistent in my definition, and as a result I was continually changing my mind about what to call something. I therefore feel it is better to code the number of spurs as absolute states rather than to try to create qualitative states that are impossible to define or to apply consistently.

#### FRENAL LINE

Character 15 (Fig. 42)

#### STATES DESCRIPTION:

Working and Ending Hypothesis: *Yes* — transverse line present on distal third of scutellum. *No* — no transverse line present on distal area of scutellum (an indentation might be seen with some difficulty or in some lights, but no well-defined line is present).

**Transformation Series:** *Yes* — *No*. CI = 13 (working), 17 (ending).

DISCUSSION: The frenal line with relation to Pteromalidae (Working Hypothesis) is plesiomorphic but apomorphic with relation to Megastigminae (Ending Hypothesis). Bouček (1988:14) suggested that the line was “probably” plesiomorphic. Unfortunately the line is homoplasious and of little practical use in understanding the phylogeny of torymids. It can be extremely clear-cut and deep (as in the monodontomerine-clade, node 14, Fig. 38), or it can be ephemeral and barely visible in some lights, or it can be absent. In the latter case a frenal area may still be delimited by obviously different sculpture than the basal part of the scutellum. This makes the frenal line difficult to code, and I made several attempts before I arrived at the states outlined above. My analysis suggests that this character is so homoplasious as to be useless in an analysis of phylogeny. Unfortunately, when present, the line has served as a ready beacon for taxonomic distinction. In the case of *Syntomaspis* and *Torymus*, for example, the line has readily diagnosed two broad groupings of taxa, yet I have seen closely related species that can scarcely be distinguished from each other except by the presence or absence of a frenal line (Grissell 1976). In my experience the frenal line is barely useful in distinguishing species groups, and its use as a generic character seems dubious at best.

#### NOTAULI

Character 16 (Fig. 42)

#### STATES DESCRIPTION:

Working and Ending Hypothesis: *Yes* — notauli present as well-defined furrows.

*Faint* — notauli present but as mere depressions or indentations, often difficult to see, or present as anterior grooves that fade out posteriorly.

**Transformation Series:** *Yes* — *Faint*. CI = 14 (working), 25 (ending).

DISCUSSION: The presence of notauli is considered plesiomorphic with reference to the outgroup. This also seems to be the consensus of workers in the Chalcidoidea (Schauff 1984; Gibson 1989; LaSalle 1987). Gibson (1985) noted that notauli are “undoubtedly a groundplan character for Hymenoptera.” Unfortunately, coding this character has not proven easy. The *Yes* state is fairly unambiguous, and the notauli are complete and readily visible as distinct grooves. In my first coding of the data, the current *Faint* state was tested as three separate states, including 1) notauli visible anteriorly but not posteriorly, 2) notauli visible, with difficulty, as extremely fine lines, and 3) notauli indicated merely as depressions in the scutum. I found that I could not consistently code taxa for these states, and regardless of my coding they were so homoplasious that little insight has been gained from their use.

## RELATIONSHIP OF NOTAULI TO SCUTOSCUTELLAR SUTURE

Character 17 (Fig. 42)

### STATES DESCRIPTION:

Working and Ending Hypothesis: *Meet* — the notauli posteriorly meet the scutoscutellar suture anteriorly. *No* — the notauli posteriorly are laterally outside the anterior edge of the scutoscutellar suture.

**Transformation Series:** *No* — *Meet*. CI (both) = 100.

DISCUSSION: An attempt was first made to analyze this character by measurement, that is, to compare the ratios of the distance between the scutoscutellar sutures anteriorly and the distance between the anterior of one suture and the posterior of the closest notaulus. This proved difficult because the lateral edges of the scutoscutellar sutures are difficult to pinpoint. When all measurements were taken, there proved to be no discontinuities between them. The measurement approach was abandoned in favor of a qualitative approach in which the scutoscutellar suture either met the notaulus or it did not. Under this division the state *Meet* was autapomorphic for *Palachia*. *No* is considered the plesiomorphic state by outgroup comparison.

Gibson (1989) discussed the relationship of the notauli to the transscutal articulation and hypothesized that widely separated notauli were plesiomorphic based on outgroup comparison to Pteromalidae. His illustrations correspond relatively well to the *Meet* state described above although he was not describing the character as I have used it. Although he treated this as the plesiomorphic condition, its use does not conflict with my interpretation, because all members of the groups he studied are probably apomorphic with regard to torymids.

## PROPODEUM

Character 18 (Fig. 45)

### STATES DESCRIPTION:

Working Hypothesis: *One* (Figs. 388, 392) — with strong, complete median carina attached to developed nucha and dorsal margin of propodeum; carina projects from surface of propodeum, spiracular sulcus evident and reaching (or curved

towards) nucha, callus convex and setose. *Two* (Fig. 412) — with two distinct, parallel submedian carinae present, spiracular sulcus evident and reaching (or curved towards) nucha, callus convex and setose. *Nocarín* (Fig. 390) — with no median carina, or, if present, a weakly developed, ephemeral line not much raised above the surface of the propodeum, or several incomplete, ephemeral carinae present (the propodeal surface may be smooth or heavily reticulately sculptured), spiracular sulcus evident and reaching (or curved towards) nucha, callus convex and setose. *Modified* (Fig. 394) — this is essentially state *One* with some modification such as foveae (e.g., *Monodontomerus* Westwood) or many strong carinae paralleling the median carina (e.g., *Perisocentrus*). *Chalci* — with multiple carinae irregularly placed over surface of propodeum, spiracular sulcus evident and reaching (or curved towards) nucha, callus convex and setose. *Multi* (Fig. 396) — with or without carinae; if present, oriented somewhat transversely across propodeum, which is somewhat elongate in the axis of the body; spiracular sulcus absent or, if present, oriented to lateral corner of propodeum; callus absent (a flattened, asetose area rarely may be present). *Propal* — without carinae, propodeum elongated in the axis of the body and projecting posteriorly as narrowed neck; spiracular sulcus absent or, if present, oriented to lateral corner of propodeum; callus absent. *Zopho* — propodeum structurally modified, with carinae that define faceted sections, scallops, and depressions (spiracular sulcus and callus condition unknown).

**Transformation Series:** *One* — *Nocarín* — *Modified*, *Zopho*, *Multi*, *Two*, *Chalci*, *Propal*. CI = 70.

Ending Hypothesis: States as above except *One* deleted and 4 states added as follows: *One\** — polymorphic state for terminal taxon with both *Nocarín* and *One* states. *Steno* — without carina, propodeum elongated in axis of body, spiracular sulcus reaching to hind margin of propodeum about mid-way between nucha and lateral corner, callus evident, flattened, with setae. *Palach* — without carina, propodeum slightly elongated in axis of body, spiracular sulcus absent, callus absent. *Tory* — This is *Nocarín* state with posterolateral corners sharply angled.

**Transformation Series:** *Nocarín* — *One\**, *Steno*, *Modified*, *Zopho*, *Multi*, *Two*, *Chalci*, *Propal*, *Palach*, *Tory*. CI = 79.

#### DISCUSSION :

**WORKING HYPOTHESIS :** This character proved difficult to elucidate and underwent three revisions to create the working transformation series given above. The primary problem was delimiting states involving the *One* and *Nocarín* conditions. In some cases a strong central carina may be present (e.g., *Monodontomerus*), and in others a weak or broken carina is present (e.g., *Paraholaspis* Masi). In several groups weak and incomplete multiple carinae are present (e.g., *Microdontomerus*, *Erimerus*), but these are easily overlooked by the casual observer as they appear merely as surface wrinkles. In my original character analysis, I coded the presence or absence of propodeal foveae as a separate character. However, after several analysis it was apparent that, when present, the foveae were always associated with the presence of a median carina, and I ultimately combined the characters into one.

By outgroup comparison the plesiomorphic condition is hypothesized to be a single, median carina. In perilampids Darling (1988a) found a distinct "median ridge" to be plesiomorphic relative to the lack of a ridge. The *Nocarín* state arose from a loss of the central carina and from this arose independently the other recognized states. *Zopho* and *Chalci* are each autapomorphic. *Two* is synapomorphic for *Ditropinotus* + *Eridontomerus*, *Modified* is synapomorphic for the monodontomerine-clade (with one reversal), *Multi* is synapomorphic for the podagrion-clade, and *Propal* is synapomorphic for the palachine-clade with the exception of the genus *Palachia*. This latter genus proved difficult to code, and I ran the analysis with the state coded as a question mark for the taxon.

ENDING HYPOTHESIS: After the above analysis was complete, I restudied the propodeal condition and added 3 more states which were autapomorphic: *Steno* (for *Stenotorymus*), *Tory* (for *Torymoidellus*), and *Palach* (for *Palachia*). A fourth state, *One\**, replaced *One* for single terminal taxa that combined *Nocarín* and *One* as a result of the synonymies proposed during the working hypothesis phase. Only *Microdontomerus*, *Platykula*, and *Zaglyptonotus* have the state. With *Megastigmus* as the outgroup, all states are considered to be derived from the *Nocarín* state. Clearly this is not very informative.

#### HIND-COXAL SETAE

Character 19 (Fig. 46)

##### STATES DESCRIPTION:

Working and Ending Hypothesis: *No* — hind coxa with no setae dorsally. *Yes\** — hind coxa dorsally with a few, widely spaced, long setae. *Yes* — hind coxa dorsally more or less densely covered with short setae.

**Transformation Series:** *Yes* — *No*, *Yes\**. CI = 20 (working), 19 (ending).

DISCUSSION: This character has not been used to distinguish genera in torymids — apparently for good reason. Because it is used in pteromalids as a generic character (e.g., Graham 1969), I thought perhaps it might have some value in torymids. By outgroup comparison the presence of dense, short setae is hypothesized as the plesiomorphic state. This character is so homoplasious that its use in reconstructing phylogeny is debatable. In my working hypothesis the absence of setae (*No* state) was coded as a question mark (as discussed under the occipital carina above). I also discovered that my coding of the states was inconsistent for the working hypothesis. For both reasons, I do not discuss coxal setae in the working hypothesis — it would be a waste of time. I do include the character states, after a reexamination of all taxa at one time, in the ending hypothesis.

#### METASTERNUM

Character 20 (Fig. 47)

##### STATES DESCRIPTION:

Working and Ending Hypotheses: *Crypto* — anterior edge of propodeal foramen placed either midway between anterior and posterior margins of hind-coxal foramen or slightly closer to posterior margin, laterally separated from each



other by a narrow area, metasternal area a square or transverse strip from half as long (anterior to posterior) as diameter of propodeal foramen to nearly as long, no metasternal shelf present. *Neopal* — anterior edge of propodeal foramen placed far posteriad of hind-coxal foramina, laterally separated from each other by a wide area, propodeum projecting posteriorly as a curved neck extending well beyond the bases of the hind coxae, metasternal area much longer than diameter of propodeal foramen, short metasternal shelf above midcoxae. *Palachia* — anterior edge of propodeal foramen placed about midway between anterior and posterior of hind-coxal foramina, laterally separated from each other by a narrow area, metasternal area shorter than diameter of propodeal foramen, a carina connects propodeal and hind-coxal foramina, metapleuron and metasternum not distinctly separated along anterior margin of latter, long metasternal shelf above midcoxae. *Chalci* — anterior edge of propodeal foramen placed closer to posterior edge of hind-coxal foramina than anterior, laterally separated from each other by a relatively wide distance, metasternal area (not including narrow translucent area surrounding each hind-coxal foramen) nearly square and slightly longer than diameter of propodeal foramen, a short carina connects propodeal and hind-coxal foramina, no metasternal shelf present; *Micropod* — forward edge of propodeal foramen placed closer to posterior edge of hind-coxal foramina than anterior (essentially touching an imaginary line drawn across the posterior edge of hind-coxal foramina), laterally separated from each other by a wide area, metasternal area between hind-coxal foramina transverse, wider than diameter of hind-coxal foramen, a short carina connects propodeal and hind-coxal foramina, metasternal shelf above midcoxae. *Podag* — propodeal foramen placed posteriad with respect to hind-coxal foramina (not touching an imaginary line drawn across the posterior edge of hind-coxal foramina), laterally separated by a wide area, metasternal area well developed and sclerotized and much longer than diameter of propodeal foramen, a lateral carina connects propodeal and hind-coxal foramina, metasternal shelf above midcoxae. *Mono* — forward edge of propodeal foramen placed closer to posterior edge of hind-coxal foramina than anterior, laterally scarcely separated, metasternal area narrowly longitudinal, subequal in length (anterior to posterior) to diameter of propodeal foramen, no metasternal shelf present.

**Transformation Series:** *Crypto* — *Mono*, [*Neopal* — *Palachia*], [*Chalci* — *Podag* — *Micropod*]. CI = 75 (working), 100 (ending).

**DISCUSSION:** This character was first proposed to help establish generic limits between *Podagrion* and *Pachytomoides* (now = *Palmon*) (Grissell and Goodpasture 1981). Subsequently it was used in several genera of pteromalids (Grissell 1983). This is the initial application of the character across the spectrum of Torymidae, and it is a complex character. My understanding of it is by no means exhaustive, and I am certain that additional analyses would prove helpful.

The basic hypothesis proposed by the transformation series is that closely spaced, abutting metasomal and hind-coxal foramina are plesiomorphic (e.g., *Crypto*), and that widely spaced foramina indicate apomorphy (e.g., *Podag*). Within members of a pteromalid subfamily previously studied (Grissell 1983) this also appears to hold true. More primitive genera of Pteromalinae (*Dinotiscus*, *Rhopalicus*) have the foramina

closer together than do putatively more advanced genera (*Pteromalus*, *Mesopolobus*).

Based on outgroup comparison, the *Crypto* state is hypothesized as plesiomorphic. *Mono*, *Chalci*, and *Neopal* are each hypothesized to have arisen independently from *Crypto*. *Chalci* gives rise to *Podag* and *Micropod*, and *Neopal* gives rise to *Palachia*. This last-named change contradicts the above suggested hypothesis, because narrow-spaced *Palachia* is derived from wide-spaced *Neopal*. Both, however, appear to be derived from *Crypto* based on the widened metasternal shelf. *Palachia* appears to be a modified reversal from *Neopal*.

The number of states I have used is, perhaps, too few especially within the podagrionine and monodontomerine clades. For example, within the monodontomerine-clade (*Mono* state) the metasternal area between the hind coxae is narrow compared to the *Crypto* state. There are, however, several interpretations of "narrowness." The most extreme condition is that of *Oopristus* and *Anneckaida*, wherein the propodeal foramen is much reduced relative to the hind-coxal foramen, and the metasternum is a mere strut-like sclerotization. The typical *Mono* state is somewhat intermediate between the *Zaglyptonotus* and *Oopristus* conditions. Somewhat similar in appearance is *Zaglyptonotus* in which the metasternum is a narrow carina that continues around from the hind-coxal foramen and has a wide, translucent lamelliform extension on either side. These extensions are probably part of the metasternum, but this is not known for certain.

The situation in the *Podag* state is analogous to that of the *Mono* state with differences in the expression of distances between foramina and placement and number of carinae. *Podagrion* is the most extreme example of the state, in which the propodeal foramen is separated from the hind-coxal foramina by a large, well-sclerotized flat plate with a single median carina. The *Micropod* state, however, is somewhat closer to the plesiomorphic condition of *Crypto*, because the propodeal foramen is only slightly posteriad of the hind-coxal foramina and are separated by a relatively narrow distance from them.

When using pteromalids as the outgroup for the working hypothesis, the states were easily coded as *Crypto* for the primitive taxa (*Lamprotatus*, *Hemadas*, *Janssoniella*), but the states were variable for Pteromalinae, and I coded the state as questionable. When using *Megastigmus* as the outgroup for the ending hypothesis, I coded the state as a question mark. Based on species of *Megastigmus* (Fig. 387) the metasternum has a widely transverse median area (i.e., the hind-coxal foramina widely separated), and the propodeal foramen is anteriorly placed with respect to the hind-coxal foramina. The state is autapomorphic for *Megastigmus*, and it would appear to be primitive, as outlined above, based on the close proximity of propodeal foramen and hind-coxal foramina.

## METAPLEURAL MARGIN

### Character 21 (Fig. 46)

#### STATES DESCRIPTION :

Working Hypothesis: *Straight* — front margin of metapleuron straight. *Sinuate* — front margin of metapleuron produced into mesepimeron.

**Transformation Series:** *Straight* — *Sinuate*. CI = 100.

Ending Hypothesis: States as above, but one new state added: *Intermed* — anterior

margin of metapleuron essentially straight, posterior margin of mesepimeron sinuate and raised above the anterior margin of the metapleuron which lies partially hidden underneath.

**Transformation Series:** *Straight* — *Intermed*, *Sinuate*. CI = 100.

DISCUSSION: Based on outgroup comparison, there is no doubt that the straight front metapleural margin is plesiomorphic and that the produced front margin is apomorphic. The intermediate state (*Intermed*) is found only in *Thaumatorymus*, and although it appears as in typical Toryminae of authors (Torymini of this study), its morphology is the reverse of that found in the tribe. It is the only taxon of questionable status with regard to this character and was not included in the working hypothesis. Its inclusion in the ending hypothesis posed no problems, but neither did it elucidate the situation. *Intermed* is hypothesized to be derived from *Straight*, but so is *Sinuate*. I expected a straight-forward transformation, but this was not substantiated by the results. Taxa with the obviously produced metapleuron (i.e., *Sinuate*) have historically been defined as the subfamily "Toryminae" of authors, and the state is presumed autapomorphic for the entire grouping of nearly 350 species and 11 genera. While there is no doubt that this is true, there is also little proof that this state defines a monophyletic unit. I used *Torymus*, by far the most speciose genus, as an exemplar to define the taxon in the broad sense (i.e., Toryminae of authors).

#### TERGAL EMARGINATIONS

Character 22 (Fig. 46, for ending hypothesis)

##### STATES DESCRIPTION:

Working Hypothesis: 0 — terga without emarginations on posterior margin, Mt2 especially rigid and "shell-like," never laterally compressed or folded medially. 1 — 1 tergum, Mt2 distinctly emarginate on posterior margin. 2 — 2 terga, Mt2-3, deeply emarginate on posterior margins. 2A — Mt2-3 greatly elongate and distinctly emarginate on posterior margins. 3 — 3 terga, Mt2-4, distinctly emarginate on posterior margins. 3A — 3 terga, Mt2-4, distinctly emarginate on posterior and lateral margins. 4 — 4 terga, Mt2-5, with emarginations either shallow or deep. *Palach* — 4 terga, Mt2-5 with emarginations and laterally flattened.

**Transformation Series:** 0 — 1, [2 — 2A], [3 — 3A], 4, *Palach*. CI = 44.

Ending Hypothesis: As above, but: 1/2 — in terminal taxon, 1 or 2 terga (Mt2 or Mt2-3) slightly to distinctly emarginate on posterior margins (this combines and redefines elements of 1 and 2 above); 1/4 — in terminal taxon, 1, 2, 3, or 4 terga (Mt2-5) distinctly emarginate on posterior margins (this combines elements of 1, 3, and 4 above).

**Transformation Series:** 0 — [1/2 — 2A, 1/4, 4], 3A, *Palach*. CI = 55.

DISCUSSION: The coding of tergal emarginations proved extremely difficult. I tried 6 different methods of coding ranging from 2 characters (relative lengths and array of emarginations) with 10 states in the beginning to one character with 3 states in intermediate analyses to the final recognition of 7 states. To arrive at these states I plotted all known tergal patterns diagrammatically and then grouped them according to the

least number of discrete states I could produce. Even so, it was often difficult to tell the difference between no emarginations (0) and a slight indentation in the posterior margin of Mt2 (1). In some analyses I ran the 0 condition as a composite of 0 + 1 with scarcely any improvement of the CI. I used the working hypothesis character states as a best-guess estimate of character-state evolution. After making taxonomic decisions based on all data and the working hypothesis tree (Fig. 37), I reanalyzed the states and combined 1 and 2 into a single state. Based on the synonymy of *Paraholaspis* with *Microdontomerus* I reassessed the states for the united taxon and created a new state for it in which species have either 1 or 2 or 1-4 emarginations.

A simple, unincised tergum is hypothesized as the groundplan based on almost all hymenopterous insects (e.g., Symphyta, Proctotrupoidea, Ichneumonoidea, Aculeata) and the pteromalid outgroup. In fact, chalcidoids seem to be one of the few hymenopterous groups where emarginate terga occur fairly frequently. In the ending hypothesis (Fig. 38) Megastigminae (node 1) and basal elements of Toryminae are hypothesized to have developed emarginations (1/2) in terga (from the unemarginate state (0) of the pteromalid outgroup). From 1/2 arose the states of 2A, 1/4, and 4 which are variations in the number of emarginate terga. State 0 is hypothesized to have arisen at node 12 as a reversal from 1/2 and to have given rise to the states of 3A (node 25) and *Palach* (node 22). In state 1/2 some taxa are found which create difficulties in precise coding because the terga are thin and liable to lateral compression. With these taxa it sometimes becomes subjective whether to call the terga emarginate or entire. If the terga are laterally compressed they may appear emarginate, if not then they appear entire. In any event, Mt2 is not shell-like, or rigid, but is usually thin and somewhat laterally collapsed or at least asymmetrical. States 1 and 2 were combined into a single character based on the working hypothesis, as were 1 and 4 to try to resolve this problem. Although the CI of the character increased I would advise against placing great faith in its soundness because of its difficulty in coding and its degree of homoplasy.

#### EXSERTED CERCI ON METASOMAL TERGUM 8

Character 23 (Fig. 46)

##### STATES DESCRIPTION :

**Working and Ending Hypothesis:** *No* — cercus arises on sclerotized portion of apparent metasomal tergum 8 (Mt8) or Mt8+9 (if fused = syntergum) (rarely, in some Eupelmidae, cercus situated on membranous area between nearly fused Mt8 and 9); cercus nearly always bump-like, not exserted. *Yes* — cercus arising on membranous area at lateral margin of Mt8, always projecting from surface as a narrow cylinder.

**Transformation Series:** *No* — *Yes*. CI = 100 (not used in ending hypothesis).

**DISCUSSION :** Exserted cerci (sometimes called pygostyles) are hypothesized by outgroup comparison to be apomorphic compared to the normal, bump-like state. All Torymidae have exserted cerci, but the condition is also found in some Pteromalidae (*Cea*, Chromeurytominae), Eulophidae (*Entia*), and Agaonidae (*sensu* Bouček 1988). In the case of *Entia*, which has no known relationship to the Torymidae, the elongation of the cerci certainly must be the result of convergent or parallel evolution. The

same may be said for its occurrence in *Cea* and Chromeurytominae, but in this case the relationship of Torymidae to Pteromalidae is not as distant as that with Eulophidae. Both *Cea* and Chromeurytominae have Mt8 and Mt9 modified and different from other pteromalids, but the condition is also different from torymids in the placement of the cerci. The cercus character was used in the working hypothesis to establish monophyly of Torymidae. In the ending hypothesis this character was not needed, as *Megastigmus* was hypothesized as the outgroup.

#### ARTICULATED METASOMAL TERGUM 9 (Mt9)

Character 24 (Fig. 46)

##### STATES DESCRIPTION :

Working and Ending Hypothesis: *No* — metasomal tergum 9 (Mt9) absent (actually fused with Mt8 and not visible = syntergum) or if visible as a separate sclerite then broad basally and separated from posterior of Mt8 only by a narrow suture. *Yes* — Mt9 a free sclerite narrowed basally and separated from posterior of Mt8 by a membranous region.

**Transformation Series:** *No* — *Yes*. CI = 100 (not used in ending hypothesis).

**DISCUSSION :** The apparent absence of Mt9 (created by the fusion of Mt8+9) or the presence of Mt9 as a sclerite which is broad basally and separated from the posterior of Mt8 by a narrow suture is hypothesized as the primitive state. The presence of Mt9 as a free sclerite which is narrowed basally and separated from the posterior of Mt8 is hypothesized to be the apomorphic state. Gibson (1989) proposed essentially the same hypothesis for eupelmid taxa in which the separation of Mt8 and Mt9 arose twice as independent secondary reversals for *Eusandalium* and *Metapelma*. In torymids the separation appears to have arisen only once. This character was used in the working hypothesis to establish monophyly of Torymidae. In the ending hypothesis this character was not needed as *Megastigmus* was used as the outgroup.

#### *Characters Initially Analyzed But Not Used*

In assessing characters and states, all those previously mentioned in the literature were used. As with the characters just discussed, the literature is not consistent in character use or description. I attempted to record character data in a consistent format for all taxa. Also, I attempted to “translate” relative characters into absolute ones by using measurements instead of the more comparative terms usually found in the literature. Several characters were first analyzed as numerical ones and subsequently converted to qualitative ones. These were discussed in the previous section as the following characters: Male Eye, Wing Venation, and Relationship of Notauli to Scutoscutellar Suture.

##### *Antennal placement:*

In previous taxonomic work the position of the antennal insertion on the face was used but not consistently. If used at all, the position was qualified by such terms as “above the middle,” “nearer the ocellus than the clypeus,” or “part of head below antennae very short” (Bouček 1978). I quantified the position of antennal placement by measuring the distance from the top of the torulus to the top of the head and from the bottom of the torulus to the free apex of the clypeus. The upper distance was divided

by the lower. Five states were recognized and ordered in the transformation series: 6 - 4 - 3 - 2 - 1, where the highest number is the lowest antennal placement. A central or lower antennal placement is considered plesiomorphic based on outgroup comparison. RESULT: Only one taxon (*Amonodontomerus* Girault) of the original 55 was defined unambiguously, based on a discrete gap in states of this character. Not only was the state autapomorphic for that taxon, it was determined by further examination that the taxon was missing one of the synapomorphies (articulated Mt9) that defined the presumed monophyletic group under examination. The taxon was eliminated from further study. Bouček (1988) subsequently synonymized the genus with *Chromeurytoma* in the Pteromalidae. A reanalysis of the character involved attempts to qualify it. The extremes of measurements were chosen and specimens were subjectively ranked according to whether the toruli were placed at the middle of the face or below. Even using the extremes of measurements an absolute method to subjectively separate states could not be found. Lacking any method of establishing discontinuities in "states," I removed the character from further consideration.

*Ratio of forecoxa to hind coxa:*

In the recognition of genera, some mention has been made of relative differences in size between the fore- and hind coxae. In some taxa the hind coxa may be four or five times larger than the forecoxa. I attempted to quantify this difference by measuring the length of the hind coxa and dividing this figure by the length of the forecoxa. Resultant ratios were rounded off to the nearest whole integer. Five states were recognized and ordered in the transformation series 1 - 2 - 3 - 4 - 6. An enlarged hind coxa relative to the forecoxa (i.e., a higher ratio value) is considered to be apomorphic by outgroup comparison. RESULT: The only discontinuity (i.e., between 4 and 6) occurred in one taxon, and after remeasurement it was found to be in error and equaled 4.0 when remeasured. Not only is the character difficult to measure, but no discontinuities appeared after remeasurement. An attempt was made to qualify the character, but no discontinuity could be found on which to base even a subjective division. Therefore the character was discarded.

*Ratio of hind femur to hind coxa:*

As just stated, hind-coxal size has been used as a character to differentiate genera. The length of the hind femur relative to the hind coxa has been used as a potential character (e.g., *Chrysochalcissa*, Bouček 1978). I attempted to quantify the character by dividing the length of the hind femur by the length of the hind coxa. After rounding to the nearest tenth, the resultant ratios ranged from 1.0 to 2.2 and were divided into two states based on ratios lower than 1.5 and 1.5 and higher. This division was purely for practical purposes. An elongate hind femur (i.e., higher ratio value) is considered plesiomorphic by outgroup comparison. RESULT: This was a continuously variable character for which no discontinuities were found. The character was discarded for this reason.

*Ratio of length to width of hind femur:*

Much of the classification of "Monodontomerinae" has been based on the morphology of the hind femur. It differs markedly in size and shape in many taxa. I analyzed

its shape qualitatively in the previous section (p. 42), and I also attempted to determine if phylogenetic information could be obtained quantitatively as well. The length of the femur was divided by its maximum width (excluding projecting teeth). The ratios were rounded to the nearest whole integer and 5 states were ordered in the transformation series 1 - 2 - 3 - 4 - 5. A narrow femur (i.e., high ratio value) is considered plesiomorphic by outgroup comparison. RESULT: There were no gaps in the "states" and measurements were not always easy to take. It was especially difficult to measure the width of the femur when modifications such as teeth were present. Because of these factors and because a qualitative assessment of the hind femur is also used in this study, I felt that the quantitative character could be discarded.

*Ratio of hind basitarsus to tibial width:*

The length of the hind basitarsus has been used as a supportive character to characterize some genera (e.g., *Neopalachia*, Bouček 1978). I attempted to quantify the character by dividing its length by the width of the apex of the tibia. The resultant ratios were rounded to the nearest whole integer and 4 states were ordered in the transformation series 1 - 2 - 3 - 4. A short tibial apex (i.e., high ratio value) is considered plesiomorphic by outgroup comparison. RESULT: This was a continuously variable character for which no gaps were found. The character was discarded for this reason.

*Ratio of metanotum to propodeum:*

One genus is known (*Zophodetus*) in which the metanotum is relatively enlarged and it was used as a generic character to distinguish the genus (Grissell 1980). This character was quantified to determine if discrete states could be found. The medial length of the metanotum was divided by the medial length of the propodeum and the resultant ratios were rounded to the nearest tenth and ordered from 0.1 to 0.7. No discontinuities were found so I arbitrarily divided the character into two states with 0.5 and below as one and above 0.6 as the other. A long metanotum (i.e., high ratio value) is considered plesiomorphic by outgroup comparison. RESULT: The ratios were continuous and were extremely close with errors in measurement easily overlapping neighboring figures. Therefore, I discarded this character.

## BIOLOGY AND PHYLOGENETICS

This section presents a brief overview of biology in the Torymidae and possible correlations with hypothesized phylogeny. It examines host information based on the host-parasite section of this work (p. 292) as well as feeding behaviors. Evidence suggests that neither host information nor feeding behaviors can be used to construct a phylogeny but that neither conflicts with the hypothetical phylogeny. Recent overviews of biology may be found in Bendel-Janssen (1977), Narendran (1984b), Wall (1984), Sellenschlo (1984a), Gauld and Bolton (1988), and Bouček (1988).

The use of the term "biology" in discussing torymids (or even chalcidoids) is largely a misnomer. In chalcidoids there are few biological facts about species. Often we know that a species is somehow associated with a host, but the exact interactions between the two are poorly known. Some associations prove to be entirely

unfounded as in the case of *Megastigmus aculeatus* Swederus, which, for many years, was thought to parasitize a tephritid present in rose hips. It was only on dissection that *aculeatus* was shown to be phytophagous in the seeds (Milliron 1949:358).

Host data should not be confused with more detailed aspects of biology such as methods of host habitat and species selection, life stage selection, paralysis (or not) of host, sex allocation, types of parasitism (such as endo- or ecto-, solitary or gregarious), mating behavior, and the like. In the end, we are often lucky simply to have host data and to make the best use of it we can. Askew and Shaw (1986:226) said, when referring to parasite biology, that the "literature is of ... limited value," and is largely "unrepresentative" of true host range data, because it is often written in the narrow context of biological control. Even host data, itself, is not always accurate, and as Noyes (1994) pointed out, can be so "misleading as to be generally useless."

Below I use the term "Torymidae" in the sense only of the subfamilies Toryminae and Megastigminae. Even though there is ambiguity about the phylogenetic position of Agaonidae, Sycophaginae, and putatively related groups, I see relatively little need to discuss them because all species are biologically autapomorphic being confined to the receptacles of fig fruits; they may be phytophages, inquilines, cleptoparasites, or parasites. Since we know the actual life-histories of less than half-a-dozen species we really know very little other than that they are associated with figs. Tables 1A and 1B (Appendix V) present a numerical overview of world Torymidae, the data of which are used in determining host-use trends within this section.

### **Megastigminae: Host Summary**

#### **Table 2 (Appendix V, p. 341)**

Megastigminae is a group of over 125 species, 90% of which are phytophagous. Larvae of these species feed internally in seeds. The left column of Table 2 summarizes the phytophagous host associations for the subfamily. These plants are arranged from presumptive primitive at top to advanced at bottom based on Bailey (1949).

About 10% of megastigminae are believed to be entomophagous. On the far right side of Table 2 are the known insect hosts of Megastigminae. The host plants on which these insects feed are shown in the center column. The plants are arranged from most primitive to most advanced, and they are placed in position relative to the plant hosts on the far left. This is so that plant taxa of phytophagous megastigmine species may be shown with phylogenetic respect to plant hosts of the insects on which entomophagous megastigminae feed. (One undescribed species (Milliron 1949:369) is known to be both phytophagous and parasitic, but is not discussed further here.)

The following hypotheses may tentatively be drawn from this data: 1) insect host taxa (right column) do not form a phylogenetically distinct grouping. These hosts occur in the Hymenoptera, Diptera, and Homoptera; the commonality of these groups appears not to be a phylogenetic relationship with each other, but rather that they form an ecological group as gall-formers or hosts enclosed within a fruit or seed pod; 2) plant taxa used phytophagously (left column) do not overlap those plant taxa on which insect hosts feed except for Anacardiaceae. Even here there is *no* overlap of feeding between genera of host plants. Because these feeding habits are mutually exclusive, the direction of possible evolution from plant host to insect, or from insect to plant host, is not readily apparent from the data; 3) the primitive Gymnospermae contain one-third of all phytophagous wasps and no entomophagous ones. Phylogenetically



this might argue that phytophagous megastigminae arose first through gymnosperms, radiated to angiosperm seed, then to insects in seed pods and finally to insects in galls. Unfortunately there has been little work on megastigmine phylogeny to corroborate this hypothesis. Indeed, the only morphological character to separate phytophagous forms from entomophagous ones appears to be a non-metallic coloration in the former and a metallic coloration in the latter, but it is presently not even clear which state is derived (see discussion in Gibson 1986:225). Bouček (1988:123) came to the conclusion that biology (or at least host range) and morphology do not corroborate each other very well in the Megastigminae.

### **Toryminae: Host Summary**

**Table 3 (Appendix V, p. 342-343)**

Table 3 is a simplified, though complete, data set for the known hosts of all Toryminae except the genus *Torymus*, for which a subset of 194 of the 317 known species was examined. In the ensuing section the basis for discussion is the putative tribal level, except for the genus *Torymus*, which is discussed as an entity in itself. This genus represents a single taxon with almost as many species (317) as the remainder of the entire subfamily taken together (426). Toryminae (at 743 species) has roughly 6 times more valid species than Megastigminae (at about 125 spp.). In Toryminae there are 5 known phytophagous species (all *Torymus*), but the majority are parasitic on a wide variety of hosts in 51 families of insects in 8 orders. For those taxa with known hosts, the percentage by host order (calculated from Table 3) is shown in Fig. 48 (data for all Toryminae), Fig. 49 (data for Toryminae without *Torymus*), and Fig. 50 (data for subset of *Torymus* as discussed above).

For Toryminae, Hymenoptera and Diptera, at 76% of all hosts (Fig. 48), are the preferred food source. This is skewed by the large proportion of *Torymus* (94%; Fig. 50) which attack these two orders, but even for Toryminae without *Torymus*, the two orders still account for 59% of hosts (Fig. 49). If tribes are ranked simply on the basis of the two highest numbers of hosts (higher number given first), the pattern is:

Hymenoptera/Diptera: Microdontomerini, Chalcimerini;

Diptera/Hymenoptera: Torymoidini, Torymini;

Hymenoptera/Lepidoptera: Monodontomerini;

Mantodea: Podagrionini (and most likely Palachiini).

Within the Diptera only 3 families are attacked with a majority of hosts being cecidomyiid gall-formers. A few Tephritidae are used as are a few Tachinidae. Within Hymenoptera, however, the host situation is more varied. Sixteen families are attacked, with the predominate hosts about evenly divided between gall-forming Cynipidae and Eurytomidae, as well as solitary nesting bees and wasps. The next largest group of hosts is mantid egg cases, which are predominantly used by the single taxon Podagrionini (this is discussed below). Lepidoptera forms the next most used group of hosts, the majority of which are attacked by 2 genera in the Monodontomerini (*Monodontomerus* and *Perissocentrus*). Coleoptera forms an extremely minor portion of the host range of Toryminae (and Torymidae as a whole). Finally, there are a number of isolated host records that appear to be accurate (e.g., Strepsiptera, psyllids, cicada eggs) and which might simply be thought of as "experiments" in feeding. These taxa might be considered "dead-ends" in terms of entering an untapped food resource, i.e., these hosts do not seem to have provided a large, unused niche in which adaptive

radiation took place, as apparently happened for the mantid egg case parasites.

Based on Table 3 (illustrated in Fig. 48), of approximately 350 host associations [i.e., "Total" Column/188 species with hosts + ("*Torymus*" Column/169 species with hosts) = 357 species with hosts, rounded to 350 as rough base number considering the difficulty and inexactitude of determining host data], 12% have been reared from mantid egg cases (41/350). This figure, however, is certainly far too low, as it accounts only for species with known host records. Only 39 species of 135 Podagrionini are actually associated with host rearings, and it is believed that all species of this tribe are associated with mantids. If this were true, then a minimum 19% of all Toryminae (135/730) would be associated with mantids. Although podagrionines are hypothesized to be the most advanced torymids, they attack relatively primitive hosts. There are several potential explanations for this anomaly. For one thing, there are no intermediary isopteroid or blatoid hosts, and few orthopteroid hosts (rarely tettigoniids), which would indicate a "progression" of feeding along possible phylogenetic lines. This suggests a possible accidental invasion of the mantoid niche, followed by explosive radiation. A mantid egg case might be likened to a gall or pupal case and would thus be a quiescent or restrained host similar in form to other hosts used by torymids. It might also be argued that, although the mantid host taxon is primitive, the use of an egg stage as host is a derived behavior relative to the use of larvae in galls.

I have verified a rearing of a *Podagrion* which is known to attack mantids but which emerged from a hesperiid pupa (see p. 236). This offers the possibility that the sister group of Podagrionini was predisposed to parasitize lepidopterous pupae and gave rise to species that shifted to the relatively empty niche of mantid egg cases and then began to radiate rapidly. The current hypothetical phylogeny places Podagrionini near Monodontomerini which includes the majority of lepidopterous parasites (Fig. 38). An additional corroboration to this hypothesis is that although egg parasitism is rare in Torymidae (only about 2% of known species excluding Podagrionini, i.e., 11 of 614 species), it is most highly developed in the Monodontomerini. In this group 7 of the known 11 cases are reported on coreids and pentatomids (*Chrysochalcissa*, *Oopristus*, *Rhynchotica*) and tettigoniids (*Amoturoides* Girault). Within other groups, egg parasitism is reported twice in the Microdontomerini (*Microdontomerus ovivorus* (Steffan) on cerambycids, *M. senegalensis* (Risbec) on mantids), once in Palachiini (*Palachia mangalae* Narendran on mantids), and once in Torymini (*Torymus oviperditor* (Gahan) on cicadas). It appears that egg parasitism was derived as an uncommon, random event within several clades, and that Monodontomerini appears more predisposed to egg parasitism than any other group of torymids except Podagrionini. This may be an indication of true phylogenetic relationship. Perhaps significantly, there is a single, questionable record of a podagrionine (*Podagrionella indarbele* Narendran and Sureshan) reared from Lepidoptera eggs (see p. 249). This emphasizes the use of both Lepidoptera and eggs, both niches which are more commonly associated with Monodontomerini than with other torymids.

It is possible that too much may be inferred from the use of eggs as hosts by torymids. It might be speculated that eggs are not the focal point, but rather that eggs may contain a hymenopterous primary parasite which has already devoured the egg content. In this sense, the egg shell would be a "pseudo-gall" which merely holds a somewhat ordinary hymenopterous host. Most of the taxa found at the base of the hypothesized tree are parasites of gall-forming insects, and it might be suggested that the

movement from galls to eggs would not be difficult to make. Because there are relatively few torymid egg parasitoids (except for those that attack mantids), exact egg-torymid interactions are unstudied. Detailed examination of this habit might prove of interest in establishing phylogenetic hypotheses in the future.

Host associations of Toryminae and Megastigminae provide grounds for much discussion for a biologically-based approach to phylogeny. I do not believe that the available host data convey any particularly convincing phylogenetic overtones. Nor are the present data even necessarily reliable, as in the case just mentioned for egg parasites. We know little about the true biological relationships of parasite and host, and much more information is needed to assess these relationships before phylogenetic inferences will mean much. It is possible that the primary orientation to galls, seed pods, aculeate nests in plant tissue, eggs in cases, and even eggs themselves, indicate an orientation to a host based more on habitat than on the host's presumptive phylogenetic hierarchy. The next section explores this idea further.

### Biological Feeding Types

In my attempts to extract phylogenetic data from host information, I looked at "biology" in a slightly different manner. This involved classifying feeding behavior based on observed and presumed larval feeding types rather than patterns of host distribution. This could be done only in a superficial way, unfortunately, because so few biological details are known for the family. Even for a single species the biological details may be contested, as in the case of *Podagrion pachymerum* (Walker), which has been reported as an internal egg parasite, an external egg parasite (one host per larva), and an egg predator (multiple hosts per larva) (Clausen 1940).

The basic feeding types found within the Torymidae, as best I can determine, are as follows: phytophagous, solitary external, predaceous (a form of solitary external), solitary internal (egg/larval in this case), gregarious external, and gregarious internal. These feeding types were placed on the final hypothetical tree presented in Fig. 38, and the simplified results are shown in Fig. 51.

Both phytophagy and external solitary feeding types occur in the basal Megastigminae. The outgroup Pteromalidae (as well as almost all other chalcidoids) is entomophagous in habit, and this would appear to be the groundplan state from which phytophagy arose as a secondary reversal. Phytophagy has arisen independently in the majority of Megastigminae and a few species of Torymini. Solitary external parasitism is represented throughout the phylogeny and occurs with certainty in Megastigminae, Microdontomerini, Torymini, Torymoidini, some Monodontomerini, and most probably Chalcimerini as well. Gregarious external and internal parasitism seems to be confined to some members of Monodontomerini. Predatory behavior appears to be confined to the Podagrionini and perhaps a species of Torymini (*Torymus oviperditor*) that feeds on cicada eggs. In Podagrionini the larvae apparently move from egg to egg of the host while inside the mantid egg case. Only one case of solitary internal parasitism has been documented in any detail, and it is a rare form of egg/larval parasitism. Oddly enough, it has arisen in the relatively primitive Megastigminae (*Megastigmus brevivalvus* (Girault), see Milliron 1949:370-371). Egg/larval parasitism would seem to be an advanced form of solitary/internal parasitism which is reported in the literature (by Clausen 1940) only for the species *Podagrion pachymerum*. As pointed out above, there is disagreement over the actual biology of this species.

If one takes the enumerated feeding characters as expressed by their presence on the hypothetical phylogenetic tree (Fig. 51) and uses them as cladogram characters to determine a hypothetical transformation series for feeding behavior the result is shown in Fig. 52. According to the phylogeny, all specialized feeding types evolved independently from the solitary external condition. Based on this transformation, solitary external gave rise to gregarious external and gregarious internal, but the precise direction (i.e., gregarious internal to gregarious external, or gregarious external to gregarious internal) cannot be determined from the data because both occur in the same genus (i.e., *Monodontomerus*). The feeding type of solitary internal (and egg/larval) arose at least basally within the Megastigminae, most likely from the solitary external entomophagous feeders. It possibly also arose independently in the Podagrionini (substantiation of exact feeding types requires more accurate data than is available in the current literature). The predatory feeding type, confined to Podagrionini, appears also to have arisen from the solitary external feeding type. Superficially, feeding habits do not disagree with the proposed phylogenetic hypothesis, but neither are they totally convincing in supporting the hypothetical phylogeny being used in this study.

**Conclusions:** The information presented above is fairly simple, and an examination within a single group of parasites demonstrates the true degree of difficulty for deriving phylogenetic information from host data. Table 4 shows biological associations of some species of *Microdontomerus* that appear specific in host choice. For example, *M. anthidii* (Ashmead) attacks bee larvae in resin or twig nests, *M. bicoloripes* (Crawford) attacks cynipids in bud galls, and *M. fumipennis* attacks moth larvae that tie leaves and live in plant stems. *Microdontomerus ovivorus*, an Old World species, feeds internally in buprestid eggs, and a nearly identical undescribed New World species attacks saturniid eggs. Most interesting is the single species *M. anthonomi*, which demonstrates a plasticity of behavior perhaps not all that uncommon in the Toryminae. This species is a solitary ectoparasite in which superparasitism has been observed (Pierce 1910). Up to eight larvae were found but only one survived. Perhaps this is a precursor to the gregarious parasitism that is found in some Monodontomerini. In addition, the species acts as a secondary parasite that attacks braconids and outcompetes pteromalids and eurytomids when multiple parasitism occurs. Finally, *M. anthonomi* not only attacks coleopterous larvae but dipterous and lepidopterous larvae as well (Turner *et al.* (1990). The species was judged to be a "host species generalist" but a "microenvironment specialist" on hosts enclosed in plant tissue.

In summary, torymids might best be classified as generalized feeders that include species that are phytophagous, carnivorous, and a few that are adapted to feed both on plant and animal tissue. As Askew (1968) stated, "the larval diet of a chalcid does not, in many cases, appear to be very critical for its development." Simple host data can be misleading when dealing with generalized feeders such as these, and detailed biological data such as feeding types would undoubtedly be more useful in assessing phylogeny than would host data alone. In generalized feeders such as the Torymidae it seems more reasonable to deduce the evolution of biological traits from a phylogeny based on phenotype rather than to deduce a phylogeny from relatively unstable or plastic biological characteristics.



- 4 (2) Marginal vein 0.5 as long as postmarginal vein and subequal in length to stigmal vein (Fig. 381); hind femur robust with numerous ventral teeth (Fig. 69) and hind tibia with apex diagonally truncate and with single, short, chisel-like spur (Figs. 379, 380) .. **Chalcimerini** (Fig. 69; p. 141)
- Marginal vein equal to (Fig. 189, uncommon) or longer than postmarginal vein (Figs. 56-61, common) and at least twice as long as stigmal vein; hind femur variable, often slender (Figs. 135-139) with at most 1 or 2 ventral teeth, but if apparently robust and with numerous ventral teeth, then apex of hind tibia either truncate at right angles with 2 apical spurs (Fig. 220) or diagonally truncate (Fig. 218) with 2 spurs and two rows of teeth (Fig. 216) ..... 5
- 5 (4) Occipital carina with dorsal margin flat, low on head, and nearer occipital foramen than hind ocelli (Figs. 231, 405) or, if carina absent, then hind femur with 2 rows of teeth in which the inner row is reduced to bumps (Fig. 224); hind femur always modified, either with single large tooth (Figs. 228-230), single median lobe (Fig. 227), or 2 rows of teeth (Figs. 216, 219, 221, 224) ..... **Monodontomerini** (Figs. 65-68; p. 117)
- Occipital carina with dorsal margin arched, either high on head nearer ocelli than occipital foramen (Figs. 81, 404, 406) or midway between ocelli and foramen (Figs. 83, 408) or, if carina absent, then hind femur without distinct teeth; hind femur most often simple (Fig. 136) or with ventral surface slightly scalloped (Figs. 137-139, 429), sometimes somewhat swollen (Fig. 142), with 1 or 2 teeth (Figs. 193-198), or rarely with a single irregular row (Fig. 140) but never 2 rows of teeth ..... 6
- 6 (5) Occipital carina absent (Fig. 399) or if present its lateral edges extending at most in line with *dorsum* of occipital foramen (Figs. 81, 83); marginal vein always relatively short, 1 to 2 times length of postmarginal vein and 2 to 5 times length of stigmal vein (Figs. 99-117) ..... **Microdontomerini** (Fig. 63; p. 72)
- Occipital carina always present, its lateral edges extending at least in line to *venter* of occipital foramen (Figs. 404, 406) and often extending more ventrally (Fig. 408); marginal vein most often relatively long, 3 to 7 times length of postmarginal vein and at least 6 times length of stigmal vein (Figs. 148-155, 186-188), but rarely subequal in length to postmarginal vein (Fig. 189) and as little as 3 times length of stigmal vein ..... 7
- 7 (6) Metapleuron with anterior margin straight (Figs. 12, 424) ..... **Torymoidini** (Fig. 62; p. 105)
- Metapleuron with anterior margin produced forward (Figs. 10, 425) ..... **Torymini** (Fig. 185; p. 98)

**Key to World Genera of Toryminae (except Torymini)**

- 1 Suture between mesepimeron and metapleuron appearing sinuous and *either*: (1) *anterior edge* of upper half of *metapleuron* curved and projecting forward as lobe into mesepimeron (Figs. 10, 425), or (2) *posterior edge* of upper *mesepimeron* curved and overlapping metapleuron (the anterior margin of which is obscured) (Figs. 280B, 368) ..... 2
- Suture between metapleuron and mesepimeron straight, the sclerites abutting each other (Figs. 11, 12, 424) ..... 4
- 2 (1) Mesepimeron and metapleuron abutting along margins, neither sclerite overlapping the other (Figs. 10, 425), but *anterior edge* of upper half of *metapleuron* projecting forward as lobe into mesepimeron; mesepimeron subdivided into upper and lower sections delimited by anterior groove; [worldwide, common] ..... **Torymini** (p. 98)
- Mesepimeron with posterior margin curved, projecting backward, and overlapping metapleuron (thus obscuring anterior margin of metapleuron) (Fig. 280B); mesepimeron not subdivided into upper and lower sections (Fig. 280B), but rarely groove on anteroventral half (Fig. 368) suggesting a partial lobe; [Palearctic, Australian, uncommon] ..... 3
- 3 (2) Metasternal shelf present (Fig. 280B); hind femur (as in Figs. 332-337) entirely enlarged, with teeth along ventral margin; hind tibia with apex diagonally truncate (as in Figs. 338-339); marginal vein longer than 0.5 times length of costal cell (as in Figs. 290-291); [Australian] ..... **Propachytomoides** Girault (see also couplet 11, below)
- Metasternal shelf absent (Fig. 368); hind femur (Fig. 354) enlarged subapically with single large tooth and minute teeth to apex; hind tibia with apex truncate at right angles; marginal vein much shorter than 0.5 times length of costal cell (Fig. 360); [Palearctic] ..... **Thaumatorymus** Ferrière and Novicky (p. 172)
- 4 (1) Metasternal shelf present (Figs. 11, 278B-285B); propodeum with spiracular sulcus absent or oriented towards lateral corner of propodeum and callus not developed (Fig. 16); hind femur always modified in some respect, usually with multiple teeth (Figs. 252-258, 331-339) but rarely with single tooth (Fig. 347) ..... 5
- Metasternal shelf absent (Figs. 10, 12); propodeum with spiracular sulcus oriented toward nucha and callus developed (Figs. 15, 17); hind femur variable, often unmodified (Figs. 136-138), with single tooth (Figs. 228-230) or, rarely, enlarged and with multiple teeth (Figs. 21-217, 219-220) ..  
..... 15
- 5 (4) Hind femur ventrally with slightly enlarged tooth (Fig. 347); hind tibia straight, apically truncate at right angles (Fig. 340); occipital carina absent; metasoma laterally compressed (nearly a single vertical plane in cross-section) and without emarginations (Fig. 340); [Afrotropical, Oriental]..... **Stenotorymus** Masi (p. 170)

- Hind femur ventrally with multiple teeth (Figs. 252-258, 331-339); hind tibia variable, often curved with apex diagonally truncate (Figs. 255, 326-328); occipital carina present (Fig. 410); metasoma not compressed or, if somewhat compressed, then with at least dorsal emarginations ..... 6
- 6 (5) Hind femur elongate, ventrally with few teeth (often two teeth most prominent) (Figs. 252-254, 256-258) or with teeth in dense comb confined to outer expansion of femur (Fig. 255); hind tibia with apex truncate at right angles (Figs. 252-253, 256), except specimens with comb-like teeth (Fig. 255) have apex obliquely truncate, and with 2 spurs (though 1 spur sometimes difficult to see); metasomal terga without lateral emarginations ..... 7
  - Hind femur ovoid, ventrally with few to many teeth along most of margin (Figs. 324, 326, 331-339), without expanded area in outer half; hind tibia with apex obliquely truncate (Figs. 324, 326-328, 332), and with 1 spur (Figs. 327-328, 332); at least metasomal terga 2-4 with lateral emarginations (Figs. 321-322) (which may be difficult to see) ..... 10
- 7 (6) Hind femur (Fig. 255) expanded apically and with minute comb-like teeth; hind tibia curved, apex obliquely truncate; [Neotropical] ..... *Neopalachia* Bouček (p. 139)
  - Hind femur (Figs. 252-254) elongate and with several long teeth; hind tibia straight, apex truncate at right angles; [extant species Old World; single fossil Neotropical] ..... 8
- 8 (7) Fossil (Dominican amber); antennal club 3-segmented (Fig. 271); hind femur with 2 sets of double teeth (Fig. 256); [Neotropical] ..... *Gummilumpus* Grissell (p. 135)
  - Extant; antennal club appearing 1-segmented (Figs. 268-269); hind femur with 2 larger teeth in addition to other teeth (Figs. 252-254, 257-258); [Old World] ..... 9
- 9 (8) Clypeus with apical margin toothed (Fig. 267); marginal vein 9 to 11 times as long as stigmal vein (Figs. 261-264); submarginal vein with setae less than height of costal cell (Fig. 261); [Palearctic, Afrotropical, Oriental] ..... *Palachia* Bouček (p. 137)
  - Clypeus with apical margin straight; marginal vein 3 to 4 times as long as stigmal vein (Fig. 259); submarginal vein with setae longer than height of costal cell (Fig. 259); [Afrotropical, Oriental] ..... *Propalachia* Bouček (p. 138)
- 10 (6) Hind tibia with apex elongately produced (Figs. 324, 326, 332, 328), the truncation at least twice width of tibia and with spur at base of truncation near basitarsus (Figs. 332, 328); [Old World] ..... *Podagrionella* Girault (p. 151)
  - Hind tibia with apex not elongately produced (Figs. 327, 338-339), the truncation subequal in length to width of tibia and with spur at apex of truncation (Figs. 327, 338-339) ..... 11



- 11 (10) Mesepimeron bulged outwardly, raised into lamelliform plate above surface of metapleuron (Fig. 280B), and overhanging (and partially obscuring) metasternal shelf; forewing with well delimited spot; [Australian] ..... *Propachytomoides* Girault (p. 156)
- Mesepimeron not bulged, abutting metapleuron, and not overhanging metasternal shelf (Figs. 278B-279B); forewing without delimited spot, rarely with diffuse stain ..... 12
- 12 (11) Antennal club ventrally divided into 3 clavomeres, of which only apical clavomere has micropilose area (Fig. 314); [Afrotropical] ..... *Mantiphaga* Ferrière (p. 150)
- Antennal club with ventral divisions most commonly obscured by micropilosity (Figs. 310-311, 313), but if 3 clavomeres visible, then micropilose area covers at least apical 2 clavomeres (Fig. 312) (latter state most common in males) ..... 13
- 13 (12) Midtibia with spur threadlike, bare, longer than basitarsus (Fig. 330); anellus about as long as wide and trumpet mouth-piece shaped in profile (Fig. 318); [Afrotropical] ..... *Micropodagrion* Ferrière (p. 157)
- Midtibia with spur thickened, setose, shorter than basitarsus (Fig. 329); anellus cylindrical, either elongate (Figs. 307, 310) or transverse (Figs. 311, 313) ..... 14
- 14 (13) Anellus as long as broad (Figs. 307, 310); forewing entirely covered with setae, without vein tracts, cells, or speculum (Fig. 289); metasternum with 2 submedian carinae between metacoxal foramina (Fig. 283A), the carinae sometimes irregular or broken (Fig. 285A); [worldwide, ?Palearctic] ..... *Palmon* Dalman (p. 158)
- Anellus transverse (Figs. 311-313); forewing with distinct vein tracts, cells, and speculum (Fig. 293); metasternum variable, but most often with single median carina between metacoxal foramina (Fig. 279A); [worldwide] ..... *Podagrion* Spinola (p. 161)
- 15 (4) Hind-tibial spurs at least twice as long as width of tibial apex (Figs. 228, 230, 357-358), the spurs usually subequal in length to hind basitarsus [a few questionable taxa will run both ways] ..... 16
- Hind-tibial spurs subequal to width of tibial apex (Figs. 218, 223, 226-227), the spurs usually obviously shorter than hind basitarsus ..... 19
- 16 (15) Hind-tibial spurs inserted at apex (Figs. 357-358); propodeum submedially reticulate or polished with at most single median carina (Fig. 238) ..... 17
- Hind-tibial spurs separated from apex (Figs. 157, 228); propodeum carinate at least laterally (Fig. 239), often completely covered with longitudinal carinae (Fig. 184) ..... 18
- 17 (16) Metasoma with at least first few terga having median emarginations (as in Fig. 91); occipital carina nearer hind ocelli than occipital foramen (Fig. 362); [Nearctic, Neotropical] ..... *Zaglyptonotus* Crawford (p. 173)

- Metasoma with terga not having median emarginations (as in Fig. 363); occipital carina nearer occipital foramen than hind ocelli (as in Fig. 231); [at least one Palearctic species falls here] ... *Monodontomerus strobili* (p. 125)
- 18 (16) Hind femur with slightly developed ventral angle (as in Fig. 182); metasoma dorsally concave; antenna with 2 or 3 anelli or reduced basal flagellomeres; [Australian] ..... *Aloomba* Girault (p. 115)
  - Hind femur with well developed ventral tooth (Fig. 228); metasoma dorsally convex; antenna with 1 anellus; [Neotropical] ..... *Perissocentrus* Crawford (p. 126)
- 19 (15) Clypeus with ventral margin greatly elongated (Fig. 235); hind femur with ventral margin having well developed tooth (as in Fig. 213); frenal line developed ..... 20
  - Clypeus with ventral margin truncate (Fig. 383), emarginate (Fig. 232), or slightly rounded (Fig. 236); other characters variable ..... 21
- 20 (19) Propodeum with weakly defined median carina arising as broad continuation of nucha, and with propodeal foveae poorly defined (Fig. 241); frenum heavily sculptured; [Neotropical] ..... *Rhynchodontomerus* Novicky and De Santis (p. 122)
  - Propodeum with well defined median carina arising from midpoint of nucha, and with propodeal foveae well defined (as in Fig. 240); frenum polished; [one north African species falls here] ..... *Monodontomerus anthidiorum* (p. 125)
- 21 (19) Hind femur ventrally with multiple teeth (Figs. 217, 220, 222, 225) or with median triangular expansion and subapical lobe(s) between expansion and apex (Fig. 227), ventrally the lobe(s) sometimes margined with fine teeth or crenulations [hind femur sometimes relatively unenlarged with hind tibia straight (Fig. 140) to relatively enlarged with hind tibia greatly curved (Fig. 69)] ..... 22
  - Hind femur with ventral surface either simple (Figs. 164, 166) or with slight angle (Figs. 160-161, 165) or with single distinct subapical tooth (Fig. 181) or, if finely serrate or crenulate (Figs. 139, 428, 429), then without lobes as above [hind femur rarely somewhat enlarged (Fig. 142) with hind tibia slightly curved but then without teeth or serrations] ..... 30
- 22 (21) Hind femur with single submedian expansion or lobe-like "tooth" and one or more lobes between expansion and apex (Fig. 227), the lobes sometimes peg-like (Fig. 355) but not sharply pointed as teeth ..... 23
  - Hind femur with distinct teeth, either comblike or individual, but without lobe(s) (Figs. 217, 220, 225) ..... 24
- 23 (22) Hind femur with single lobe between submedian "tooth" and apex, the lobe with fine teeth or serrations (Fig. 227); propodeum with median carina subtended by lateral foveae (as in Fig. 240); [Afrotropical] ..... *Pradontomerus* Bouček (p. 127)

- Hind femur with several lobe-like teeth between submedian “tooth” and apex, the lobes sometimes peg-like (Fig. 355) but not sharply pointed as teeth; propodeum evenly reticulate; [Palearctic] ..... *Exopristus* Ruschka (part) (p. 167)
- 24 (22) Hind femur with irregularly sized and spaced teeth (Figs. 140, 222) .... 25
  - Hind femur with regularly sized and spaced, comb-like teeth (Figs. 217, 220, 225) ..... 27
- 25 (24) Hind femur (in cross-section) triangularly expanded, ventral surface flattened for reception of tibia and covered with minute bumps (Fig. 221) and with inner basal tooth; hind tibia evenly curved (Fig. 222) and with apical spurs thickened, the inner spur much longer than outer spur (Fig. 223); [Oriental, Australian] ..... *Rhynchotocida* Bouček (p. 131)
  - Hind femur (in cross section) vertical (inner surface evenly curved from ventral to dorsal edges), without flattened surface or bumps and without inner basal tooth; hind tibia curved only basally (as in Fig. 355) and with apical spurs unmodified and subequal in length [Palearctic] ..... 26
- 26 (25) Occipital carina present; both sexes with metasomal terga wider than long and medially with barely perceptible emarginations (Fig. 364); [Palearctic] ..... *Exopristus* Ruschka (part) (p. 167)
  - Occipital carina absent; females with metasomal terga 2 and 3 longer than wide, creased medially with Mt2 deeply emarginate (Fig. 92), males with terga slightly longer than wide, flat, and Mt2 and Mt3 deeply emarginate (Fig. 93); [Palearctic] ..... *Idarnotorymus* Masi (p. 93)
- 27 (24) Marginal vein subequal in length to stigmal vein and 0.5 times length of elongated postmarginal (Fig. 381); hind tibia with single, thickened and truncate apical spur (Figs. 379-380); [Palearctic] ..... *Chalcimerus* Steffan and Andriescu (p. 142)
  - Marginal vein 4 to 6 times as long as stigmal vein and longer than post-marginal vein (Figs. 242-248); hind tibia with two pointed apical spurs which vary in thickness (Figs. 218, 220, 225) ..... 28
- 28 (27) Frenal line present; hind tibia with spurs of unequal length (Fig. 220); malar keel present (as in Fig. 237); clypeus apically convex (as in Fig. 236) [Oriental, Afrotropical] ..... *Anneckeida* Bouček (p. 130)
  - Frenal line absent; hind tibia with spurs subequal in length (Figs. 218, 225); malar keel absent; clypeus apically emarginate (Fig. 232) ..... 29
- 29 (28) Occipital carina present; hind tibia with apex diagonally truncate (Figs. 217-218); hind femur with outer and inner rows composed of subequally long teeth (Fig. 216); face without tufts of setae at base of scape and ventral edge of clypeus; [Afrotropical, Australian, Oriental] ..... *Chrysochalcissa* Girault (p. 128)

- Occipital carina absent; hind tibia with apex truncate at right angles (Fig. 225); hind femur with inner row of teeth reduced to bumps (Fig. 224), the bumps sometimes difficult to see; face with tufts of setae at base of protuberant scape and along ventral edge of clypeus (Figs. 232-233); [Palearctic] ..... *Oopristus* Steffan (p. 129)
  
- 30 (21) Forewing with marginal and stigmal veins conspicuously thickened relative to submarginal vein, postmarginal vein equal in length or shorter than stigmal vein (Figs. 373-374), and with marginal vein slightly removed from margin of wing (Fig. 373; may be somewhat difficult to see); malar distance very much longer than intermalar distance (Fig. 371); mandibles reduced, scarcely visible, tips not meeting medially when closed, apically without teeth; [Afrotropical, Australian] .... *Echthrodape* Burks (p. 166)
- Forewing with marginal and stigmal veins not conspicuously thickened relative to submarginal vein (Figs. 56-59), with postmarginal vein longer than stigmal vein (Figs. 148-155), and with marginal vein at edge of wing margin; malar distance subequal to or shorter than intermalar distance (Figs. 72-77); mandibles normal, visible, and tips meeting medially when closed, apically with teeth ..... 31
  
- 31 (30) Occipital carina well developed, dorsal margin not greatly arched but nearly horizontal (Figs. 231, 405), closer to occipital foramen than to hind ocelli (head usually tilted forward with dorsoposterior aspect conspicuously concave and occipital carina easy to see), and reaching hypostomal carina (head must be removed to see this); hind femur ventrally with abrupt tooth (Figs. 213-215); metasomal terga heavily sclerotized, without apicomedian emarginations ..... 32
- Occipital carina absent (Fig. 399), weakly or questionably developed (Figs. 401, 403) or, if apparent, then medially arched and midway between hind ocelli and occipital foramen (Fig. 361) or closer to former (Fig. 404) (head usually vertical with dorsoposterior aspect slightly concave and the carina, if present, easy to see), and not reaching hypostomal carina; hind femur ventrally either without tooth (Figs. 177-178), or angulate (Figs. 172-174), or vaguely serrate (Figs. 428-429); metasomal terga with or without apicomedian emarginations, often weakly sclerotized ..... 34
  
- 32 (31) Frenal line absent, frenum not delimited, setae covering scutellum nearly to apex; [Australian] ..... *Amoturoides* Girault (p. 124)
- Frenal line developed, frenum delimited and without setae, varying from highly polished to sculptured similarly to anterior of scutellum ..... 33
  
- 33 (32) Hind femur somewhat swollen with broadly rounded tooth some distance from apex (Fig. 226); metasoma with hypopygium prominent, broadly scoop-shaped, with ovipositor sheaths curved sharply upward and not projecting beyond apex of metasoma, and with ovipositor frequently protruding from sheaths as short, straight barb (Fig. 64); [Nearctic] ..... *Zdenekius* Grissell (p. 121)

- Hind femur narrow with sharp tooth near apex (Figs. 213-215); metasoma with hypopygium (if seen at all) pointed, and with ovipositor sheaths exerted well beyond apex of metasoma and usually covering ovipositor (Fig. 65); [Holarctic, Neotropical, Oriental] ..... *Monodontomerus* Westwood (p. 125)
  
- 34 (31) Marginal vein long, 3 to 7 times length of postmarginal vein and at least 6 times length of stigmal vein (Figs. 148-155); occipital carina present, its lateral edges extending at least in line with *dorsum* of hypostomal foramen (Figs. 39 (Character 1, state 2), 404) ..... 35
  - Marginal vein short, 1 to 2.5 times length of postmarginal vein and 2 to 5 times length of stigmal vein (Figs. 99-117); occipital carina absent (Fig. 399) or, if present, its lateral edges not (or scarcely) extending in line with *venter* of occipital foramen (Figs. 39 (Character 1, state 1), 81, 83, 361) ... 38
  
- 35 (34) Antenna with 1 anellus (Figs. 169-171), though exceptionally small specimens of a population may sometimes have 2 anelli (Figs. 168, 175); [Holarctic, Afrotropical] ..... *Pseudotorymus* Masi (p. 107)
  - Antenna with 2 or more anelli ..... 36
  
- 36 (35) Hind-tibial spurs (Fig. 158) modified as elongate, polished, apically black spines differing from fore- and midtibial spurs which are covered with short bristles; [Nearctic, Neotropical] ..... *Platykula* Huber (p. 114)
  - Hind-tibial spurs unmodified, both spurs covered with short bristles similarly to fore- and midtibial spurs (visible at 100X, but at lower magnification giving the spurs a fuzzy appearance; Fig. 156) ..... 37
  
- 37 (36) Propodeum laterally carinate with posterolateral corners sharply angled (Fig. 183); [Australian] ..... *Torymoidellus* Bouček (p. 113)
  - Propodeum laterally unmodified with posterolateral corners rounded (Fig. 392); [Worldwide] ..... *Torymoides* Walker (p. 110)
  
- 38 (34) Fossil (Dominican amber); clypeus concave (Fig. 86); propodeum carinate in complex manner with well defined horizontal and vertical ridges and depressions (Fig. 145); [Neotropical] ..... *Zophodetus* Grissell (p. 75)
  - Extant; clypeus truncate or slightly rounded (Figs. 72-77); propodeum at most with one median (Fig. 388) or two well defined submedian carinae (Fig. 412), otherwise sometimes with a few irregular, weakly defined, vertical carinae ..... 39
  
- 39 (38) Occipital carina visible in dorsal view as finely polished line raised distinctly above surface sculpture (Figs. 81, 83, 361) ..... 40
  - Occipital carina absent (Fig. 399) or, if vaguely indicated under some lighting conditions (Figs. 401, 403), then formed of irregular sculpture scarcely raised above other surface sculpture [a few questionable specimens run either way in couplet] ..... 44

- 40 (39) Propodeum with two submedian carinae (as in Fig. 412); hind femur minutely serrate ventrally (as in Figs. 428, 429), the teeth sometimes produced as slender, sharp barbs that are difficult to see except at 50 or 100X; [Holarctic] ..... *Eridontomerus* Crawford (p. 96)
- Propodeum either without carinae or, if present, then with single median carina (Fig. 388) or several irregular, incomplete carinae; hind femur variable, only rarely ventrally with serrations or wavy margin (Fig. 353), but then without sharp barbs ..... 41
- 41 (40) Forewing with marginal + postmarginal veins equal to 0.33 times length of wing *and* postmarginal vein much longer (almost twice) than stigmal vein (Figs. 56, 359); hind femur ventrally concave subapically, angulate basal to concavity (Figs. 353, 356) ..... 42
- Forewing either with marginal + postmarginal veins equal to 0.20 times length of wing (Fig. 57) *or*, postmarginal vein equal to or shorter than stigmal vein (Fig. 58); hind femur variable, but ventrally usually convex subapically (Figs. 135-139) ..... 43
- 42 (41) Hind femur ventrally sharply angulate subapically (Fig. 353); female with metasomal terga 2 and 3 oblong and Mt2 deeply excised (Fig. 365), male with metasomal terga transverse and entire; [Holarctic] ..... *Cryptopristus* Förster (p. 165)
- Hind femur at most slightly angulate and with wavy margin subapically (Fig. 356); both sexes with metasomal terga 2 and 3 transverse and apically entire (Fig. 363); [Holarctic] ..... *Glyphomerus* Förster (p. 169)
- 43 (41) Antenna with 1 anellus (Figs. 127, 128); forewing venation reduced, marginal + postmarginal veins 0.20 times wing length and postmarginal vein longer than stigmal vein (Fig. 57); [Holarctic, Afrotropical] ..... *Adontomerus* Nikol'skaya (p. 76)
- Antenna with 2 or more anelli; forewing with marginal + postmarginal veins equal to 0.33 times wing length and postmarginal and stigmal veins subequal in length (Fig. 58); [Holarctic, Neotropical, Australian (introduced), Afrotropical] ..... *Idiomacromerus* Crawford (part) (p. 85)
- 44 (39) Hind tibia with 1 apical spur (Figs. 136, 138); male with eye reduced (in all cases where males are known) (Figs. 88-89) ..... 45
- Hind tibia with 2 apical spurs (Figs. 135, 138-139) (occasionally outer spur sometimes difficult to see in very small specimens, less than 1 mm); male with eye normal (Figs. 84-85) ..... 47
- 45 (44) Antennal clava of female with apical spicula (Figs. 118-119); anellus in both sexes wider than long and funicle with basal 1 to 5 segments reduced (appear to be, or are, anelli, see text) (Fig. 118); [Holarctic] ..... *Pseuderimerus* Gahan (p. 90)
- Antennal clava of female without apical spicula (Fig. 120); anellus in both sexes wider than long to longer than wide and funicle with basal segments not reduced (Fig. 120) ..... 46

- 46 (45) Hind femur simple, without subapical angle or tooth (Fig. 137); propodeum without median carina; [Nearctic] ..... *Erimerus* Crawford (p. 92)  
 — Hind femur with subapical angle or tooth; propodeum with inverted “Y”-shaped median carina; [?Oriental: this genus is placed provisionally from the literature, see discussion of genus]..... *Ophiopinotus* Husain and Kudesia (p. 97)
- 47 (44) Hind femur ventrally minutely serrate or scalloped (Figs. 428, 429), the teeth sometimes produced as slender, sharp barbs that are difficult to see except at 50 or 100X; propodeum with 2 complete submedian carinae (Fig. 412) ..... 48  
 — Hind femur ventrally without serrations (Fig. 138), though margin sometimes wavy; propodeum either without carinae or, if present, then with single median carina (Fig. 388) or several irregular, incomplete carinae .... 49
- 48 (47) Antenna (Fig. 122) with 2 or 3 anelli, apical funicular segment considerably larger than 2nd funicular segment (i.e., second anellus) and funicular segments closely appressed; male with club and funicular segments 7 and 8 ventrolaterally having micropilosity (Fig. 124) (in dorsal view, apical half of flagellum diagonally truncate, Fig. 123); [Holarctic] ..... *Eridontomerus* Crawford (p. 96)  
 — Antenna (Fig. 125) with 1 anellus, apical funicular segment slightly larger than 2nd funicular segment, funicular segments often somewhat separated; male with club and funicular segments lacking micropilosity (in dorsal view, apical half of flagellum cylindrical, Fig. 126); [Holarctic] ..... *Ditropinotus* Crawford (p. 94)
- 49 (47) Antenna with 1 anellus (Fig. 130); [Holarctic, Afrotropical] ..... *Microdontomerus* Crawford (p. 78)  
 — Antenna with 2 or more anelli; [Holarctic, Neotropical, Australian (introduced), Afrotropical] ..... *Idiomacromerus* Crawford, part (p. 85)

### Microdontomerini, New Tribe

Type genus: *Microdontomerus* Crawford

The tribe Microdontomerini is composed of 67 valid species (plus 5 synonyms) in the following genera: *Adontomerus* (with *Mellitotorymus*, n. syn.), *Ditropinotus*, *Eridontomerus*, *Erimerus*, *Idiomacromerus* (with *Liodontomerus*, n. syn.), *Idarnotorymus*, *Microdontomerus*, *Pseuderimerus* (with *Lochitomorpha* n. syn.), and *Zophodetus*. *Ophiopinotus* is listed here provisionally (as *incertae sedis*).

The tribe is Holarctic in distribution with a single species (*Idiomacromerus gallicola*, generic placement not confirmed) questionably found in the Afrotropical Region and a single species (*Idiomacromerus insuetus*) either introduced into the Neotropical Region or misidentified. Only a single fossil species from Dominican amber (*Zophodetus woodruffi*) can arguably be listed as Neotropical.

Microdortomerini vies with Torymini as the most diverse group of torymids in biological habit, attacking all of the known host orders for the family (an undescribed species of *Microdortomerus* attacks Hemiptera). It is the only group that attacks Strepsiptera. It is commonly associated with gall-forming insects in grasses and seed-feeding insects in legumes, but a few species are known to attack eggs of insects. Some species are facultatively hyperparasitic as well. No phytophagous species are yet known. Hosts for 45 percent of the species are unknown (Table 3).

Microdortomerini is formed of taxa of relatively simple appearance (Fig. 63). Most members of the tribe are 2-4 mm (rarely 5 mm) in length excluding the ovipositor, which is rarely as long as the mesosoma and metasoma combined. Specimens are dull and drab in color, generally being black, olive green, or occasionally bronze. A few brightly colored species are known (e.g., *Erimerus wickhami*, *Microdortomerus senegalensis*). Members of Microdortomerini share plesiomorphic characters except for the reduction of the occipital carina, which is considered as a reversal within Toryminae, and the wing venation, which is derived with respect to pteromalid or megastigmine venation.

**DIAGNOSIS.** - Microdortomerini is defined by the *marginal vein 2 to 4.5 times the length of the stigmal vein and 1.5 to 2.5 times the length of the postmarginal vein* (Figs. 99-117); *the occipital carina absent* (Fig. 399), *vaguely indicated* (Figs. 401, 403) *or, when present, with ventrolateral edges not extending below imaginary line drawn horizontally across dorsum of occipital foramen, its dorsum nearer to the hind ocelli than the occipital foramen* (Figs. 81, 83); *and the usually simple hind femur* (Figs. 135-138) that uncommonly may be barely serrate or scalloped (Figs. 139, 428-429), *enlarged* (Fig. 142), or *toothed* (Fig. 140). Most torymids without an occipital carina are placed here. In only two other non-Microdortomerini taxa is the occipital carina absent: *Oopristus* and *Stenotorymus*, both of which have the hind femur modified, either with an enlarged tooth (Fig. 347) or with a row of outer teeth and an inner flat plane with a row of bumps (Figs. 224-225).

**DESCRIPTION.** - Occipital carina absent (Fig. 399) or present as an indefinite ridge seen only at certain angles of view and/or under certain lighting (Figs. 401, 403) and expressed only dorsally (Figs. 39 [Character 1, state 1], 81, 83,) with its ventrolateral edges not extending below imaginary line drawn horizontally across dorsum of occipital foramen, and its dorsum nearer to the hind ocelli than the occipital foramen; antennal club formed of 3 flagellomeres indicated by distinct annulations that completely encircle club, without ventral micropilosity (except males of *Eridontomerus*, Fig. 124); propodeum (Figs. 388, 412) with spiracular sulcus evident and reaching (or curved towards) the nucha, callus convex and setose; anterior metapleural margin straight; metasternum (Fig. 389) with anterior edge of propodeal foramen about midway between anterior and posterior margins of hind-coxal foramen, metasternal area transversely narrowed to strip half as long (anterior to posterior) as diameter of propodeal



foramen, without metasternal shelf; shortened marginal vein 2 to 4.5 times length of stigmal vein and 1.5 to 2.5 times length of postmarginal vein, stigma width much less than stigmal vein length (Figs. 99-117); hind femur simple (Figs. 135-138), sometimes barely serrate or scalloped (Figs. 139, 428-429), enlarged or swollen (Fig. 142), or toothed (Fig. 140); hind tibia straight (slightly curved in some *Adontomerus*), with apex truncate at right angles and with 1 (rarely, Figs. 136-137) or 2 spurs at ventral corner (Figs. 135, 138-140); metasomal terga not laterally emarginate, usually slightly dorsomedially emarginate (Figs. 90, 94-95, 97), rarely greatly emarginate (Figs. 91-93, 96).

PHYLOGENY . - On the ending hypothesis tree (Fig. 38B) Microdontomerini arises at node 3, one branch of the multifurcation at node 2. Node 2 is diagnosed by the reversal from megastigmine (Fig. 38A) to pteromalid wing venation and node 3 by the change from pteromalid to monodontomerine wing venation (Fig. 42, Character 8). The *Mono* state arises again from the pteromalid state at node 13 and is homoplasious for Toryminae. As explained under the character state discussion (p. 40), the *Mono* state might be composed of 2 states with Microdontomerini having the marginal vein 2 to 4.5 times the length of the stigmal vein but Monodontomerini having the marginal vein 4 to 6.5 times the stigmal vein. Based on the overlap I did not feel justified in separating these into 2 states. The *Mono* state is the same for Microdontomerini and Monodontomerini in having the marginal vein 1.5 to 3 times longer than the postmarginal vein. Both tribes differ from Torymini/Torymoidini, which have the marginal vein 6 (rarely slightly less) to 12 or more times as long as the stigmal vein and 3 to 7 times as long as the postmarginal vein.

Based on the ending hypothesis, Microdontomerini and Torymini/Torymoidini are considered more closely related to each other than to Monodontomerini due largely to the change from a simple hind femur to the toothed state at node 11 (Fig. 38D). This reflects, to some degree, the difficulty in interpreting hind-femoral states and the sporadic nature of the states. In general, Microdontomerini have simple hind femora, but in one clade of the tribe, node 7, the hind femur is autapomorphically modified from the simple state to the *Serrate* state and in some species of *Adontomerus* the hind femur is somewhat swollen. This indicates a predilection towards the hind-femoral modifications which arise at nodes 11, 17, 19, 20, 21 and for various isolated taxa (e.g., *Neopalachia*, *Exopristus*, *Pradontomerus*). Torymini and Torymoidini also demonstrate the tendency for taxa with a simple, primitive hind femur to show homoplasy for this character. In Torymini a few taxa have a single large tooth (e.g., *Diomorus* and a very few species of *Torymus*) whereas in the latter tribe a few taxa have a pronounced angle or slight tooth (e.g., *Pseudotorymus* and *Torymoides*). In Monodontomerini all taxa have a prominent tooth and some have single or double rows of teeth. This evidence, in itself, demonstrates a tendency towards homoplasy in the hind femur, but based on predominance (a technically questionably criterion), it would seem as if Microdontomerini + Torymini/ Torymoidini are primitive relative to Monodontomerini, and that the hind femur of the former grouping has a rare tendency to evolve an independently derived and modified state. As independent support of this premise, while Microdontomerini + Torymini/Torymoidini retain the primitive state of the propodeum (i.e., *Nocarin*), Monodontomerini changes to the derived, *Modified* state. The metasternum also changes at node 15 from the *Crypto* to the *Mono* state,

which indicates that primitive Monodontomerini (i.e., *Zdenekius*, *Rhynchodontomerus*) retain the primitive metasternal state found in Microdontomerini + Torymini/Torymoidini but that more advanced members of the tribe exhibit a derived modification of the metasternal area.

Although the loss of an occipital carina is not noted until node 4, this is due in part to the questionable status of the carina for *Zophodetus* (an amber inclusion). Were it not for this genus, node 3 would also be defined by the major or complete loss of the occipital carina (i.e., *No* state). As suggested by the analysis of this character (p. 32), loss is considered a reversal, and the state is considered derived within the Torymidae. Also, even though the state is coded as an absence, a partial or obscure carina may still be present within the definition of the state.

**SUMMARY.** - The ending hypothesis suggests that Microdontomerini is monophyletic, primitive, and more closely related to Torymini/Torymoidini than to Monodontomerini.

### *Zophodetus* Grissell

Figs. 37(D), 38(B), 86, 112, 121, 144-145

*Zophodetus* Grissell 1980:253. Type-species: *Zophodetus woodruffi* Grissell (orig. desig. and monotypic, FSCA, examined).

NUMBER OF SPECIES (catalog p. 291). - 1.

DISTRIBUTION . - NEOTROPICAL (Dominican Republic).

HOST. - Unknown.

KEYS TO SPECIES. - None.

AGE. - Tertiary, Oligocene, amber.

**RECOGNITION .** - Within Microdontomerini the presumably extinct genus *Zophodetus* is recognized by its concave clypeus (Fig. 86) and complexly carinate propodeum (Fig. 145), both autapomorphies. Other characters which aid in recognition are the simple hind femur (Fig. 144), the marginal vein about 4 times the length of the stigmal vein (Fig. 112), 1 anellus (Fig. 121), and metasomal terga 1-4 slightly emarginate. Also the antennae are inserted closer to the median ocellus than to the apex of the clypeus (Fig. 86), but this is a recognition character only. (The state of the occiput is discussed below.)

**PHYLOGENY .** -

**Working Hypothesis (Fig. 37D):** On the working tree, *Zophodetus* arises at node 15 as part of a trifurcation defined by taxa with most of the metasomal terga having emarginations. The taxon is defined by the concave clypeus (Fig. 86) and carinate propodeum (Fig. 145), which are autapomorphies. The placement of *Zophodetus* at node 15 is due to coding that assessed the wing venation as microdontomerine (i.e., *Mono* state) but the occipital carina as torymoidine (i.e., *Yes* state). For reasons stated next, I recoded the occipital carina as questionable with somewhat predictable results.

**Ending Hypothesis (Fig. 38B):** On the ending tree (Fig. 38B) *Zophodetus* arises

as the basal element of node 3. It is diagnosed by the same 2 autapomorphies as just discussed: the concave clypeus and the elaborately carinate propodeum. A third diagnosed character is the homoplasious state of 4 slightly emarginate metasomal terga, which is hypothesized as derived from the *1/2* state. Four different states for this character are found within the Microdokterini (*1/2, 2A, 1/4, 4*), but this should be construed as an indication of homoplasy rather than relationship. In *Zophodetus* the occipital carina appears to be well developed dorsally and laterally on the right side, but its presence on the left side is questionable due to visibility through the amber matrix. The apparent carina may be an artifact of a collapse of the back of the head, but I can not be certain of this. On the right side, the apparent carina appears to run to the hypostomal carina, but again, it is difficult to be certain of this. As a result of my inability to see the carina with assurance, I coded it as questionable in the ending analysis. This resulted in *Zophodetus* being placed as a basal member of the Monodokterini, based on wing venation (node 3, *Mono* state), as opposed to Torymoidini (node 9, *Tory* state). Determination of the precise state of the occipital carina would, of course, bear on the phylogenetic placement of *Zophodetus*, but as the taxon is known only from a single specimen in amber, its relationships must remain somewhat speculative. Based solely on wing venation, it would appear to be correctly placed within the Microdokterini.

DISCUSSION. - In my original description and discussion of *Zophodetus* (Grissell 1980), I was unsure of its placement but suggested a relationship near *Microdokterus*. The current analysis also suggests this, and its placement as the basal element of Microdokterini indicates that it is among the most primitive taxa of Toryminae. The torymid fauna appears to have been well developed during the Oligocene, based on the presence in Dominican amber of both presumably primitive taxa such as *Zophodetus* and presumably advanced taxa such as *Gummilumpus* and *Podagrion* (unreported specimens of latter in FSCA).

#### *Adontomerus* Nikol'skaya

Figs. 37(C), 38(B), 57, 82-83, 90-91, 106-109, 127-129, 141-143

*Adontomerus* Nikol'skaya 1955:339. Type-species: *Adontomerus eriogasteris* Nikol'skaya (orig. desig. and monotypic, ZIAN, examined).

*Mellitotorymus* Steffan 1964:101-102. Type-species: *Mellitotorymus gregalis* Steffan (monotypic, MNHN, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 178). - 7.

DISTRIBUTION. - PALEARCTIC (Commonwealth of Independent States, Bulgaria, Yugoslavia, Hungary, Italy, Sardinia, Spain, Jordan, Algeria).

HOSTS. - Species have been reared from cocoons of Lasiocampidae (Lepidoptera), galls of Cynipidae (Hymenoptera), and cocoons of Megachilidae (Hymenoptera).

KEYS TO SPECIES. - Zerova and Seregina (1992) gave a key to 3 species in Commonwealth of Independent States.

RECOGNITION. - Within Microdokterini, *Adontomerus* is recognized by a combination of a simple to swollen hind femur (Fig. 141-143), the presence of an occipital

carina (expressed only dorsally) (Fig. 83), the marginal vein 2 to 2.5 (rarely 3) times the length of the stigmal vein (Figs. 106-109), and 1 anellus (Fig. 127, though see discussion below). Additionally, metasomal terga 2 and 3 in both sexes are at least slightly (Fig. 90) to noticeably emarginate medially (Fig. 91).

#### PHYLOGENY AND SYNONYMY. -

Working Hypothesis (Fig. 37C): *Adontomerus* (node 9) is defined by states involving tergal emarginations (node 8), notauli (node 9), and the presence of an occipital carina (*Above* state). It is 2 steps removed from *Mellitotorymus* at node 5, which was also defined by the occipital carina (*Above* state). The first step (node 5 to 8) involves metasomal tergal emarginations and was, I discovered on further analysis, coded inconsistently. Although *Mellitotorymus* was coded as having no emarginations, Mt2 and 3 are faintly emarginate (Fig. 90). *Adontomerus* is the same, and the taxa cannot be distinguished based on this character. The second step (node 8 to 9) involves an interpretation of the faintness or completeness of the notauli. This character was difficult to interpret, and analysis resulted in its recognition as homoplasious, which left these taxa without defining character states. Although *Adontomerus erio-gasteris*, the type species of the genus, has slightly elevated propodeal spiracles, another species placed therein, *A. nesterovi*, does not. The species *A. amygdali* (transferred from *Plastotorymus*, see p. 78) has elevated spiracles, but I do not consider the spiracles as a defining state for the genus *Adontomerus*. As a result of the working hypothesis, I placed *Mellitotorymus* as a junior subjective synonym of *Adontomerus*. The single known species of *Mellitotorymus* is a parasite of megachilid bees, and one of the 7 known species of *Adontomerus* is also a parasite of megachilids. This is perhaps additional evidence that points towards synonymy.

Ending Hypothesis (Fig. 38B): *Adontomerus* arises at node 4, which is diagnosed by the *No* state of the occipital carina (*nb.* that the state allows the presence of a partial carina). It arises as a trifurcation with *Microdontomerus* and node 5, but *Adontomerus* is not defined by apomorphies. *Microdontomerus* has 3 different character states, but *Adontomerus* simply retains the primitive states, namely the propodeum without a median carina, the hind coxa with setae, and metasomal terga 2 and 3 with slight to deep emarginations. Node 5 is a change from 1 anellus to 2, but again *Adontomerus* retains the primitive state. *Adontomerus* and *Microdontomerus* are hypothesized as being closely related, which does not surprise me. At one time I considered them synonyms. I have discussed the evidence for this as well as the relationship of *Adontomerus* to *Idiomacromerus* in additional detail under *Microdontomerus* (see p. 78).

I believe that the phylogenetic conclusions belie my inability to code character states as well as I might have. Subtle diagnostic differences between these taxa suggest they might all be treated as valid genera. For example, in addition to the above 3 changes cited for *Adontomerus* and *Microdontomerus*, *Adontomerus* retains a partial occipital carina (absent in *Microdontomerus*) (partial presence and total absence are both conditions found in the state called *No*). In addition, the marginal vein is 2 to 2.5 (rarely 3) times longer than the stigmal vein (Figs. 106-109) but 3.5 to 4.5 in *Microdontomerus* (Figs. 110-111). I was not able to code this as a distinct subset of the *Mono* state for the purposes of higher classification, but it appears to be of some possible significance in the evolutionary history of these two taxa.

DISCUSSION . - Based on the definitions of *Adontomerus* (given above) and *Microdontomerus* (given below), I transfer the following 4 species to *Adontomerus*: *Microdontomerus crassipes*, *M. impolitus*, *Plastotorymus amygdali*, and *Paraholaspis robusta* (all **new combinations**). The latter two species were transferred to *Microdontomerus* by Bouček (1976b, 1982), but I disagree with this placement based on the synapomorphies outlined above. In the single paratype female of *Adontomerus impolitus* that I have examined, the second flagellomere (= 1st funicular) of the left antenna (Fig. 129) appears to be an anellus (based on lack of multiporous plate sensilla), while that of the right antenna (Fig. 128) is simply reduced but still retains the MPS. In the male paratype examined, both antennae have 2 anelli (as in some *Microdontomerus*, and all *Idiomacromerus*). In the original description and illustrations, *impolitus* was described as having a single anellus. Based on its partial occipital carina, presumed single anellus, and marginal vein only twice the stigmal vein, this species would be placed in *Adontomerus*, but the interpretation of the antennal condition is subjective enough to place the species taxon in *Idiomacromerus*. This is further evidence, in my opinion, that *Microdontomerus*, *Adontomerus*, and *Idiomacromerus* are very closely related taxa.

### *Microdontomerus* Crawford

Figs. 37(B, C, D, F), 38(B), 87, 94-96, 110-111, 130-135, 388-389, 399

- Microdontomerus* Crawford 1907b:179. Type-species: *Torymus anthonomi* Crawford (orig. desig. and monotypic, USNM, examined).  
*Antistrophoplex* Crawford 1914:125. Type-species: *Antistrophoplex bicoloripes* Crawford (orig. desig. and monotypic, USNM, examined).  
*Paraholaspis* Masi 1921a:168-169. Type-species: *Paraholaspis cothurnata* Masi [= *annulata* Spinola] (monotypic, MCSN, examined).  
*Plastotorymus* Masi 1921b:235-236. Unnecessary replacement name for *Paraholaspis* Masi 1921a, believed preoccupied by *Paraholaspis* Berlese 1918:174 (Arachnida).

NUMBER OF SPECIES (catalog p. 202). - 8.

DISTRIBUTION . - This genus is most abundant in the Nearctic, with 4 described species and at least 6 undescribed species. Two species are reported from the Palearctic and 2 are Afrotropical. Reported distributions are summarized as follows: NEARCTIC (transcontinental), PALEARCTIC (Spain, Italy, Algeria, Libya), AFROTROPICAL (Senegal). [The genus was reported in India (see Farooqi 1986, David *et al.* 1990), but this is probably a misidentification based on the confusion in names that existed at the time.]

HOSTS . - Species are reported from megachilid bees and cynipid gall-formers (Hymenoptera), tephritids (Diptera), buprestid eggs and curculionids (Coleoptera), mantid eggs (Mantodea), and coleophorids, gelichiids, lasiocampids, and tortricids (Lepidoptera). Species have also been documented as facultative hyperparasites of braconids (Hymenoptera). At least one undescribed Nearctic species attacks saturniid eggs.

KEYS TO SPECIES . - None.

RECOGNITION . - Within Microdontomerini, *Microdontomerus* is recognized by a combination of a simple hind femur (Fig. 135), the absence of an occipital carina (Fig. 399), the marginal vein 3.5 to 4.5 times the length of the stigmal vein (Figs. 110-111), and 1 anellus in females (funicular 1 may be reduced in atypically small specimens of a species (Figs. 130-134), and males may have 2 anelli even when females have 1). Additionally, the metasomal terga of females are normally slightly emarginate (Fig. 94-95), but in females of a few species Mt2-5 are deeply emarginate (Fig. 96; males of all species have Mt2 at most slightly emarginate, even when they are deeply emarginate in the female).

PHYLOGENY AND SYNONYMY . -

Working Hypothesis: (Fig. 37B): Because of the confusion and complexity surrounding the generic names I primarily treat their synonymy in this section. Some comments are made about phylogeny, but I discuss this matter more completely in the Ending Hypothesis, below. In my analysis I coded character states for the type species of *Microdontomerus* and *Liodontomerus* (now = *Idiomacromerus*), as well as current generic synonyms that differed in at least one character state from the type species of both genera (e.g., *Lochites*). This was an attempt to assess potential generic phylogeny with some objectivity. I also added additional species of questionable generic placement that differed from a type species by one or more character states. This would create either a "broadening" of a single generic definition or indicate the need for more refined definitions of genera. The latter taxa included both described species questionably placed (e.g., *Liodontomerus indicus*, *Microdontomerus crassipes*) and an undescribed species that I could not place to genus (*Microdontomerus* A). This resulted in 4 terminal taxa previously considered in the genus *Microdontomerus* and 6 terminal taxa previously considered in the genus *Liodontomerus*.

As a result of coding all of these taxa, the basal multifurcation at node 5 displayed 8 branches all of which included members either part of, or related to, *Microdontomerus* and *Idiomacromerus*. I next discuss these taxa as well as accepted synonyms in their chronological order (i.e., as listed above in the synonymy).

***Antistrophoplex***: I did not include the genus *Antistrophoplex* in my present analysis, because after preliminary study I could find no character state differences to separate it from *Microdontomerus*. The genus is a synonym of *Microdontomerus* based on my comparison of type specimens and reared series. Bouček (1982) reported this synonymy based on my suggestion to him. The main character used to separate the genera (i.e., emarginate metasomal tergum 2) is an artifact of drying. In *Antistrophoplex bicoloripes* (type of genus) the metasoma is normally compressed from side to side, giving tergum 1 a split appearance. In specimens from the same series, however, tergum 1 is flat enough to show that only a very slight emargination exists (Fig. 95), and there is little difference between terga in the type species of these 2 genera (cf. with *Microdontomerus*, Fig. 94). Even if there were, I have demonstrated that the tergal emarginations are homoplasious (see p. 52). Bouček (1976b:347) earlier synonymized *Senegalella* and *Paraholaspis* with *Antistrophoplex* (and thus eventually *Microdontomerus*), but I do not agree with the placement of *Senegalella*, which I treat as a synonym of *Pseudotorymus* for reasons stated under the latter genus (p. 107).

*Paraholaspis* (node 15) / *Plastotorymus*: Steffan (1962:30) was the first to point out that *Plastotorymus* was an unnecessary new name for *Paraholaspis* of Masi. Bouček (1965:544) followed this synonymy as do I. Although Bouček (1976b, 1982) synonymized this genus with *Microdontomerus*, I placed the monotypic *Paraholaspis* in my analysis based on its type, *P. cothurnata* (now = *annulata*), to determine its hypothetical phylogenetic position. The genus arose at stem 15 with no apomorphies, but it does differ from other members of the node by lacking the occipital carina (the negative state of this character was coded as questionable as discussed for the character in the “Phylogenetic Analyses” section). *Paraholaspis* differs from typical *Microdontomerus* in females only by having metasomal terga 2–6 deeply split medially (Fig. 96; males with Mt2 only emarginate) whereas known *Microdontomerus* species have these terga essentially entire. It arises two steps higher (node 15) than *Microdontomerus* (node 5) based solely on this difference, and as part of the trifurcation that includes *Zophodetus*.

Askew and Nieves (1988) suggested that *Paraholaspis* was a valid taxon and should not be included with *Microdontomerus*. They stated that *Paraholaspis* differed in the following characters: the hind coxal edge bare, but it is nearly bare in some species of *Microdontomerus* and completely bare in the type-species *M. anthonomi* (in addition to which hind-coxal setae appear to have no generic significance as discussed in the “Phylogenetic Analyses” section); the hind femur only moderately broad, which is true also in *M. anthonomi*; the hind tibia with its inner apical spur not twice as long as its outer spur, which is true for *M. anthonomi*; and a fine, but distinct median propodeal carina. Several species of *Microdontomerus*, including *M. anthonomi* (which was miscoded in the data), have such a carina, while most do not. Additionally, it can be noted that *Paraholaspis* differs from the type of *M. anthonomi* in its brilliant metallic color. Most New World *Microdontomerus* (including *anthonomi*) are reddish brown or black. Color comparisons do not hold up well, however, because within a single species, or even a single rearing, (e.g., *M. anthidii*) the color may vary from black to dull metallic red to green.

In addition to the factors just listed, I have examined 6 undescribed Nearctic species which I place as *Microdontomerus*, and one of them has Mt2–6 deeply emarginate as does *Paraholaspis annulata*. Even though I had thought that *P. annulata* should remain a distinct taxon, I cannot see any basis from phylogenetic evidence to justify this position. My conclusion is that *P. annulata* is an Old World derived species of *Microdontomerus* and that it has a New World parallelism in at least one undescribed species. As the genus was synonymized by Bouček (1976b, 1982), my work provides additional evidence in support of his decision.

Among 6 undescribed New World *Microdontomerus* are forms with Mt2 and 3 (and Mt2–6) distinctly emarginate, forms with a median propodeal carina (as for *P. annulata*), and forms with the hind coxa distinctly bare or just barely setose. I see no basis for recognizing each unique combination of characters as a distinct genus-level taxon. Additionally, I have found several Old World specimens identified as “*Paraholaspis*” in the collection of the USNM that vary as do the New World species. Two specimens, one from Egypt and one from Iran, are identical to *Paraholaspis sensu* authors in all respects, including the brilliant coloration, except that only metasomal terga 2 and 3 are emarginate, and these just barely. These specimens, it could be hypothesized, are closer to the *Microdontomerus*-like ancestor and parallel in development to

the New World forms.

*Microdoktermerus* (node 5) / *Idiomacromerus* (node 5): The working tree itself is unresolved concerning these two genera and their relationships. Putative synonyms are spread over a number of basal branches between nodes 5 and 15. Most of these terminal taxa are relegated to synonymy, as discussed under *Idiomacromerus* (p. 85), and it is pointless to cite the working tree as providing much in the way of phylogenetic information at this point. I discuss the relationships in the Ending Hypothesis, below and under the genus *Idiomacromerus*.

?*Microdoktermerus* sp. (node 10): This undescribed taxon was included in my analysis because it had metasomal terga 2 and 3 emarginate and had the hind coxa slightly setose dorsally. This differed from the type species of *Microdoktermerus*, which has no tergal emarginations (or extremely minute on Mt2) and has the hind coxa asetose dorsally. ?*Microdoktermerus* sp. arose at node 10, 2 steps from *Microdoktermerus* (node 5): the first step is a change from 0 to 2 metasomal tergal emarginations (node 8) and the second a change from a setose coxal dorsum (*Yes*) to only slightly setose (*Yes\**; node 10). Both of these characters are homoplasious. Although ?*Microdoktermerus* sp. and *Lochimerus* arise at node 10, neither is defined by apomorphies. This is because the anelli were not read into the Working Hypothesis tree, and the absence of an occipital carina was coded as questionable data (see Phylogeny). If both are considered, then ?*Microdoktermerus* sp. (anelli state *I*; carina state *No*) becomes an undescribed species of *Microdoktermerus*. The position of *Lochimerus* (anelli state 5; carina state *No*) is more problematic and is discussed under *Idiomacromerus*.

Ending Hypothesis (Fig. 38B): *Microdoktermerus* arises at node 4, which is diagnosed by the *No* state of the occipital carina. It arises as a trifurcation with *Adontomerus* and node 5. *Microdoktermerus* has 3 character state changes: the propodeum from *Nocarin* to *One\**, the hind-coxal setae from *Yes* to *Yes\**, and metasomal terga from *I/2* to *I/4*. *Adontomerus* retains the primitive states for the characters just listed. Node 5 is a change from 1 anellus to 2, and both *Microdoktermerus* and *Adontomerus* retain the primitive state.

Unfortunately, these states are homoplasious, rather difficult to code, and create difficulties in interpreting phylogeny. The tree suggests that *Adontomerus* and *Microdoktermerus* should probably best be treated as synonyms with node 5 as a sister group. In the case of *Adontomerus* and *Microdoktermerus*, I believe that retention of the names is of some value based on the discussion which follows. After that discussion I explain also the relationship of *Microdoktermerus* with *Idiomacromerus*.

*Microdoktermerus* (node 4) / *Adontomerus* (node 4): With reference to the 3 character state changes outlined above, I do not believe they lend much credibility for establishing monophyly of either taxon or a taxon of both combined. In the case of the propodeum, for example, *Adontomerus* does not have a carina, but the state is variable within *Microdoktermerus* (coded as such with the state *One\**, which combines taxa which have the *Nocarin* and *One* states). The hind-coxal setae also are variable for *Microdoktermerus*, ranging from none to sparsely setose (I miscoded this for *Microdoktermerus*, but the consistency is so low for the character I don't think it matters). The tergal emarginations, though technically coded correctly for *Microdoktermerus*, are inclusive of the states found in *Adontomerus*, so the character does not help establish distinctions between the two.



In recoding the states for occipital carina in the ending hypothesis, I defined the state of *No* to include both the absence of the carina and its reduction to a band confined to the dorsal region of the head. I did this because the two conditions are not always easy to differentiate. In the case of *Microdontomerus* and *Adontomerus* the distinction is clear: the former has no carina while the latter does. Secondly, the wing venation may also help in this regard, but I did not fully appreciate the distinction until the analysis was complete. In *Microdontomerus* the marginal vein is 3.5 to 4.5 times as long as the stigmal vein, whereas in *Adontomerus* the marginal vein is 2 to 2.5 times (rarely 3) as long. Thirdly, whereas *Microdontomerus* is largely Holarctic in distribution, *Adontomerus* so far is known only from the Palearctic (7 species). This might suggest a possible vicariant event in which *Adontomerus* was derived from the more cosmopolitan *Microdontomerus*, or it might suggest that *Microdontomerus* was the derived group which became a more successful invader of the New World. This latter hypothesis more clearly fits the morphological evidence because *Microdontomerus* would be considered the more derived taxon based on the loss of the occipital carina, the elongation of the marginal vein (relative to the stigmal vein), and the 3 derived states mentioned above (homoplasious though they may be). Not unexpectedly, the known species of both genera are parasitic on similar hosts in the Lepidoptera and Hymenoptera.

The evidence just presented argues in favor of retaining morphological and nomenclatural distinctions, but my treatment of the genus *Idiomacromerus* would argue equally well against it. In *Idiomacromerus* forms with or without the occipital carina are included within the definition of the genus. In that taxon, however, the carina, when present, is often difficult to see or interpret, as it is effaced and vague. In *Microdontomerus* and *Adontomerus* the carina is either absent or well developed (dorsally). Arguably the differences are small, and *Adontomerus* could be combined with *Microdontomerus*, in which case *Adontomerus* would become a subjective junior synonym. I am taking a more conservative approach to the resolution of this question. Because the wing venation of *Microdontomerus* and *Adontomerus* differs enough to diagnose them (both taxa overlap *Idiomacromerus* but not each other), I am using this as additional evidence with relation to the occipital carina upon which to retain them as distinct taxa. My hypothesis is that *Microdontomerus* is the more derived taxon of the two.

***Microdontomerus* (node 4) / *Idiomacromerus* (node 5):** *Microdontomerus* arises one step lower (node 4) than *Idiomacromerus* (node 5) which is diagnosed based on the change from 1 anellus to 2 (node 5) and then to 2\* (2, 3, or 5 anelli). *Idiomacromerus* is also defined (within the node) by the hind coxa with sparse dorsal setae, but as this is the same state found in *Microdontomerus* it offers no additional phylogenetic information. Similarly, the state of the propodeum offers no additional help. The propodeal state for *Microdontomerus* (*One\**) combines propodea with no carina (*Nocarin*) or a single carina and is thus not a true synapomorphy with respect to *Idiomacromerus* (*Nocarin*). The metasomal state 1/4 for *Microdontomerus* similarly includes members which may have 1/2 (the plesiomorphic condition) as found in *Idiomacromerus*. In *Microdontomerus* (and *Adontomerus*) I considered a comparison of the length of the marginal vein to the length of the stigmal vein as a potential phylogenetic character (later abandoned for phylogenetic purposes), but both taxa overlap the condition for *Idiomacromerus*, and so this is of no help in reconciling the problem

of relationship. In effect, the only potential source of phylogenetic information to be gleaned from morphology appears to lie in the antenna. The change in anelli, therefore, becomes the single defining point (it is somewhat irrelevant whether it is more than 2 (i.e., 2\*) for the remainder of this discussion).

The genus *Microdontomerus* was treated as distinct from *Idiomacromerus* (as *Liodontomerus*) based on the former having 1 anellus and the latter having 2 or sometimes more anelli (Gahan 1914, Szelenyi 1957b). In the transformation series analysis, 2 anelli are hypothesized to be a derived reversal from a single anellus (see p. 34). This makes sense within Torymidae because it seems more straightforward to begin with "normal" funicular segments and to reduce them to form anelli, rather than to begin with anelli and enlarge them to become funicular segments. Under this hypothesis, *Microdontomerus* + *Adontomerus* is the plesiomorphic sister group to *Idiomacromerus*. In studying *Microdontomerus*, including the type-species *M. anthonomi*, I became aware that while a single anellus is the groundplan state for the genus, both females and males may occasionally have 2 anelli in dwarf (or atypically small) specimens (Fig. 130). Additionally, an undescribed Nearctic species has females with 1 anellus and males with 2 or 3 anelli. Alternatively, females and males of the Palearctic species *Liodontomerus* (now = *Idiomacromerus*) *mayri* have one distinct anellus and a reduced second flagellomere. Thus, even the apparently practical use of anelli is not without problems and must be tempered as the basis for defining genera. It would be possible, in my opinion, to use this sort of data to place *Idiomacromerus* as a subjective junior synonym of *Microdontomerus*, but where this state has proven consistent for two taxa, as in the case of *Torymoides* and *Pseudotorymus*, there is some practical, as well as potentially phylogenetic, significance in accepting the condition as informative. At present the anelli may be used with some reservation to determine generic placement, and in my opinion it better serves the eventual clarification of phylogeny to take the nomenclaturally conservative approach in this particular situation.

Biological information may also be of limited use in reconciling relationships between the two groups. *Microdontomerus anthonomi* (the type-species) is a primary and secondary parasite of weevils and bruchids in seed pods of legumes and gall-forming Lepidoptera, tephritids, and braconid parasites associated with flower heads of composites and malvaceous plants (Turner *et al.* 1990). Additional hosts in *Microdontomerus* include bees, cynipid gall-formers, eggs of buprestids, and eggs of saturniids (undescribed Neotropical species). *Idiomacromerus bimaculipennis* (the type-species) is reared from eurytomids in seed pods of *Rhus*. [*Liodontomerus perplexus*, type-species of *Liodontomerus*, is reared from eurytomids in seed pods of alfalfa.] Additional hosts of *Idiomacromerus* include cynipid gall-formers and hosts in seed heads of composites and poppies.

Although both *Microdontomerus* and *Idiomacromerus* parasitize hosts enclosed in plant tissue (except for the egg parasites), where overlap of host-habitat occurs the specific host is different. For example, *Microdontomerus* attacks seed-feeding bruchids in legume pods, but *Idiomacromerus* attacks seed-feeding eurytomids; *Microdontomerus* attacks gall-forming Lepidoptera, but *Idiomacromerus* attacks gall-forming Hymenoptera. These differences perhaps should be considered as general guidelines, because the exact host relationships of both genera are poorly known. *Microdontomerus anthonomi*, biologically probably the best known species, is both a

primary parasitoid on bruchids, weevils, and tephritids and a facultative secondary parasitoid on braconids associated with these hosts (Turner *et al.* 1990). Within reason, there is some indication that *Microdontomerus* and *Idiomacromerus* differ in host usage, and this supplies an additional rationale for retaining generic concepts for the present.

DISCUSSION . - The recognition and definition of *Microdontomerus* has been somewhat difficult to elucidate and requires some discussion, especially with regard to *Adontomerus* and *Idiomacromerus*, itself a study in complexity. The species involved in these genera are confounding due, in part, to their initially vague historical definitions, the degree of acceptable character state variation used to define the taxa, and their frequent and confusing transfer from one genus to another. Askew and Nieves (1988:358), for example, commented that species of *Microdontomerus* and *Liodontomerus* (now = *Idiomacromerus*), along with their collection of synonyms, had "... increased morphological variation within the genera to the point where morphological distinctions between them are blurred and need to be based on combinations of characters." Some of these "synonyms" are monotypic Palearctic "genera" that differ in one character state from the already ill-defined *Idiomacromerus* or *Microdontomerus*. The relationship of both to *Adontomerus* has not previously been recognized.

Part of the problem of "blurring" of taxa has been solved by the removal of several species, which I demonstrate to be wrongly placed. For example in *Microdontomerus* Bouček (1976b) synonymized *Senegalella* with *Antistrophoplex* which he later (1982) synonymized under *Microdontomerus*. However, I transfer *Senegalella* to *Pseudotorymus* (see p.107 for reasons). Bouček (1982) placed *Lochitimorpha* in *Liodontomerus* (now = *Idiomacromerus*) but I transfer it to *Pseuderimerus* (see p. 90 for reasons). Similarly Bouček transferred *Torymus mesembryanthemumi* (in 1976b) and *Hemitorymus africanus* (in 1978) to *Antistrophoplex* (and thus *Microdontomerus*), but I place these species in *Pseudotorymus* (see p. 254 and 258 for reasons). Also, I transfer several species placed in *Microdontomerus* by Bouček (1982) and Askew and Nieves (1988) to the genus *Adontomerus*. These include (cited in original combinations) *Microdontomerus crassipes*, *M. impolitus*, *Paraholaspis robusta*, and *Plastotorymus amygdali*. With the removal of these taxa the definitions of *Microdontomerus*, *Adontomerus*, and *Idiomacromerus* each becomes more discrete, if not still somewhat problematic.

There is no doubt in my mind that *Microdontomerus*, *Idiomacromerus*, and *Adontomerus* (along with their synonyms) are extremely closely related. In fact for a period of time I considered the entire assemblage congeneric and had placed all species in the genus *Microdontomerus*. I still have reservations that this may be more accurate, but I have adopted some practical constraints to try to resolve our understanding of the phylogeny of these genera. I have made every attempt to retain a conservative nomenclature, one that does not cause more confusion than it tries to correct. To do so has required a slight degree of "compromise" between absolutely strict phylogenetic interpretation and nomenclatural practicality.

***Idiomacromerus* Crawford**

Figs. 37(B, C), 38(B), 58, 72-81, 84-85, 97-105, 138, 401

- Lochites* Förster 1856:43-44. Type-species: *Lochites papaveris* Förster (monotypic, ?NMW, USNM, examined). Preocc. by *Lochites* Gistl 1848 (Protozoa).
- Idiomacromerus* Crawford 1914:124-125 [26 September 1914]. Type-species: *Idiomacromerus bimaculipennis* Crawford (orig. desig. and monotypic, USNM, examined).
- Liodontomerus* Gahan 1914:159 [16 December 1914]. Type-species: *Liodontomerus perplexus* Gahan (orig. desig. and monotypic, USNM, examined). **New synonymy.**
- Lochitisca* Ghesquière 1946:368. Objective replacement name for *Lochites* Förster nec Gistl.
- Lochimerus* Szelenyi 1957b:382-383. Type-species: *Liodontomerus balasi* Szelenyi (orig. desig. and monotypic, HNHM, examined).
- Liutorymus* Steffan 1962b:31. Type-species: *Liutorymus regillus* Steffan (monotypic, IZ, examined).
- Liodontomerus* subgenus *Conolochites* Bouček 1982:189-190. Type-species: *Liodontomerus (Conolochites) nitens* Bouček (orig. desig. and monotypic, BMNH, examined).

NUMBER OF SPECIES (catalog p. 195). - 26.

DISTRIBUTION . - Most species of *Idiomacromerus* (19) are Palearctic and 2 are Afrotropical. One species is endemic to the Nearctic, but several have probably been introduced. Their reported distribution is summarized as follows: HOLLAND-ARCTIC (widespread throughout), NEOTROPICAL (Mexico), AUSTRALIAN (New Zealand, introduced), AFROTROPICAL (Madagascar).

HOSTS . - This genus has been reared from numerous gall-forming and seed-feeding insects. Hosts include gall-forming Cynipidae (Hymenoptera) on Asteraceae, Rosaceae, and Papaveraceae; galls of Cecidomyiidae (Diptera); seeds of Fabaceae and Anacardiaceae infested with Eurytomidae (Hymenoptera); unknown gall-formers on racemes of Orchidaceae; and Mengenillidae (Strepsiptera).

KEYS TO SPECIES . - Partial keys for Nearctic species were provided by Burks (1958), for Palearctic species by Szelenyi (1957a, 1959), for Hungary by Erdős (1960), and for Commonwealth of Independent States by Nikol'skaya and Zerova (1978).

RECOGNITION . - Within Microdontomerini, *Idiomacromerus* is recognized by a combination of a simple hind femur (Fig. 138), the occipital carina absent or weakly expressed (Fig. 401), marginal vein 2 to 4.5 times as long as the stigmal vein (Fig. 99-105), 2 or more anelli, and the unreduced eyes of the male (Figs. 84-85, cf. Figs. 88-89). Additionally, in females, Mt2 and 3 are at most somewhat emarginate (Figs. 97-98), in males only Mt2 is very slightly emarginate medially.

PHYLOGENY AND SYNONYMY . -

Working Hypothesis (Fig. 37B): The basal multifurcations at node 5 and 8 say little about relationship and are based largely on a change in character state involving tergal emarginations, a highly homoplasious character. As can be seen from these branches, most of the taxa have no apomorphies when the state of the anellus is not included in the analysis, or when the occipital carina is coded as questionable for the

*No* state (see Phylogeny). Most of the taxa included under *Idiomacromerus* (i.e., list of synonyms above) differ only in the physical structure of a single character state that varies from one monotypic genus to another. Monotypic taxa are essentially species-level taxa, and to know how a genus is defined requires more than one species. After establishing the tree, I compared these taxa one to the other to see what state was defining each branch. If the branches were defined by states that appeared to be homoplasious, or that were difficult to elucidate (e.g., tergal emarginations), or that were difficult to code consistently, then I tentatively placed the taxa together to determine what then would define the group. The discussion which follows summarizes each generic taxon previously considered valid and now included under the name *Idiomacromerus* and the reasons for their synonymy. Then I present the results of the ending hypothesis.

Historically the nomenclature of *Idiomacromerus* (as *Liodontomerus*) has been unsettled and somewhat complex. Peck (1951) synonymized *Lochites/Lochitisca* (node 8) with *Liodontomerus* (node 8). Bouček (1982) reduced *Lochimereus* (node 10), *Lochitimorpha* (node 5), and *Liotorymus* (node 5) to subgenera of *Liodontomerus* and described *Conolochites* (not treated in analysis, see below) as another subgenus. I transfer *Lochitimorpha* to *Pseuderimerus* (node 6) for reasons which I discuss under the latter generic name. I synonymize *Liodontomerus* under *Idiomacromerus* (node 5) for reasons given below (p. 87). I have not attempted to recognize subgenera, but the currently recognized definitions given by Bouček (1982) are subjective enough so as to preclude easy recognition without access to all taxa at one time for comparative purposes. Each "subgenus" is based on 1, or at most 2, species, and for this reason probably represent only derived taxa in an otherwise speciose group.

***Lochites* (node 8) / *Lochitisca*:** The generic name *Lochites* was discovered to be preoccupied, and *Lochitisca* was proposed as a replacement name by Ghesquière (1946). Peck (1951) synonymized *Lochitisca* (and thus *Lochites*) with *Liodontomerus*. I retained the name *Lochites* for purposes of analysis, because it differed in one character state (occipital carina) from *Liodontomerus*, and I compared the type-species of both (i.e., *Lochites papaveris* and *Liodontomerus perplexus*). In the working hypothesis *Lochites* and *Liodontomerus* arose at node 8, where they differed solely on the basis of the occipital carina. In the Working Hypothesis a *No* state (*Liodontomerus*) was coded as a question mark and thus does not appear on the tree as an apomorphy for *Liodontomerus* (see p. 32), whereas the *Yes* state found in *Lochites* is considered the groundplan for Torymidae. The implication of this treatment is discussed next.

***Idiomacromerus* (node 5) / *Lochites* (node 8):** *Idiomacromerus* arises with the basal multifurcation at node 5. It is one step removed from *Lochites* (node 8), based on a supposed lack of tergal emarginations in the former (coded 0) and the presence of Mt3+4 with weak emarginations in the latter. This coding, however, is incorrect. In reexamining terga I have come to the conclusion that the difference between *Lochites* (coded as 2) and *Idiomacromerus* (coded as 0) is due to the difficulty of interpreting tergal emarginations and that this is reflected in the homoplasious nature of the character on the tree (see "Phylogenetic Analyses" section, p. 52 for discussion). Both taxa agree in possessing an occipital carina (groundplan state *Yes*) and disagree in this respect from *Liodontomerus* (state *No*). Therefore if one were to establish a classification based on the presence or absence of an occipital carina, the only difference in fact

between *Lochites* and *Liodontomerus*, then the preoccupied name *Lochites* would have to be replaced by the older name *Idiomacromerus* and *Liodontomerus* would remain a valid taxon.

***Idiomacromerus* (node 5) / *Liodontomerus* (node 8):** The relationship of *Idiomacromerus* (node 5) to *Liodontomerus* (node 8) is the same as to *Lochites* (node 8). As explained for *Lochites*, I miscoded (or misinterpreted) the tergal emarginations and the only actual differences between *Idiomacromerus* and *Liodontomerus* are the presence of an occipital carina in the former (absent in type-species of *Liodontomerus perplexus*) and some aspects of facial proportions (as discussed below). Unfortunately even the carinal difference is not clear cut. It is often difficult to tell if a carina is present or not. The carina requires a subjective assessment and may be seen in some angles of light but not others. Even within a series of the same species the decision is not straightforward. In *Idiomacromerus bimaculipennis*, for example, some specimens have a distinct, crisp edge to the carina, while in others one must look at various angles before finding the merest outline of the carina. Often the distinction between a carina and a slight fold or alignment of reticulations is not all that great. As we are dealing with only the 2 type-species, if each is diagnosed as a genus-grade clade, then we would have to assume that each is a monophyletic unit. I am not certain this assumption is valid without an examination of all included species.

*Idiomacromerus bimaculipennis* differs from *Liodontomerus perplexus* also in antennal placement and facial proportions, with the toruli higher on the face and with a relatively longer distance between the eyes in *bimaculipennis* (Fig. 80) than in *perplexus* (Fig. 77). Other Palearctic type-species of genera (e.g., *Liotorymus regillus* Fig. 79; *Lochimerus balasi* Fig. 76; *Lochites papaveris* Fig. 74) differ from each other in position of antennal insertion and facial proportions, but I have already dismissed the torulus character as not being of generic rank (see p. 54), and I am not convinced that facial proportions are of generic rank either. Again, if each facial proportion or torulus placement is diagnosed as a genus-grade clade, then we would have to assume that discrete differences exist that define monophyletic units.

As I can see no clear-cut, workable (or even practical) solution to the recognition of monophyletic groupings between *Idiomacromerus* and *Liodontomerus*, I place the two in synonymy. Unfortunately, the less well known name is the older of the two by several months.

***Lochimerus* (node 10):** Bouček (1982) placed *Lochimerus* as a subgenus of *Liodontomerus*. Only one species is known, *Lochimerus balasi*. I placed the taxon as a valid genus in my analysis to see where it would arise on the tree. There is only one step difference between *Lochimerus* and *Liodontomerus* (nodes 8 to 10), and this is the result of the hind coxa having relatively fewer and more widely spaced setae in *Lochimerus*. As I pointed out in the "Phylogenetic Analyses" section (p. 49), at best this is probably a species, or species group, character. *Lochimerus* does differ from typical *Liodontomerus* in having reduced flagellomeres in addition to the 2 anelli. It is somewhat debatable whether *Lochimerus* has 2 anelli and 3 reduced funiculars or 5 anelli. Regardless of the true number, it appears to be a reduction phenomenon and appears to have little impact on the phylogenetic placement of *Lochimerus*. I agree with Bouček (1982) in his placement of *Lochimerus* with *Liodontomerus* (and thus of *Idiomacromerus*). The species *balasi* has the toruli placed very low on the face (Fig. 76) compared to other *Idiomacromerus* (Figs. 72-75, 77, 79-80).

***Liotorymus*** (node 5): Bouček (1982) placed *Liotorymus* as a subgenus of *Liodontomerus* and placed *Liodontomerus splendens* (*lapsus* for *splendidus*) Szelenyi in the same subgenus. Based on the type species, *Liotorymus regillus*, I placed the taxon as a valid genus in my analysis to see where it would arise on the tree. There is only a one step difference between *Liotorymus* (node 5) and node 8, and this is the result of coding the terga for *Liotorymus* as “?” (i.e., unknown). I now know that the terga should have been coded as 2. As *Liotorymus* differs in no coded characters from *Lochites*, its treatment should be the same as that taxon for phylogenetic purposes, and I therefore treat it as an *Idiomacromerus*, based on the above discussion for *Lochites*. The taxon does differ, however, in having the marginal vein almost 4.5 times longer than the stigmal vein (Fig. 105) whereas most other species of *Idiomacromerus* have the marginal vein 2 to 3 times the length of the stigmal vein (Figs. 100, 102-104). The species *Liodontomerus splendidus* (now = *Idiomacromerus*) has the marginal vein about 3.5 to 4 times as long as the stigmal vein (Fig. 101), so it is possible that if more species are found that have a long marginal vein, and the state appears to remain consistent, a sub-genus level taxon could be recognized. The likelihood of finding intermediate vein forms seems a more likely possibility to me.

***Conolochites*** (not on tree): Bouček (1982) described *Conolochites* as a subgenus of *Liodontomerus*, based on some rather subjective differences in habitus. I did not include it as a terminal taxon in my analysis, as it did not differ in any character states from *Liotorymus*. It has an occipital carina. Because I have not studied all Old World species of *Liodontomerus*, I cannot propose a system of subgeneric taxa. I see little difference between this subgenus and the subgenus *Liotorymus*, and in my opinion they are the same. If subgenera were recognized, I would place *Conolochites* and *Liotorymus* together.

***Eridontomerus* A** (node 5): This is a reared, undescribed species from California, for which I could make no initial satisfactory generic placement. In overall phenetic appearance it approaches *Eridontomerus*. After analysis it was found to be part of the multifurcation at node 5. It is 3 steps (nodes 8, 11, 12) removed from *Eridontomerus* and lacks the autapomorphy that defines node 12 (the double propodeal carinae) as well as the autapomorphy that defines node 11 (the serrate hind femur). It arises with *Microdontomerus* (node 5), differing only in possessing a dorsal weak occipital carina (*Above*) (it differs also by having 3 anelli, but this was not read into the working analysis). It is 1 step from *Liodontomerus* (node 8), from which it differs by having metasomal tergum 2 emarginate (*Liodontomerus* with Mt2 and 3 emarginate), by having an extremely weak occipital carina (absent from the type species of *Liodontomerus*), and by possessing 3 anelli (2 in *Liodontomerus*). The subject of metasomal tergal emarginations is discussed in the “Phylogenetic Analyses” section (p. 52), and not much weight is placed on them because of the amount of homoplasy. The presence of an occipital carina, weak though it may be, and the 3 anelli agrees with my interpretation of *Idiomacromerus* rather than of *Microdontomerus* and, in my opinion, this taxon simply represents an undescribed species of the former.

Ending Hypothesis (Fig. 38B): On this tree, *Idiomacromerus* arises at node 5 as part of a trifurcation. The node is diagnosed by the change in anelli from 1 to 2. *Idiomacromerus* is defined by the apomorphy of 2\* anelli (single terminal taxon having 2, 3, or 5 anelli--or reduced basal flagellomeres-- within the taxon) and the hind-coxal setae sparse and widely spaced (*Yes*\*). Both of these states are homoplasious. The

genus retains the primitive state of the hind femur (*Simple*) which changes at node 7 to *Serrate* and retains the hind-tibial spur number of 2 and the unreduced male eye which change at node 6 to 1 and reduced respectively. *Idiomacromeris* is hypothesized to be derived with respect to *Microdoktermeris* and *Adontoktermeris*, based on the reduction of the second flagellomere (= anellus) and loss of multiporous plate sensilla. I have discussed *Idiomacromeris* in relation to both of these genera above under *Microdoktermeris* (see p. 81).

DISCUSSION. - The genus *Idiomacromeris* is a complex of similarly appearing species, many of which have been given generic rank based on slight differences in numbers of reduced flagellomeres, sculpture, body shape, antennal placement, and so forth. As a result of my study, I believe that most of this variation is only of species-level ranking. My emphasis has been on studying the type-species of each genus, and I have not been able to study all species of the group. It is possible that some taxa assigned to this genus in the catalog are misplaced. In the past, *Lochitimorpha* (with its only described species *indicus*) was placed in *Liodontoktermeris*, but I transfer it to *Pseuderimeris* and give reasons for my action under that genus (see p. 91).

The 5 neotropical species described by Kieffer and Jorgensen (1910) as *Lochites* (= *Idiomacromeris*) are, in my opinion, *Torymoides*. The types are presumed lost, and no one has seen specimens to confirm their correct generic placement. The fact that all were reared from cecidomyiid galls provides some evidence for suspicion, because known hosts of *Idiomacromeris*, as broad-ranging as they are, include only one Old World species (*Idiomacromeris balasi*) that attacks cecidomyiids. In their descriptions, Kieffer and Jorgensen (1910) state that the stigmal club is nearly sessile and "Torymus-like," and that 2 anelli are present. Because Kieffer and Jorgensen also described species of *Torymus*, we must presume that they could tell the difference between *Torymus* and non-*Torymus* taxa. The most closely *Torymus*-like taxon likely to fit all of the descriptive and biological facts is *Torymoides*. This genus has a sessile (*Torymus*-like) stigma, 2 anelli, is reared from cecidomyiids, and is found throughout the New World (both described and undescribed species). Based on this hypothesis, I transferred these 5 species to *Torymoides* in the catalog (p. 263).

After removing the above taxa from *Idiomacromeris*, I am of the opinion that among described Nearctic *Idiomacromeris* only *I. bimaculipennis* is truly Nearctic and that the remaining 3 described species, considered Holarctic in distribution, are introduced from the Palearctic into the Nearctic: *Liodontoktermeris insuetus*, *L. longfellowi*, and *L. perplexus*. Respectively, these species parasitize the clover chalcid (*Bruchophagus gibbus*) on *Melilotus* sp. and *Trifolium* sp., the trefoil chalcid (*B. platyptera*) on *Lotus corniculatus*, and the alfalfa chalcid (*B. roddi*) on *Medicago sativa*. Each of these plants is endemic to the Old World and only reached the New World by introduction (Bailey 1949). Each of the 3 eurytomid hosts is found throughout the Palearctic as are each of the 3 parasites. They are contained in mature seed of the hosts and are thus easily transported. It is less parsimonious to assume that 3 different eurytomid hosts and 3 different torymid parasites were native New World taxa that moved onto introduced plants and then were carried back to the Old World.

There is at least one undescribed Nearctic species (as discussed above, see "Eridontoktermeris A") that is related to Palearctic forms and that is reared from seed pods of



an endemic umbellifer in California. The genus, therefore, appears to be truly Holarctic in distribution.

*Pseuderimerus* Gahan

Figs. 37(B), 38(B), 88-89, 114, 118-119, 136

*Pseuderimerus* Gahan 1919a:124. Type-species: *Pseuderimerus mayetiolae* Gahan (orig. desig. and monotypic, USNM, examined).

*Lochitimorpha* Szelenyi 1957b:382. Type-species: *Lochitimorpha semiaenea* Szelenyi (orig. desig. and monotypic, HNHM, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 252). - 8.

DISTRIBUTION . - Three species are reported from the Nearctic, 4 species from the Palearctic, and a single species is known from northern India. Reported distribution is summarized as follows: NEARCTIC (USA: California), PALEARCTIC (Tadzhikistan, Czechoslovakia, Hungary, Morocco, Sudan), ORIENTAL (India: Delhi).

HOSTS. - Reared from Eurytomidae (Hymenoptera) and Cecidomyiidae (Diptera) in wheat and barley stems (Poaceae), and from Eurytomidae in seeds of umbellifers (Apiaceae).

KEYS TO SPECIES. - Erdös (1960) gave a key to species of Hungary, and Zerova and Seregina (1990) to species of the Commonwealth of Independent States.

RECOGNITION . - Within Microdontomerini, *Pseuderimerus* is recognized by a simple hind femur (Fig. 136), the hind tibia with 1 apical spur (Fig. 136), the female with an apical spicula on the antennal club (autapomorphy; Figs. 118-119), females and males with a single, distinctly wider than long "anellus" (Fig. 118; but see discussion below) plus 1 to 5 reduced basal flagellomeres, and males with eyes reduced (Figs. 88-89).

PHYLOGENY AND SYNONYMY. - In my analyses, both working (Fig. 37B, node 6) and ending (Fig. 38B, node 6), *Pseuderimerus* + *Erimerus* always occur together based on two synapomorphies: the hind tibia having one apical spur (reduction from groundplan state of 2) and the reduction in size of male eyes (reduction from groundplan state of *Norm*). The eye state occurs only once in the subfamily Toryminae, but the single hind-tibial spur occurs twice, once here and again at node 24 (ending hypothesis; Fig. 38F). These are considered to be independent derivations of the state, arising far apart as they do in apparently unrelated groups. In the working hypothesis *Pseuderimerus* + *Erimerus* were additionally grouped by the lack of occipital carina which was coded as questionable for the state (see Phylogeny).

Working Hypothesis (Fig. 37B): Some taxa were associated with node 6, which must be discussed before moving on to the ending hypothesis, in which I discuss the relationship of *Pseuderimerus* with *Erimerus*.

*Lochitimorpha* (node 5): Bouček (1982) placed *Lochitimorpha* as a subgenus of *Liodontomerus* (now = *Idiomacromerus*). Only one species is known, *Lochitimorpha semiaenea*. In the working hypothesis I placed the taxon as a valid genus to see where it would arise on the tree. For *Lochitimorpha* there is a one step difference between it

and *Liodontomerus* (from node 5 to 8), and this is the result of the metasomal terga being coded as having no emarginations in *Lochitimorpha* and 2 in *Liodontomerus*. Actually *Lochitimorpha* has a very slight emargination on Mt2 and should have been coded as 1, but as this character has proven both difficult to code and homoplasious, this single difference between the taxa appears of little significance at the generic level.

After additional study I found an error in coding and a new character which substantially alters the placement of *Lochitimorpha*. The error in coding involved the number of hind-tibial spurs. Szelenyi (1957b) stated that "the shorter spur of the hind tibiae [was] minute." In examining the holotype I had a difficult time seeing a second spur, but there were several setae at the tip of the tibia, and I assumed that one of these was a second spur. However, based on the number of spines, I now believe that these are not the same as a true tibial spur and that only one hind-tibial spur is present. Secondly I also discovered that the apex of the club of *Lochitimorpha semiaenea* has a hyaline spicula, as is found only in *Pseuderimerus*. *Lochitimorpha*, therefore, shares the synapomorphies of a single hind-tibial spur and the spicula of the club with *Pseuderimerus*. I disagree with Bouček (1982) in his synonymy of *Lochitimorpha* with *Liodontomerus* and remove it from that genus. I place *Lochitimorpha* as a junior subjective synonym of *Pseuderimerus*. A final test of this hypothesis will be if the unknown males of *Pseuderimerus semiaenea*, **new combination**, have reduced eyes, another shared character with *Pseuderimerus*.

***Liodontomerus indicus*** (node 6): I coded this species as a terminal taxon (Fig. 37B, node 6) because it differed from typical *Liodontomerus* in having 5 reduced flagellomeres (or 2 anelli and 3 reduced funiculars) (2 in *Liodontomerus*), one hind-tibial spur (2 in *Liodontomerus*), and eyes reduced in the male (normal in *Liodontomerus*). On the whole it seemed phenetically more closely related to *Pseuderimerus*, which has one hind-tibial spur and the male eyes reduced. It differed from *Pseuderimerus*, however, in having 5 reduced flagellomeres (*Pseuderimerus* with 4), metasomal terga 2 and 3 emarginate (*Pseuderimerus* with only metasomal tergum 2 emarginate, i.e., Tergmar3 = 1), and less setae on the hind coxa (Cx3seta = Yes). In the working hypothesis, *Liodontomerus indicus* arose at node 6 with *Pseuderimerus* and not at node 8 with *Liodontomerus*. It differs, as expected, only in the characters just enumerated. As tergal emarginations and hind-coxal setae are shown to be homoplasious (see p. 49-52), these characters are best not used to define genera. The difference between 4 and 5 reduced flagellomeres is not considered significant enough to establish generic limits (see also discussion of anelli below). For these reasons, I transfer *Liodontomerus indicus* to the genus *Pseuderimerus*, **new combination**.

***Erimerus*** A (node 7): For a discussion of this taxon see *Erimerus* (p.92).

Ending Hypothesis (Fig. 38B): *Pseuderimerus* and *Erimerus* (node 6) appear phenotypically quite different: the former small (body under 2 mm) and the latter large (5 to 6 mm). They would appear at first to have no relationship with each other, but there is little, in fact, that separates them phylogenetically. *Pseuderimerus* females have a spicula on the antennal club, an apparently derived state found in no other tolymid genus. Although the hind-coxal setae (Cx3seta) are reduced in *Pseuderimerus* (a derived state), this condition scarcely varies from the plesiomorphic groundplan. The number of anelli differs between *Pseuderimerus* and *Erimerus*, with *Pseuderimerus* having the derived state, and I discuss this next.

Although I coded the type species of *Pseuderimerus* as having 4 anelli, this is

questionable. In slide preparations it appears as if only the first flagellomere (= anellus) is "different" from the others, i.e., it has no setae or sensilla. Flagellomeres 2, 3, 4, and 5 have setae but no sensilla (and thus would be anelli by operational definition) and are much reduced, and flagellomeres 6, 7, and 8 have setae and sensilla. Gahan (1933) stated that in *Pseuderimerus* only the 1st flagellomere was a "true ring joint." There is some area for disagreement, even when a prepared slide is examined, but enumeration of "anelli" becomes even more doubtful when the antenna is examined under the typical dissecting scope (Fig. 118). In *Erimerus*, only the first flagellomere is "different" from the others, and it has setae but no sensilla (Fig. 120), but in this case the flagellomere is much elongated, being twice as long as wide, and thus does not appear to be a typical "ring-like" anellus. It is difficult to clearly define "anellus" in this case. If diagnosed by the absence of setae, then *Pseuderimerus* has 1 anellus and *Erimerus* has none. If diagnosed by the absence of sensilla *Pseuderimerus* has 5 anelli and *Erimerus* 1. There are, however, a half-dozen undescribed species of *Pseuderimerus* (as defined by the autapomorphic spicula) in which the number of reduced flagellomeres ranges from 2 to 5. The inherent difficulty in using the concept of anellus is obvious (I discuss this further in the "Phylogenetic Analyses" section, p. 34).

DISCUSSION . - Based on at least 5 or 6 undescribed Nearctic species of *Pseuderimerus* in the USNM collection, species are more common than suspected.

#### *Erimerus* Crawford

Figs. 37(B), 38(B), 63, 113, 120, 137

*Erimerus* Crawford 1914:123. Type-species: *Torymus wickhami* Ashmead (orig. desig. and monotypic, USNM, examined).

NUMBER OF SPECIES (catalog p. 192). - 1.

DISTRIBUTION . - NEARCTIC (USA: Utah, Arizona).

HOST . - The only known species was reared from galls on Poaceae, probably from Eurytomidae, a common group of gall-formers in grass stems.

KEYS TO SPECIES . - None.

RECOGNITION . - Within Microdontomerini, *Erimerus* is recognized by a simple hind femur (Fig. 137), the hind tibia with 1 apical spur (Fig. 137), females and males with 1 "anellus" that is as long or longer than wide (Fig. 120), and without other reduced flagellomeres, female without spicula on antennal club, and males with reduced eyes (as in Figs. 88-89).

PHYLOGENY . - In my analyses, both working (Fig. 37B, node 6) and ending (Fig. 38B, node 6), *Erimerus* + *Pseuderimerus* always occur together based on two synapomorphies: the hind tibia having one apical spur (reduction from groundplan state of 2) and the reduction in size of male eyes (reduction from groundplan state of *Norm*). Relationships between the two genera were discussed under *Pseuderimerus*. Although the taxa at first appear phenetically distinct, this difference is largely due to the fact that *E. wickhami*, the only described species, is much larger in size (up to 6

times longer than some species of *Pseuderimerus* including ovipositor) and has the mesosoma metallic blue and the metasoma dull orange compared to Nearctic species of *Pseuderimerus*, which are black or greenish black (or males black with yellowish metasoma). The slight differences in the basal flagellomeres (as discussed under *Pseuderimerus*) and the apical spicula on the female antenna of *Pseuderimerus* suggest that the two are generically distinct with *Pseuderimerus* being the more derived of the two taxa. There is a slight difference in the tergal emarginations, with metasomal tergum 2 in *Erimerus* entire but slightly incised in *Pseuderimerus* (this difference is discussed below). Both taxa attack hosts in grass nodes, which is a further indication of close relationship.

***Erimerus* A** (Fig. 37B, node 7): This taxon is an undescribed species which differed from the type of *Erimerus* in having Mt2 angularly emarginate medially (as in *Pseuderimerus*). It was placed in my working hypothesis to determine its possible influence in the phylogeny. According to that analysis (Fig. 37B), it arose at node 7 with *Pseuderimerus* and 1 step up (6) from *Erimerus*. This association was due to the comparable tergal emarginations (coded 1) and ignored the states of the anelli which were not read into the data (see p. 34 for reasons). Because metasomal tergal emarginations are considered highly homoplasious and because I subsequently found an autapomorphy for *Pseuderimerus* (the spiculate antennal club) in the ending hypothesis, *Erimerus* A is now considered an undescribed species of *Erimerus* based on the absence of the spicula and the elongate basal flagellomere (= anellus).

DISCUSSION .- Within reared series of *Erimerus wickhami* smaller individuals occur (2-3 mm) in which the mesosoma is concolorous with the metasoma and the entire body is therefore orange. These striking specimens would appear to be a different species but differ in no morphological way from larger specimens in which the mesosoma is metallic blue. There is also at least one undescribed Nearctic species which is similarly colored, morphologically different, but in the size range of *Pseuderimerus*. As with this latter genus, *Erimerus* may be more speciose than is currently suspected.

### ***Idarnotorymus* Masi**

Figs. 37(C), 38(B), 92-93, 117, 140

*Idarnotorymus* Masi 1916:59-60. Type-species: *Idarnotorymus pulcher* Masi (monotypic, MCSN, examined).

*Slanecia* Bouček 1955:307-309. Type-species: *Slanecia elongata* Bouček [= *pulcher* Masi] (orig. desig., NMP, not examined).

NUMBER OF SPECIES (catalog p. 195). - 1.

DISTRIBUTION . - PALEARCTIC (Italy, Hungary, Bulgaria, Czechoslovakia, Uzbekistan.)

HOST. - The only known species was reared from Eurytomidae (Hymenoptera) in stems of Poaceae.

KEYS TO SPECIES . - None.

RECOGNITION . - Within Microdontomerini, *Idarnotorymus* is recognized by a hind femur that has finely pointed teeth on its ventral edge (Fig. 140). There are no

propodeal carinae as in *Ditropinotus* + *Eridontomerus*. Additionally the notauli become obscure in the posterior half of the scutum, and in females metasomal tergum 2 and 3 are much longer than wide, Mt2 is deeply cleft, and Mt3 has a slight dorsal crease along its margin (in males both Mt2 and Mt3 are emarginate, though Mt3 is less so than Mt2).

PHYLOGENY . - For both the working and ending hypotheses (Fig. 37C, node 11; Fig. 38B, node 7) *Idarnotorymus* is placed as the sister group to *Ditropinotus* + *Eridontomerus* based on the serrate condition of the hind femur. Because both hypotheses agree, I treat only the ending hypothesis. (In the working hypothesis the occipital carina was coded as questionable, and the anelli were not read into the analysis, but both were accounted for in the ending hypothesis; see Phylogeny for reasons.)

*Idarnotorymus* differs from node 8 (Fig. 38B) in having the plesiomorphic state of no propodeal carinae (*Nocarin* vs. *Two* in *Ditropinotus* + *Eridontomerus*). The condition of the state "serrate" is slightly different than found in *Ditropinotus* + *Eridontomerus* because in *Idarnotorymus* the femur has irregular, finely pointed teeth on its ventral edge (Fig. 140), whereas in *Ditropinotus* + *Eridontomerus* the edge is more truly serrate (Figs. 139, 428-429). The condition in *Idarnotorymus* is essentially autapomorphic, a distinction not realized until after conclusion of the analysis. Two other states define *Idarnotorymus*: the notauli fade out in the posterior half of the scutum and metasomal tergum 2 is elongate and emarginate, while Mt3 is elongate and dorsally folded (Fig. 92). Both states separate *Idarnotorymus* from *Ditropinotus* + *Eridontomerus* which have complete, deep notauli and Mt2 and 3 barely emarginate. The tergal condition is seen only in the genus *Cryptopristus*, to which *Idarnotorymus* bears an overall phenetic resemblance but is easily distinguished by the synapomorphy that defines the clade (note that in *Cryptopristus* males the terga are entire, but in *Idarnotorymus* males, Mt2 and 3 are noticeably split).

DISCUSSION . - Erdős (1963:283-285) synonymized *Slanecia* with *Idarnotorymus* and Bouček (1965:545) followed this placement. At present the generic name *Idarnotorymus* is retained even though it is monotypic. The only described species is parasitic on *Tetramesa* (Eurytomidae) in grass nodes and is thus biologically identical to *Ditropinotus* + *Eridontomerus* which feed in the same habitat. It is possible that the phenetic similarities between these taxa are simply convergent. Discovery of additional species of *Idarnotorymus* might help verify or alter its generic status and might also be helpful in resolving questions of relationship within the clade.

### *Ditropinotus* Crawford

Figs. 37(C), 38(B), 115, 125-126, 403, 412, 428-429

*Ditropinotus* Crawford 1907b:178. Type-species: *Ditropinotus aureoviridis* Crawford (orig. design. and monotypic, USNM, examined).

NUMBER OF SPECIES (catalog p. 187). - 2.

DISTRIBUTION . - NEARCTIC (USA: transcontinental), PALEARCTIC ("Central Asia").

HOST . - Reared from Eurytomidae (Hymenoptera) and possibly Cecidomyiidae (Diptera) in wheat stems (Poaceae).

## KEYS TO SPECIES. - None.

RECOGNITION . - Within Microdontomerini *Ditropinotus* is recognized by a combination of a serrate hind femur (Figs. 428-429), 2 submedian propodeal carinae (Fig. 412), and 1 anellus (Figs. 125-126). Two additional characters may be used (albeit with some difficulty) for recognition purposes to distinguish between *Ditropinotus* and *Eridontomerus*. In *Ditropinotus* the occipital carina is either absent or barely indicated by irregular sculpture scarcely raised above the surface sculpture (Fig. 403), whereas in *Eridontomerus* the carina is present dorsally as a finely polished line raised above the surface sculpture. This difference is often somewhat subjective, because it can be difficult to see the carina in some *Eridontomerus*, and it can easily be overlooked. A second character, for identification of males only, is that in *Ditropinotus* the funiculars are longer than broad and the flagellum is essentially parallel-sided (Fig. 126). This character was not used in the generic analysis because it was believed to be only of specific value. This may have been an unwarranted assumption.

PHYLOGENY . - In both the working and ending hypotheses *Ditropinotus* and *Eridontomerus* arise together with *Idarnotorymus* as a sister group. Therefore I treat only the ending hypothesis in which *Ditropinotus* arises at node 8 based on the possession of submedian propodeal carinae (state *Two*). It differs from *Eridontomerus* based on states of the anelli and the hind-coxal setae. Both sexes of *Ditropinotus* have 1 anellus (plesiomorphic) whereas in *Eridontomerus* both sexes have 2 or 3 anelli (derived state 2\*). Also, in *Ditropinotus* the hind coxa has sparse dorsal setae (apomorphic) compared to the more setose hind coxa (plesiomorphic) found in *Eridontomerus*. This latter character is homoplasious and probably of little significance. Based on the shared propodeal carinae and similar biology (both attacking grass node borers or gall-formers) these taxa are phylogenetically allied and are sister groups at a minimum. Based on the reduced basal funiculars, *Eridontomerus* appears to be more derived than *Ditropinotus*.

The occipital carina was coded as *No* for both taxa (as explained under "Phylogenetic Analyses" p. 32, the *No* state includes taxa with a reduced or indefinite carina) because it is either absent, not well developed, or difficult to interpret. There is some difference in the occiput between these two taxa as explained above under Recognition, but the expression of even a remedial carina appears to be of little help in establishing phylogeny within the clade (node 3). *Idiomacromerus*, for example, has species with or without the carina. It appears that within this clade the occipital carina is undergoing modifications that are homoplasious in nature, and some care must be taken when interpreting character state development and applying names based solely on evidence from the occipital carina.

DISCUSSION . - It is probable that both *Ditropinotus* and *Eridontomerus* are adventive to the New World through their association with wheat. *Eridontomerus* contains 11 species in the Palearctic Region, one of which it shares with the Nearctic. *Ditropinotus* contains 2 species in the Palearctic one of which it shares with the Nearctic. Wheat is "unquestionably of Old World origin" (Baker 1970), and so the possibility of introduction not only of the plant's most common pests, *Mayetiola destructor* (Hessian fly) and *Tetramesa tritici* (wheat jointworm), but also of the parasites of these

pests is highly likely. Thus, these genera probably do not form part of the evolutionary history of the New World fauna.

*Eridontomerus* Crawford

Figs. 37(C), 38(B), 116, 122-124, 139

*Eridontomerus* Crawford 1907b:178, 179. Type-species: *Eridontomerus primus* Crawford [= *isomatidis* Riley] (orig. desig. and monotypic, USNM, examined).

*Dibaomerus* Erdős 1954:150. Type-species: *Cryptopristus laticornis* Förster (orig. desig., NMW, not seen).

NUMBER OF SPECIES (catalog p. 189). - 12.

DISTRIBUTION . - Eleven species occur in the Palearctic, 1 in the Nearctic (probably introduced). Reported distribution is summarized as follows: NEARCTIC (USA, essentially transcontinental), PALEARCTIC (Algeria, Hungary, Germany, Mongolia, Kazakhstan).

HOST. - Reared from Eurytomidae (Hymenoptera) and Cecidomyiidae (Diptera) in grass stems (Poaceae).

KEYS TO SPECIES. - The genus was revised in Europe by Ruschka (1923) and Erdős (1960). Later, Erdős (1954) gave a key to world species, but because a number of species have been described since then the key is out of date. Zerova and Seregina (1991) gave a key to the 7 known species in the Commonwealth of Independent States (repeated in English, 1992).

RECOGNITION . - Within Microdontomerini, *Eridontomerus* is recognized by a combination of a serrate hind femur (Fig. 139), 2 submedian propodeal carinae (as in Fig. 412), and 2 or 3 anelli (Figs. 122-124). Also, the occipital carina is usually present dorsally as a polished ridge above the normal surface sculpture (see discussion under *Ditropinotus* Recognition and Phylogeny). [A recognition character, for identification of males only, is that the funiculars are wider than long, the flagellum is apically much wider than basally, and the distal half of the flagellum is diagonally truncated (Figs. 123-124). These were not used in the generic analysis because they were believed to be only of specific value. This may have been an unwarranted assumption.]

PHYLOGENY . - In both the working and ending hypotheses *Eridontomerus* and *Ditropinotus* arise together with *Idarnotorymus* as a sister group. In the ending hypothesis, *Eridontomerus* + *Ditropinotus* arise at node 8 based on the presence of submedian propodeal carinae (*Two*; as in Fig. 412), a state which is hypothesized as more derived than that found in *Idarnotorymus* (*Nocarini*). Based on the reduced basal flagellomeres, *Eridontomerus* appears to be more derived than *Ditropinotus*. I discuss relationships also under *Idarnotorymus* and *Ditropinotus*.

DISCUSSION . - As explained under *Ditropinotus*, I believe *Eridontomerus* was introduced into the Nearctic Region within historic times.

Microdoktermerini: *Incertae Sedis**Ophiopinetus* Husain and Kudesia

*Ophiopinetus* Husain and Kudesia 1987:175. Type-species: *Ophiopinetus pinetus* Husain and Kudesia (orig. desig. and monotypic; type depository unstated, types not examined).

NUMBER OF SPECIES (catalog p. 225). - 1.

DISTRIBUTION . - ?ORIENTAL (?India).

HOST . - Unknown.

KEYS TO SPECIES . - None.

RECOGNITION . - Based on the description (see below for additional comments), this genus is recognized by a combination of a single hind-tibial spur, a single anellus, the hind femur with an apical, ventral angle, a well developed genal carina, and the propodeum with an inverted "Y" carina.

DISCUSSION . - The original description of this genus is a travesty of modern-day systematics and speaks to the need of stronger editorial and scientific regulation in taxonomy for acceptable minimal standards of valid publication. There is no indication of number of specimens examined (probably only 1), no type-locality, no country of collection (presumably India), and no type depository. In spite of these deficiencies, under the rules of the International Code of Zoological Nomenclature, this taxon is considered validly published. Repeated requests to several institutions to examine the specimens on which this genus is based were met with no reply. Narendran (1994) had similar experiences. For all intents and purposes the type is not available to the scientific community and should be considered destroyed.

I do not believe that either the description or the illustrations provide a basis to extract detailed information about the taxon. If valid, the genus appears to be related to taxa in the Microdoktermerini based on the wing venation, lack of an occipital carina, and angulate hind femur. Based on the presumed synapomorphy of a single hind-tibial spur (a second spur might have been overlooked as is easily done), it would appear to be part of node 6 (ending hypothesis, Fig. 38B), but this cannot be confirmed from the second synapomorphy of the reduced male eye (males unknown). It differs from known members of node 6 by having an angulate hind femur. It differs from all other genera studied (except *Anneckkeida*) by having a genal carina (unless the authors meant genal sulcus, which is the common condition) and by having the propodeal carina in the form of an inverted "Y" (similar to a few species of the podagrion-clade at stem 25). Based on the unique combination of characters as set forth above, I can only suggest that this taxon is uniquely derived from among the microdoktermerine lineage and place it as an *incertae sedis* until specimens can be found.



### Tribe Torymini (Revised Status)

The tribe Torymini is composed of 355 valid species (plus 177 synonyms) in the following genera: *Allotorymus* Huber, *Austorymus* Bouček, *Diomorus* Walker, *Ecdamua* Walker, *Lissotorymus* Kamijo, *Mesodiomorus* Strand, *Odopoa* Walker, *Ovidia* Girault, *Physothorax* Mayr, *Plesiostigmodes* Ashmead, and *Torymus* Dalman. The vast majority of this tribe's species are Holarctic, but the tribe has a few taxa in all zoogeographic regions.

Members of Torymini have a predilection for gall-forming cynipids and cecidomyiids and are rarely associated with Coleoptera or Lepidoptera. A few egg parasites are known (e.g., on cicadas), and a few species are entirely phytophagous. *Torymus*, the most numerically speciose genus of Torymini (and all Torymidae), has hosts reported for most of its 317 species (based on a subset of almost 200 species: Table 3), but the remaining genera (38 species total) have hosts known for only one-fourth of their species (Table 3).

Torymini (*sensu* Grissell) is the taxon historically referred to as Toryminae of authors. Genera of this tribe are listed below in a format similar to other genera in this study, but no diagnoses or phylogenetic implications are given (as explained earlier in the introduction to this work).

Torymini is formed of taxa relatively unmodified in appearance (Fig. 185), although occasionally some rather modified phenotypes are seen (e.g., *Ecdamua*, *Diomorus*). Members of the tribe range from about 1 to 5 mm excluding the ovipositor, which may be many times the length of the mesosoma and metasoma combined (some species measure up to 30 mm including the ovipositor). Many species are brightly metallic colored in green, blue, and red, or in combinations of these colors.

**DIAGNOSIS.** - Torymini is defined by the *forward projecting anterior metapleural margin* (Figs. 10, 425) (autapomorphic). Additional characters that aid in recognition are the relatively long marginal vein (Figs. 186-191) usually about 6 to 15 times as long as the stigmal vein, but uncommonly only about 4.5 times as long (as in *Diomorus*, Fig. 192) and 1 to 10 times as long as the postmarginal vein, the occipital carina (Figs. 406, 408) which nearly or completely reaches the hypostomal carina, and the usually simple hind femur (Fig. 185; rarely with 1 or 2 teeth: Figs. 193-198).

**DESCRIPTION.** - Occipital carina dorsally arched (Figs. 406, 408), nearer to hind ocelli than to occipital foramen and with ventrolateral edges extending nearly to imaginary line drawn horizontally across dorsum of hypostoma (e.g., most *Torymus*) or reaching this carina near base of mandibles (*Ecdamua*, some *Diomorus*: Fig. 408; in this case it is more ventrolaterally narrowed than in Podagrionini Fig. 410); antennal club formed of 3 flagellomeres indicated by distinct annulations that completely encircle club, without ventral micropilosity; propodeum (Fig. 390) with spiracular sulcus evident and reaching (or curved towards) nucha, callus convex and setose; anterior metapleural margin projecting forward (Fig. 10, 425); metasternum (Fig. 391) with anterior edge of propodeal foramen placed about midway between anterior and posterior margins of hind-coxal foramen, metasternal area transversely narrowed to strip half as long (anterior to posterior) as diameter of propodeal foramen, without metasternal shelf (Fig. 10); marginal vein 6 to 15 times longer than stigmal vein (rarely 4-5 times)

and 1 to 10 times longer than postmarginal vein, stigma width equal to or greater than stigmal vein length (Figs. 186-192); hind femur usually simple, though sometimes with single (Figs. 193-195, 198) or double teeth (Figs. 196-197); hind tibia usually straight (slightly curved in some *Diomorus*), with apex truncate at right angles, and with 2 spurs at ventral corner; metasomal tergum 2 not laterally emarginate, usually dorsomedially emarginate.

**PHYLOGENY** . - In both the working and ending hypotheses, Toryminae of authors was the most unstable taxon on the tree due mostly to the wide range of character states found within the group. In no instance did "Toryminae" end up as the sister taxon to what has been called "Monodontomerinae" or even to Megastigminae. It always ended up somewhere between taxa of the putative "Monodontomerinae." This is not surprising when one considers that within Torymini, character states which are used to define genera in non-Torymini are simply species characters or, at best, species-group characters. For example, aspects of the antenna, clypeus, hind femur, propodeum, frenal line, notauli, head shape, hind-coxal setation, spur length, and metasomal terga are all used to define species or species-groups within *Torymus*, but not genera (Grissell 1976). In the working hypothesis the states for many of these characters had to be coded as question marks for Torymini, and this accounted for much of the instability of placement for the taxon. It arose as part of node 13, 16, 17, or 18 depending on the tree selected (Fig. 37).

In the ending hypothesis (Fig. 38) Torymini was not included as a taxon for the purposes of establishing a tree. The theory was to first establish a stable tree without the conflict induced by the presence of Torymini, then to place Torymini on that tree assuming that it was monophyletic. When a tree was chosen, the most primitive states (as defined by node 1 of the ending hypothesis, Fig. 38A) of characters known to vary within Torymini were estimated to be the ground-plan for the taxon, and Torymini was placed in the analysis by the least number of state changes. By this means, Torymini was estimated to fit the ending hypothesis (Fig. 38C) either as part of node 9 or adjacent to it along with the multifurcation at node 2 (Fig. 38).

**DISCUSSION** . - "Toryminae" is an easily recognized monophyletic unit that has been elevated to a higher rank than appears to be the case based on phylogenetic study. Ease of recognition, however, is criterion neither for acceptance nor for rejection as a hierarchical category. Monophyletic simply means that all members of the group are derived from a common ancestor and thus are more closely related to each other than to members of other groups. In assuming that the projecting (or sinuate) anterior mesepimeral margin is a synapomorphy shared by all Torymini, I am assuming that it has evolved only once from a common ancestor.

I have studied enough species (over 100) of the genus *Torymus* to accept that these species are all related, but I have not studied the majority of other genera (11) in the tribe. My analysis is based on the supposition that the unique, sinuate mesepimeron is a true synapomorphy that unites all Torymini, but this may be open to argument (see also "Phylogenetic Analyses," p. 52).

Technically speaking, my treatment of Torymini is easily attacked by traditionalists and by cladists alike. I have adapted my approach so as to preserve as much historical

hierarchical nomenclature as possible, realizing that my phylogenetic analyses are not as perfect as they might be. I have attempted to be nomenclaturally conservative while at the same time preserving phylogenetic integrity. To be phylogenetically correct I should probably assign Torymoidini + Torymini a "tribal" rank, thus creating the tribe Torymini with subtribes Torymina and Torymoidina. Alternatively I could adopt the "phylogenetic sequencing convention" of Nelson (1972, 1974), creating a supertribe that includes both taxa (i.e., Torymini and Torymoidini) and a supertribe for all the taxa at the next branch above. Either way introduces a degree of refinement which is out of proportion to the analyses I provide. It seems most appropriate at this time to be conservative, to recognize an imperfect situation, and to take the best advantage of it.

I clearly cannot support the treatment of Toryminae of authors as a sister-group to the remaining "monodontomerines." Alternatively, treating it as a subfamily requires the creation of a number of additional subfamilies which creates a sophistication unwarranted by my analyses. In my opinion Torymini and Torymoidini are derived from a common ancestor, and Torymini is mostly closely related to *Pseudotorymus*. As I explain under Torymoidini, both appear to be derived from a microdontomerine ancestor, and within Torymidae the three groups are all relatively primitive.

The following generic treatments are provided as an overview of the tribe and to allow comparison with all other genera in the Toryminae.

#### *Allotorymus* Huber

*Allotorymus* Huber 1927:104. Type-species: *Syntomaspis splendens* Provancher (orig. desig. and monotypic).

NUMBER OF SPECIES (catalog p. 179). - 1.

DISTRIBUTION. - Apparently widespread in Canada, and known from Colorado in the United States.

HOST. - Unknown.

KEYS TO SPECIES. - Grissell (1976) gave a key which included this genus and its only species.

TAXONOMY. - *Allotorymus splendens* is most likely a modified species of *Torymus*.

#### *Austorymus* Bouček

*Austorymus* Bouček 1988:145-146. Type-species: *Austorymus nitidus* Bouček (orig. desig. and monotypic).

NUMBER OF SPECIES (catalog p. 181). - 1.

DISTRIBUTION. - Australia.

HOST. - Unknown.

KEYS TO SPECIES. - Bouček (1988) provided a key to the genus and thus its only known species.

***Diomorus* Walker**

Figs. 190-195, 408, 411, 413, 420

*Diomorus* Walker 1834:159. Type-species: *Diomorus nobilis* Walker (= *armatus* Boheman) (monotypic).

*Dihomerus* Schulz 1906:148. Unjustified emendation.

NUMBER OF SPECIES (catalog p. 183). - 14.

DISTRIBUTION . - All zoogeographic regions except Australia where it was apparently introduced.

HOSTs . - Members of this genus have been reared as parasites of larvae of other Hymenoptera, especially aculeate wasps. Reports of species from cynipid galls are most likely rearings from aculeates nesting in old galls, and this may be true for *Diomorus aiolomophi* as well, which is reported from eurytomid grass-stem galls.

KEYS TO SPECIES . - Europe: Hoffmeyer 1930d:254, Graham 1992b:112. Hungary: Erdős 1960:44-46. Commonwealth of Independent States: Nikol'skaya and Zerova 1978:670, Zerova and Seregina 1991b:7. Africa: Risbec 1955:573-574. India: Narendran and Sureshan 1989:10-11, Narendran 1994:24.

TAXONOMY . - Breland (1938b) discussed the phylogenetic placement of *Diomorus* noting that it scarcely differed from *Torymus* except in host choice. Graham (1992b) defined the genus somewhat more clearly.

***Ecdamua* Walker**

Figs. 189, 198

*Ecdamua* Walker 1862:387-388. Type-species: *Ecdamua macrotelus* Walker (monotypic).

*Monodontomerella* Girault 1925/384:98. Type-species: *Monodontomerella longipilum* Girault (monotypic).

NUMBER OF SPECIES (catalog p. 188). - 5.

DISTRIBUTION . - This genus is found in the Afrotropical and Indo-Australian areas.

HOST . - Williams (1928:84-85) reported an unknown species of *Ecdamua* associated with nests of *Polemistus luzonensis* (Sphecidae) in the Philippines. The nests were made in beetle borings in wood posts. Bouček (1988) pointed out that the related genus *Diomorus* may also be found in such situations. Compton and Nefdt (1988) briefly discuss the extremely long ovipositors of females of this genus.

TAXONOMY . - Bouček (1988:147) synonymized *Monodontomerella*.

***Lissotorymus* Kamijo**

*Lissotorymus* Kamijo 1961:66. Type-species: *Lissotorymus laevigatus* Kamijo (orig. desig. and monotypic).

NUMBER OF SPECIES (catalog p. 201). - 1.

DISTRIBUTION . - Known only from Japan.

HOST. - From cynipid galls on oak.

### *Mesodiomorus* Strand

*Mesodiomorus* Strand 1911b:93-94. Type-species: *Mesodiomorus compressus* Strand (orig. desig. and monotypic).

NUMBER OF SPECIES (catalog p. 202). - 1.

DISTRIBUTION. - This genus was reported from Taiwan, but Bouček (1988) stated that it was possibly also found in the Malaysian Peninsula, Borneo, and the Celebes (based presumably on undescribed species).

HOST. - Unknown.

### *Odopoa* Walker

*Odopoa* Walker 1871a:36. Type-species: *Odopoa atra* Walker (monotypic).

*Odopoa*: Dalla Torre 1898:315. Misspelling.

*Australorymus* Girault 1925/384:97. Type-species: *Australorymus dentatinotus* Girault (monotypic).

*Ua* Girault 1929/430:2. Type-species: *Ua maria* Girault (monotypic)

*Pauliana* Risbec 1952:375. Type-species: *Pauliana philippiae* Risbec, (monotypic).

NUMBER OF SPECIES (catalog p. 224). - 4.

DISTRIBUTION. - *Odopoa* is restricted to the Indo-Australian and Afrotropical regions.

HOST. - Known only from flower-galls on *Philippia* sp. (Ericaceae).

TAXONOMY. - Bouček (1988) summarized the little information known for the genus and placed it in the monotypic new tribe "Odopoiini." This will require further assessment.

### *Ovidia* Girault

*Ovidia* Girault 1924/378:172. Type-species: *Ovidia conicicollis* Girault (monotypic).

NUMBER OF SPECIES (catalog p. 225). - 1.

DISTRIBUTION. - This genus is known only from Australia.

HOST. - Unknown.

TAXONOMY. - The generic name was described again by mistake by Girault (1926/399:60-61).

### *Physothorax* Mayr

Figs. 196-197

*Physothorax* Mayr 1885:159, 196. Type-species: *Physothorax disciger* Mayr (desig. by Gahan and Fagan 1923).

?*Plesiostigma* Mayr 1885:158, 226-227. Type-species: *Plesiostigma bicolor* Mayr (monotypic).

NUMBER OF SPECIES (catalog p. 231). - 9.

DISTRIBUTION. - Members of this genus are found only in the Neotropical Region and southern tip of Florida.

HOST. - Species are associated with the receptacles of figs (Moraceae). At least one species is known to parasitize the larvae of cecidomyiids in the fig.

KEYS TO SPECIES. - Burks (1969a) gave a key to Nearctic species of the genus, but this is outdated by Bouček (1993) who keyed most of the known species.

TAXONOMY. - The synonymy of *Plesiostigma* was proposed questionably by Bouček (1993), who could not find the types of most of the species described by Mayr that are supposed to be in the Vienna Naturhistorisches Museum. (Dr. Max Fischer informed me that he could not find material of *P. bicolor* in the Vienna Museum when I recently inquired.) From the description and illustrations of *Plesiostigma bicolor*, the males are winged, the antenna 12-segmented (with 7 funiculars and no apparent anelli), the pronotum is large (nearly one-third the length of the mesosoma), the notauli sharp, the scutellum "rather rhombic," the sessile stigmal vein slightly inflated and at right angles to the marginal/postmarginal veins, the hind femur with a "more or less indistinct tooth," and the body partly green and partly yellow. These characters could pertain to *Physothorax* except for the single hind-femoral tooth. All known species of *Physothorax* have 2 large teeth and sometimes additional small ones. The genus *Plesiostigma* is probably best placed here with reservation.

### *Plesiostigmodes* Ashmead

*Plesiostigmodes* Ashmead 1904a:243, 400. Type-species: *Plesiostigmodes brasiliensis* Ashmead (orig. desig. and monotypic).

NUMBER OF SPECIES (catalog p. 233). - 1.

DISTRIBUTION. - Known only from Brazil.

HOST. - Unknown.

TAXONOMY. - The genus was originally placed in the "Monodontomerinae" by Ashmead (1904a) and has been cited therein ever since (e.g., Crawford 1914, Szelenyi 1957b, De Santis 1980). I examined the only known specimen, and it is a Torymini based on the forward projecting metapleuron.

### *Torymus* Dalman

Figs. 10, 20, 22, 24, 28, 60, 185, 187-188, 390-391, 406, 416, 425

*Callimome* Spinola 1811:146-148. Type-species: *Ichneumon bedeguaris* Linnaeus (desig. by Curtis 1835:552). Suppressed by Int. Comm. Zool. Nomen., Opinion 155, 1944.

*Misocampe* Latreille 1818:213. Type-species: *Ichneumon bedeguaris* Linnaeus (desig. by Gahan and Fagan 1923:91). Suppressed by Int. Comm. Zool. Nomen., Opinion 155, 1944.

*Torymus* Dalman 1820:135, 178. Type-species: *Ichneumon bedeguaris* Linnaeus (desig. by Ashmead 1904a:242).

*Misocampus*: Stephens 1829:395. Emendation of *Misocampe*.

*Syntomaspis* Förster 1856:43-44. Type-species: *Torymus eurynotus* Förster (= *cyaneus* Walker, see Bouček and Graham 1978a) (desig. by Gahan and Fagan 1923:139).

*Lioterphus* Thomson 1876:60, 99. Type-species: *Torymus pallidicornis* Boheman (= *nitidulus* Walker) (desig. by Ashmead 1904a:241).

*Callimomus* Thomson 1876:60, 77. Type-species: *Callimomus scaposus* Thomson (desig. by Ashmead 1904a:241).

*Nannocerus* Mayr 1885:159, 195. Type-species: *Nannocerus biarticulatus* Mayr (monotypic).

*Hemitorymus* Ashmead 1904a:243. Type-species: *Hemitorymus thoracicus* Ashmead (monotypic).

NUMBER OF SPECIES (catalog p. 273). - 317.

DISTRIBUTION. - The genus occurs worldwide, but by far the largest number of species are confined to the Holarctic Region. A few species are found in the Neotropical, Oriental, Afrotropical, and Australian regions.

HOSTS. - *Torymus* species have been associated with large numbers of different hosts, but not many specific biologies have been worked out. The majority are associated with cynipid and cecidomyiid gall-formers on numerous plants. Species have also been reared from insect eggs and larvae of Coleoptera, Lepidoptera, Diptera, and Hymenoptera. Some species are known to be phytophagous, and yet others have been shown to feed on both plant and insect tissue. Specific records may be found in host lists such as those provided in Peck (1963), Grissell (1979), De Santis (1967, 1979, 1980, 1983, 1989), and Wall (1984).

KEYS TO SPECIES. - In general there are surprisingly few keys to species of *Torymus* and scarcely any comprehensive ones. In the Nearctic, Huber (1927) produced a key to the then known species. Grissell (1976) provided keys to Nearctic species groups and to western Nearctic species. In the Palearctic there are several old keys (or key-like papers) available, the most notable of which are Mayr (1874), Thomson (1876), Schmiedeknecht (1914), and Hoffmeyer (1930d). Less satisfactory keys include limited regions such as Hungary (Erdös 1960). The only modern key is that by Nikol'skaya and Zerova (1978), which treats the species of the European part of the Commonwealth of Independent States and is most likely derivative from the older keys as well as Nikol'skaya (1952). Much of these keys' emphasis is on body color and ovipositor length, neither of which can be used without considerable allowance for biological and morphological variation.

TAXONOMY. - This genus is a large and complex one. Many species remain to be described. The generic concept for *Torymus* might be considered rather indefinite, and, considering the number of species involved, rightly so. Bouček and Graham (1978a, b) recognized *Callimomus* as a species group of *Torymus* and regarded *Lioterphus* and *Syntomaspis* as subgenera. Bouček (1993) also regards *Nannocerus* as a subgenus. Earlier I recognized five species groups based on the Nearctic fauna (Grissell 1976), and most of the Palearctic species appear to belong to two of these groups (*bedeguaris* and *tubicola* groups). Graham and Gijswijt have been studying the Palearctic fauna for some time (Graham in *litt.*) and eventually it will be possible to integrate our knowledge of the Nearctic and Palearctic faunas. There are many systematic problems yet inherent in the genus *Torymus*, and their resolution will not be easy.

### Torymoidini, New Tribe

Type genus: *Torymoides* Walker

Torymoidini is composed of 91 valid species (plus 13 synonyms) in the following genera: *Aloomba*, *Platykula*, *Pseudotorymus* (with *Senegallela* and *Thiesia* new synonyms), *Torymoidellus*, and *Torymoides* (with *Ameromicrus* and *Pondorymus* new synonyms). The *nomen nudum* *Eridontomeroidella* mercifully is recognized as a member of *Pseudotorymus*. The tribe is numerically most abundant in the Australian and Palearctic regions, with relatively few species in each of the other zoogeographic regions.

In spite of having far fewer species than Torymini, Torymoidini is almost as diverse in host selection. Hymenoptera and Diptera similarly provide the most host records, but no egg parasites or phytophagous species are yet known in the tribe. The hosts for 60 percent of species are unknown (Table 3).

Torymoidini is formed of taxa relatively unmodified in appearance (Fig. 62). They appear to be little more than derived Microdontomerini. Members of the tribe range from about 2 to 4 mm excluding the ovipositor, which is usually shorter than the body length. Many species are brightly metallic colored in green or blue, but non-metallic species are known as well.

**DIAGNOSIS.** - Torymoidini is defined by the *straight anterior metapleural margin* (Fig. 424, and as in Fig. 12) and by the *relatively long marginal vein 6 to 12 times the stigmal vein and 3 to 7 times the postmarginal vein* (Figs. 148-155). Additional characters that aid in recognition are the occipital carina with ventrolateral edges extending below imaginary line drawn across dorsum of hypostoma (Fig. 404) and the simple to barely toothed hind femur (Figs. 159-166).

**DESCRIPTION.** - Occipital carina dorsally arched (Fig. 404), nearer to hind ocelli than to occipital foramen, with ventrolateral edges extending below imaginary line drawn across dorsum of hypostoma; antennal club formed of 3 flagellomeres indicated by distinct annulations that completely encircle club, without ventral micropilosity; propodeum (Fig. 392) with spiracular sulcus evident and reaching (or curved towards) nucha, callus convex and setose; anterior metapleural margin straight (Fig. 424); metasternum (Fig. 393) with anterior edge of propodeal foramen placed about midway between anterior and posterior margins of hind-coxal foramen, metasternal area transversely narrowed to strip half as long (anterior to posterior) as diameter of propodeal foramen, without metasternal shelf (Fig. 424); elongated marginal vein 6 to 12 times longer than stigmal vein, 3 to 7 times longer than postmarginal vein, stigma width equal to or greater than stigmal vein length (Figs. 148-155); hind femur simple to angulate (Figs. 159-166); hind tibia straight, with 2 spurs; metasomal tergum 2 not laterally emarginate, dorsomedially emarginate.

**PHYLOGENY.** - In my working hypothesis (Fig. 37) members of what I now recognize as Torymoidini arose at nodes 13, 16, 17 and 18. In my reanalysis in preparation for the ending hypothesis (Fig. 38) I reexamined and recoded several character states (as discussed below under generic headings), and synonymized several taxa. In the ending hypothesis, genera now placed in Torymoidini arise at node 9 based on the change



of wing venation from the *Ptero* state (Fig. 38C) to the *Tory* state, in which the marginal vein is long, the stigmal vein is reduced, and the postmarginal vein is reduced (Figs. 148-155). The marginal vein is 6 to 12 times longer than the stigmal vein, 3 to 7 times longer than the postmarginal vein, and the width of the stigma is equal to or greater than the length of the stigmal vein. In the more primitive Microdontomerini, the marginal vein is 2 to 4 (rarely 4.5) times longer than the stigmal vein, 1.5 to 2 times longer than the postmarginal vein, and the width of the stigma is equal to or shorter than the stigmal vein. The Torymoidini (and Torymini) pattern is unique among torymids and although similar wing venation reappears later in highly derived forms of the family (e.g., *Podagrion*), I hypothesize that such wing venation is independently derived and thus a parallel or convergent development.

At the time of the working hypothesis I did not realize that the occipital carina occurred in several additional states than I coded. Based on a reanalysis, the ending hypothesis suggests that in Torymoidini, as well as the basal sister group Megastigminae and the basal genus *Glyphomerus*, the occipital carina is well-developed, dorsally arched, nearer to the hind ocelli than to the occipital foramen, but falls short of nearly reaching (or rarely reaching) the hypostomal carina (Fig. 404) as in Torymini (Figs. 406, 408). In this state alone, Torymoidini appears slightly less advanced than Torymini which, in a few cases (e.g., *Diomorus*, Fig. 408), displays a nearly to fully complete carina approaching that found in advanced groups such as Palachiini and Podagrionini.

Although I have tried to find other characters to support the monophyly of Torymoidini, I have not been successful. One character that might prove useful, but only in a putative, hypothetical way, is the structure of the metasoma. As I discussed in the phylogenetic analysis (p. 52) and pointed out in the discussions of taxa in the Microdontomerini, metasomal tergal emarginations are difficult to code, are highly homoplasious as defined by my analysis, and are widely variable within some otherwise well-defined taxa (e.g., *Torymus*). The sole use of such states to define branching patterns is dubious at best and highly distorted at worst. But I have studied a number of species involved in node 9 (and Torymini), and it is generally true that taxa in these groups tend to have metasomal terga 2-5 emarginate (and often sharply laterally compressed) whereas the more primitive Microdontomerini tend to have only metasomal terga 2 and sometimes 3 slightly emarginate (very rarely Mt2-5 emarginate in several species of *Microdontomerus*). One might conclude that these are the groundplan conditions for both clades, thus demonstrating a tendency for Microdontomerini to retain the hypothetically primitive conditions of unemarginate terga whereas Torymoidini (and Torymini) has a greater tendency towards emarginate metasomal terga. While this is possibly of phylogenetic value, it is not always so easy to appreciate these differences in routine examinations.

In my opinion, there is good reason that attempts at phylogenetic interpretation should prove less than satisfactory. Based on examination of many thousands of specimens, the relatively more primitive Torymoidini (e.g., *Pseudotorymus* and basal species of *Torymoides*, especially those once referred to as *Ameromicrus*, e.g. *A. violaceae* and *A. piceae*) are not far removed from some of the more primitive species of the microdontomerine genera (e.g., *Idiomacromerus* and *Microdontomerus*). This is borne out by the ending hypothesis tree. The only difference so far as I can tell resides in the wing venation and occipital carina.

*Pseudotorymus* Masi

Figs. 37(D), 38(C), 153, 156, 167-182

*Holaspis* Mayr 1874:83. Type-species: *Torymus militaris* Boheman. (desig. by Ashmead 1904:242, 377, depository unknown). Preöcc. by Gray 1863 (Reptilia).

*Eridontomeroidella* Girault in Ramakrishna Ayyar 1919:935. Type-species: "*Eridontomeroidella gibboni* Girault" (monotypic). *Nomen nudum*.

*Pseudotorymus* Masi 1921b:235. Objective replacement name for *Holaspis* Mayr nec Gray 1863.

*Senegalella* Risbec 1951a:289. Type-species: *Senegallela acythopeusi* Risbec (desig. by Bouček 1976b:347, MNHN, examined). **New synonymy.**

*Thiesia* Risbec 1951a:292. Type-species: *Thiesia gallephila* Risbec (monotypic, MNHN, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 253). - 43.

DISTRIBUTION. - This genus is most abundant in the Palearctic (30 species) and Afrotropical (7 species) regions with 4 species known from the Oriental region and a single species known from the Nearctic (but I have seen several undescribed species from this region). Reported distribution is summarized as follows: NEARCTIC (USA: 1 species widespread in southern Canada and northern US), PALEARCTIC (widespread throughout region into northern Africa), ORIENTAL (India), AFROTROPICAL (Senegal, Rwanda (Republic of the Congo), Madagascar, Mali, Sudan, Nigeria, Mozambique, South Africa).

HOSTS. - Members have a broad host association including Curculionidae (Coleoptera) in leguminous seed pods; Bruchidae (Coleoptera) from galls on Orchidaceae, Combretaceae, Asteraceae, Rubiaceae, and Fabaceae; Cecidomyiidae (Diptera) associated with Fabaceae, Cruciferae, Salicaceae, Rosaceae, Lamiaceae, Scrophulariaceae, and Apiaceae; Eurytomidae (Hymenoptera) in grass stems (Poaceae); Cynipidae (Hymenoptera) in pods of Papaveraceae; Tenthredinidae (Hymenoptera); and Pyralidae (Lepidoptera).

KEYS TO SPECIES. - Keys for *Pseudotorymus* (*sensu stricto*) were given by Ruschka (1923) and Hoffmeyer (1930d, 1931:259-261) to European species; Erdös (1960:62) gave a key to the species of Hungary, and Nikol'skaya and Zerova (1978) gave a key to the European part of the Commonwealth of Independent States.

RECOGNITION. - Within Torymoidini, *Pseudotorymus* is recognized by having 1 anellus (but see phylogeny and discussion sections below), unmodified hind-tibial spurs (Fig. 156), and an unmodified propodeum (as in Fig. 392).

PHYLOGENY AND SYNONYMY. -

Working Hypothesis (Fig. 37D): *Pseudotorymus* (node 18) arises 2 steps above *Senegalella* (node 16), based on the hind femur state changes from *Simple* (node 16) to *Angle* (node 17) to *Tooth* (node 18). In *Pseudotorymus* the hind coxa has dorsal setae, but the absence of hind-coxal setae in *Senegalella* was coded as a question mark. The reason for using this convention was discussed under the introductory "Phylogenetic Analyses" section of this paper. The absence of this character state was not reflected in the working hypothesis tree and was largely ignored for purposes of

analyses. Upon examining several hundred specimens of *Pseudotorymus* (as defined by the presence of a toothed hind femur) from around the world, I have found specimens in Thailand, Egypt, and Cyprus (all in USNM) which have the hind coxa dorsally bare as in *Senegalella*. Thus the exclusion of the character for generic purposes appears warranted.

The use of the hind-femoral tooth to establish generic limits is problematic based on conditions found in other taxa. In species of *Torymoides*, sister group to *Pseudotorymus*, the femur ranges from unmodified (Fig. 166) to barely angulate (Fig. 165), to distinctly angulate (Fig. 162). In nearctic species of the genus *Torymus* the toothed or angulate hind femur occurs in 2 of the 5 species groups. Even within a single species some variation may occur in the hind femur. For example, in *Torymoides amiabilis* the femur may be essentially simple (with an poorly defined angle) (Fig. 159) or definitely toothed (Fig. 161). This is true also for an undescribed species of *Pseudotorymus* that I have seen (Figs. 172-174). There appears to be similar variation within a single population of *Senegalella leguminosae*, but in this case the more obvious angulation is seen in the smaller (Fig. 177), rather than larger (Fig. 178), specimens.

Based on the above morphological characters used to define *Pseudotorymus* and *Senegalella*, and as a result of the working hypothesis, I placed *Senegalella* as a junior subjective synonym of *Pseudotorymus*. The 5 species of *Senegalella* are all reported as Afrotropical (but I have seen specimens that would be placed in this genus from India, Philippine Islands, and Thailand), while the majority of *Pseudotorymus* are reported from the Palearctic (including North Africa) with a few species in the New World (mostly undescribed). On the basis of its unmodified hind femur, *Senegalella* appears to represent a relatively primitive sub-Saharan species group of what is otherwise typical *Pseudotorymus*.

In my working hypothesis (Fig. 37D), the phylogenetic placement of *Pseudotorymus* is difficult to establish. First because of the synonymy of *Senegalella*, thus lumping taxa on nodes 16 and 19, and second because of synonymy involved with *Torymoides* and other taxa involving nodes 9, 13, 16 and 17 (see discussion under *Torymoides*). For this reason a discussion of relationships between *Pseudotorymus* and other taxa is given in the next section.

Ending Hypothesis (Fig. 38C): In the ending hypothesis *Pseudotorymus* (node 9) is considered the primitive sister group to the multifurcation at node 10 which includes *Torymoidellus*, *Torymoides*, *Aloomba*, and *Platykula*. This is based on the change from metasomal terga 1 and 2 emarginate (plesiomorphic) to 1-4 emarginate and two changes at node 10: 1) a change from the retention of the primitive anellus state of 1 in *Pseudotorymus* to 2 and, 2) a similar change in hind-coxal setae from present to absent at node 10. To dismiss the first and last characters, the presence or absence of hind-coxal setae and of tergal emarginations are homoplasious characters. The hind-coxal setal state is variable even within *Pseudotorymus*, as I discussed above. With regards to the anellus, I have seen in several series of *Pseudotorymus* (as *Senegalella*) a tendency in small specimens towards the reduction of funicular 1 (i.e., flagellomere 2) into a ring-like "anellus." Although the flagellomere has multiporous plate sensilla (and is thus not an anellus by operational definition), it is still ring-like in appearance. This is disturbing, because the only diagnosed difference between the complex of 35+ species of *Pseudotorymus* (*sensu* Grissell, node 9) and of 35+ species of *Torymoides*

(*sensu* Grissell, node 10) is that the former genus is defined by having 1 anellus, and the latter 2 or more. Obviously, the recognition of these two taxa is a bit uncertain and they may, in time, be synonymized. Conservatively speaking, I believe there is some nomenclatural value in retaining the two names for now.

DISCUSSION. - *Eridontomeroidella* was first mentioned in press by Ramakrishna Ayyar (1919), who attributed the genus and species to Girault in a list of parasites of Indian crop pests. He stated (p. 32) that Girault was publishing the new species "in some journals not accessible to us." Apparently Girault never published the name. Gahan (1922b:41) commented on a similar problem with the name *Eurytoma indi* Girault (= *mellipes* Gahan), which was the presumed host of *E. gibboni*. Both species were from leguminous pods of "dhaincha" supposedly containing the phytophagous *Eurytoma mellipes*. In 1940 (page 3) Pruthi and Mani again mentioned *Eridontomeroidella gibboni* Girault and illustrated it (pl. I, Fig. 1) with the note that no description could be found. They mention rearing it from the pod of a second species of leguminous plant, namely "agathi." Six specimens are present in the USNM collection that bear the manuscript name *E. gibboni*. Additionally, they bear locality and host data as well as USNM type numbers. A typical Girault slide of a mangled head is also present. There can be no doubt that these are the specimens which Girault intended to describe. They are identical in all respects with *Senegalella* (and are, in fact, *S. leguminosae*). I have discussed Girault's manuscript name at length in order to categorically dispose of it.

Bouček (1976b:347) synonymized *Senegalella* with *Antistrophoplex* (now a synonym of *Microdontomerus*). As I have shown above, however, it should be placed as a synonym of *Pseudotorymus*. Dr. J. R. Steffan (MNHN, Paris) kindly loaned to me specimens of *Senegalella acythopeusi*, the type of the genus. From the 4 slides representing 10 specimens sent, I can associate only 2 specimens with the original data given by Risbec. One slide, containing 1 female, bears the label "Bambey" (type-locality) and "*Acythopeus tragardi*" (type-host) and another slide bears 1 female with the data "Bambey," "fleurs Aubergine 11-5-46." These I consider to be part of the syntype series. The specimen reared from *Acythopeus* is herein designated lectotype, and the other is designated paralectotype. I have remounted the lectotype on a point and both specimens are in the Museum National d'Histoire Naturelle, Paris.

Based on the types of *Thiesia gallephila* loaned to me by Steffan, *Thiesia* is a synonym of *Pseudotorymus*. Risbec (1951a) compared *Thiesia* with *Senegalella*, and separated the two taxa based on 2 anelli and 6 flagellomeres in the former and 1 anellus and 7 flagellomeres in the latter. *Thiesia* appears to have 2 anelli but this is simply because the specimens are extremely small (less than 1.5 mm in length), and the 2nd flagellomere is ring-like. Multiporous plate sensilla are present so that it is not a "true" anellus, at least by operational definition. Bouček (1978:133) commented on a single, undescribed species of *Antistrophoplex* (= *Microdontomerus*) from Africa that has 1 anellus in larger specimens and 2 anelli in smaller ones, and I have seen a similar situation in a Nearctic species of *Torymus* (Grissell 1976:82). The fact *Thiesia gallephila* and *Senegalella* (now = *Pseudotorymus*) *leguminosae* are similarly colored, have the same color pattern (especially the all white tibiae), and are morphologically identical except for antennae and size (the smaller *T. gallephila* is about 1.5-2 mm and *P. leguminosae* is about 2-3 mm), indicates to me the possibility that they are the same

species. Only by studying reared series or with biological studies can this problem be resolved. Risbec (1954c:535) synonymized *Thiesia* with *Lochities* (now = *Idiomacromerus*), but this is incorrect.

### *Torymoides* Walker

Figs. 37(D), 38(C), 62, 151, 154-155, 159-166, 392-393, 404, 414-415, 417, 424

*Torymoides* Walker 1871b:37-38. Type-species: *Torymoides amabilis* Walker (monotypic, BMNH, examined).

*Dimeromicrus* Crawford 1910a:127. Type-species: *Dimeromicrus ashmeadi* Crawford (orig. desig. and monotypic, USNM, examined).

*Macrodontomerus* Girault 1913/175:100. Type-species: *Macrodontomerus unimaculatus* Girault (monotypic, QM, examined).

*Didactyliocerus* Masi 1916:69. Type-species: *Didactyliocerus dispar* Masi (monotypic, MCSN, examined).

*Ameromicrus* Nikol'skaya 1954:411-412. Type-species: *Ameromicrus violaceus* Nikol'skaya (monotypic, ZIAN, examined). **New synonymy.**

*Pondorymus* Bouček 1978:124. Type-species: *Pondorymus latus* Bouček (orig. desig. and monotypic, BMNH, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 263). - 48.

DISTRIBUTION. - Although *Torymoides* is widespread throughout the world, its species are most abundant in the Australian Region, which contains nearly half the known total (18 of 45). A third of the species are Palearctic (16), 1 is Afrotropical, 2 Nearctic, 5 Neotropical, and 6 Oriental. I have seen a few undescribed Nearctic species. Reported distribution is summarized as follows: NEARCTIC (USA: Widespread from northern U.S. southward to Texas), NEOTROPICAL (Mexico, St. Vincent, St. Kitts, Montserrat, Nicaragua, Peru, Brazil, Argentina), PALEARCTIC (widespread throughout the Commonwealth of Independent States, Europe, Japan, and extending into northern Africa), AUSTRALIAN (Australia, New Zealand), ORIENTAL (India, Sri Lanka, Nepal, Taiwan, Philippine Islands), AFROTROPICAL (South Africa).

HOSTS. - Reared from Cecidomyiidae (Diptera) galls on Fabaceae, Asteraceae, Chenopodiaceae, and Euphorbiaceae, from unknown gall-formers on Fabaceae, Chenopodiaceae, and Myrtaceae, from Tephritidae (Diptera) gall-formers on Asteraceae, and from Pinaceae seeds (possibly parasitic on Torymidae (Hymenoptera) in the seeds).

KEYS TO SPECIES. - Bouček (1970a), Doganlar (1989), and Zerova and Seregina (1993) published keys to world species of *Ameromicrus*. Narendran (1994) gave a key to the Indian species of *Torymoides*.

RECOGNITION. - Within Torymoidini, *Torymoides* is recognized by having 2 anelli (or rarely more as in Fig. 146-147), unmodified hind-tibial spurs (as in Fig. 156), and an unmodified propodeum (Fig. 392).

PHYLOGENY AND SYNONYMY. -

Working Hypothesis (Fig. 37D): Bouček (1988) synonymized *Dimeromicrus* with

*Torymoides*, but I included the genus in my working hypothesis before this synonymy. In the analysis, *Dimeromicrus* (node 16) arises one step below *Torymoides* (node 17,) based on the simple hind femur in the former and the angled hind femur in the latter. To define the genus *Dimeromicrus* I used the type-species *Dimeromicrus ashmeadi*. After some study, it was apparent that although a feebly angled margin of the hind femur may be discerned with some difficulty, it becomes largely a matter of opinion as to whether this is simple, slightly angulate, or markedly angulate. After studying more than 350 specimens of *Torymoides amabilis*, the type-species of *Torymoides*, composed of several long series of specimens collected in one locality at one time, it is apparent that femora may vary anywhere from simple (Fig. 159) to noticeably angulate (Figs. 160-161). Thus, assigning generic placement to specimens based on hind-femur states becomes an arbitrary judgment, because there is no disjunct gap between states. I agree with Bouček (1988) that *Dimeromicrus* should be synonymized.

*Macrodontomerus* and *Didactyliocerus* were synonymized with *Torymoides* by Bouček (1988). I have seen the types and agree with these placements. There were no character state differences on which to differentiate them, and they were not placed in my analysis.

*Ameromicrus* was considered by Bouček (1988) to be closely related to *Torymoides* and perhaps a species group of it. I did not include it in my analysis, because I could find no character state differences with which to distinguish it from *Torymoides*. It does differ, at least in the type and the species *A. violaceus* and *A. piceae*, by having the marginal vein relatively shorter than in *Torymoides* (about 6 times the stigmal vein length vs. about 8 times), but this does not seem to warrant generic status, because, for example in *Pseudotorymus*, this much variation can be found between species of the same genus. For these reasons I place *Ameromicrus* as a subjective junior synonym of *Torymoides*.

Although *Pondorymus* (node 9) arises basad of *Torymoides* (node 17) on my tree, this was due to several errors in coding. First, the metasomal tergal emarginations were coded as “?” because I had not seen the type at the time of analysis. They should have been coded as 4 because Mt2-5 are all barely emarginate. Thus, instead of arising at node 8 (metasomal tergal emarginations 2), *Pondorymus* would have arisen at node 15 (Mt emarginations 4). The wing veins should have been coded as “torymus-like” (*Tory*) and not “monodontomerus-like” (*Mono*). *Pondorymus* would then have arisen at node 16 with wing vein *Tory*.

*Pondorymus* is autapomorphic in having 3 reduced funiculars (anelli), but anelli were not read into the working hypothesis data (see introduction Phylogeny for explanation). As *Pondorymus* differs in no other states from *Torymoides*, I conclude that it is simply a single derived taxon within *Torymoides*. I place *Pondorymus* as a junior subjective synonym of *Torymoides*. I have seen specimens from Australia that also have 3 anelli but are otherwise simply *Torymoides*. There is an undescribed Nearctic species that has at least 3 anelli and perhaps as many as 5 anelliform flagellomeres. Males have the scapes greatly inflated and nearly covering the entire face. This equals the taxon Genus A (unknown) at node 13. I thought perhaps it might be placed as an undescribed genus, but now I believe it is simply a highly derived species of *Torymoides*.

One additional character should be discussed for the sake of completeness. It was

not used in my character analysis because of the suspected variation in the state, including variation between sexes of the same species. In the type-species of *Macrodontomerus*, *Didactyliocerus*, *Dimeromicrus*, and *Torymoides*, the mesepimeron has no median dividing sulcus and appears as a flat, or slightly convex plate. The majority of species assigned to *Torymoides* and *Dimeromicrus* have a median sulcus. Bouček (1988) discussed this problem and pointed out that in species of *Torymoides* the sulcus may appear in any state from absent, to "shallow and visible only at a certain angle," to "long, curved and moderately deep." He also pointed out that in males of both *Macrodontomerus* and *Didactyliocerus* the groove is "more or less indicated." I have not seen many specimens of these genera and cannot confirm Bouček's comment. In many dozens of male *Torymoides amabilis* the sulcus is not present. In any case, it is probable that the condition of this sulcus may be helpful at the species level, but probably not at the generic level.

Ending Hypothesis (Fig. 38C): In the ending hypothesis, *Torymoides* arises as part of a four branch multifurcation at node 10 which includes *Torymoidellus*, *Aloomba*, and *Platykula*. The node is defined by the change from 2 anelli to 1, and by the loss of setae on the hind coxa. This latter character is homoplasious and, as I demonstrated for *Pseudotorymus*, is at best a species character. Within the node, *Torymoides* is defined by having 2 or more anelli (state 2\*, other taxa with 2) and metasomal terga 2-5 emarginate (all others with Mt2+3 emarginate at most). In this particular use of anelli the character is unsuited for establishing relationship (or identity), because a convention for variability was used in which 2 or more anelli was coded as a character (I explain in the "Phylogenetic Analyses" section, p. 34, why this convention was used). In this case it was not helpful because two anelli is the most common state for *Torymoiäes* (and all other taxa at node 10), but further reductions may occur. The occurrence of 4 metasomal terga having emarginations is found in *Pseudotorymus* (node 9), but this character is homoplasious and probably tells little about true relationships. Relationships within node 10 are questionable due, in part, to the fact that two of the taxa are defined by autapomorphies (*Torymoidellus* - propodeal structure, *Platykula* - hind-tibial spurs spine-like) and one (*Aloomba*) has a unique combination of derived characters. It is possible that each of these taxa is simply a derived species of *Torymoides* and that all should be placed in this genus. *Torymoidellus* and *Aloomba* are each known from a single species in Australia. *Platykula* is known from a single nearctic species and at least one undescribed species from the Neotropics. *Torymoides* is a widespread taxon, and it would not be unexpected to find closely related, derived taxa associated with it. Whether these warrant generic status is questionable, but I retain the names, pending further study.

DISCUSSION. - As discussed under *Pseudotorymus*, the only diagnosed difference between the complex of 43 species of *Torymoides* (*sensu* Grissell) and 38 species of *Pseudotorymus* (*sensu* Grissell) is that the former genus is defined by having 2 or more anelli and the latter 1 anellus. The recognition of these two taxa is based on an admitted homoplasy, but I believe there is some nomenclatural value in retaining the two names until species-level revisions are attempted.

*Torymoides* appears to be an ecological homologue of *Torymus* in Australia. For this region there are 18 species of *Torymoides* and 2 introduced species and 2 endemic ones of *Torymus* (1 of which is apparently undescribed, Bouček 1988). Palmer *et al.*

(1993) pointed out that a cecidomyiid endemic to California (*Rhopalomyia californica*) and introduced into Australia to control *Baccharis halimifolia* came under attack by a native species of *Torymoides*. In California the cecidomyiid is attacked by two endemic species of *Torymus* (Grissell 1976). The cecidomyiid was established in Australia in 1982. By 1991, 4 endemic parasites had moved over to the introduced cecidomyiid and a single species of *Torymoides* accounted for up to 80% of total parasitism.

***Torymoidellus* Bouček**

Figs. 38(C), 148, 183

*Torymoidellus* Bouček 1988:136. Type-species: *Torymoidellus reticulatus* Bouček (orig. desig. and monotypic, BMNH, examined).

NUMBER OF SPECIES (catalog p. 263). - 1.  
 DISTRIBUTION. - AUSTRALIAN (Australia).  
 HOST. - Unknown.  
 KEYS TO SPECIES. - None.

RECOGNITION. - Within Torymoidini, *Torymoidellus* is recognized by having 2 anelli, unmodified hind-tibial spurs, and the propodeum laterally carinate with the posterolateral corners sharply angled (Fig. 183).

PHYLOGENY. - *Torymoidellus* was not included in the working hypothesis, because it was described after its completion. It was placed in the ending hypothesis (Fig. 38C) where it arises at node 10 as part of a quadrifurcation involving *Torymoides*, *Aloomba*, and *Platykula*. The node is defined by the change from 2 anelli to 1 and by the loss of hind-coxal setae (which is homoplasious and a species-group character at best). It differs from the other three genera (and other torymids) by having an autapomorphically structured propodeum (Fig. 183), which is laterally carinate and with the posterolateral corners sharply angled. Based on this single state I retain the genus as valid, but it is possible that it is just a derived species of *Torymoides*. In some other genera of Torymini (e.g., *Torymus*) the propodea of species vary considerably. However, I have not seen evidence of much propodeal variation in *Torymoides*, and so it seems most reasonable to recognize this distinctive modification until intermediate forms should prove otherwise.

Based on the tree, *Torymoidellus* appears equally closely related to either *Platykula* or *Aloomba*, but both have derived, modified hind-tibial spurs. As I discuss under *Torymoides*, it is possible that all three taxa are derived taxa which should be placed in *Torymoides*, but this needs further study.

DISCUSSION. - Bouček (1988) suggested that *Torymoidellus* was closely related to *Torymoides* but differed from it in the "relatively longer" pronotum, the propodeum that was "steep" and with carinate corners, and the mesepisternum that was "anteriorly nearly carinate." The pronotal length is, in my opinion, so relative as to be of little diagnostic value. The mesepisternum is only questionably carinate, being angulate at most, and its construction is more a matter of degree of angle than of a true, developed carina. Bouček (1988) in his key (but not description) stated that *Torymoidellus* had



2-toothed mandibles and *Torymoides* had 3-toothed mandibles. I could not confirm this in the specimens I examined, but it is further evidence suggesting that this taxon is different from typical *Torymoides*. Mandibular teeth have not been well studied, and I know of only one other case of a deviation from the normal 3-toothed condition. In *Monodontomerus mandibularis* each mandible has only 2 teeth (one enlarged and one reduced), but the remainder of species have 3. It is probable that tooth number and/or size is a species character.

***Platykula* Huber**

Figs. 37(C), 38(C), 149, 158

*Platykula* Huber 1927:106. Type-species: *Syntomaspis albihirta* Ashmead (orig. desig. and monotypic, USNM, examined).

NUMBER OF SPECIES (catalog p. 233). - 1.

DISTRIBUTION . - Reported from a single state in the Nearctic (Florida), but I add the following new state records based on material in the USNM: Michigan, Maryland, Virginia, North Carolina, Missouri. At least 2 undescribed species are known from the Neotropical Region (Brazil, Chile).

HOST. - Unknown.

KEYS TO SPECIES. - None.

RECOGNITION . - Within Torymoidini, *Platykula* is recognized by having 2 anelli, an unmodified propodeum, and 2 apical hind-tibial spurs slightly longer than apical width of hind tibia, and spine-like (wiry) (Fig. 158).

PHYLOGENY . -

Working Hypothesis (Fig. 37C): *Platykula* arises as part of a 7 part multifurcation at node 8 and in association with several taxa at 13 (note that Genus A (unknown) is now placed as *Torymoides* as a result of the working hypothesis discussed under that genus). My analysis of *Platykula* was based on the monotypic Nearctic type-species of the genus (i.e., *Platykula albihirta*) and two undescribed species from Brazil and Chile coded as *Platykula* A. These taxa differ from each other only in that *Platykula* has a median propodeal carina (state = *One*) and *Platykula* A has no carina (state = *Nocarin*). In my analysis both arose at node 14 based on the synapomorphy of the elongated and spine-like hind-tibial spurs (Fig. 158). The two taxa differed only as expected based on the propodeal carina. A case could be made that each represents a generic-level taxon, but as stated in the phylogenetic analysis (p. 47), these 2 states were problematic to code and were homoplasious. Thus they would appear not to be reliable states on which to base generic-level taxa. For purposes of further discussion, *Platykula* A is now considered to be a species of *Platykula*, and the propodeal condition is considered variable.

Assuming that *Platykula* is monophyletic, based on the hind-tibial spurs, the question arises as to its placement relative to the other taxa on the tree. Based on its position in the working hypothesis (Fig. 37C, nodes 8, 13, 14) there is no resolution to this problem in the tree. Its association with Genus A (now = *Torymoides*) suggested a possible placement near that taxon.

Ending Hypothesis (Fig. 38C): In this hypothesis, *Platykula* arises at stem 10 as part of a quadrifurcation in association with *Torymoides*, *Torymoidellus*, and *Aloomba*. The stem is defined by the change from 1 to 2 anelli and the loss of the hind coxal setae. This last character is homoplasious and of no phylogenetic value. *Platykula* is defined by the presence of spine-like hind-tibial spurs (Fig. 158) and the propodeum which is variable for a single carina (state = *One*) or no carinae (state = *Nocarin*). The latter character was coded as a convention for a variable state as *One\** (see phylogeny, p. 47) and is not terribly informative. *Torymoides* has a simple propodeum (state = *Nocarin*) *Torymoidellus* has an autapomorphic propodeum (= *Tory*), and *Aloomba* has a modified propodeum (= *Modified*) as found in Monodontomerini (much like *Perissocentrus*).

*Platykula*, *Torymoidellus*, and *Aloomba* appear to be equally derived with respect to each other and, in my opinion, all could either be considered genus-level taxa or species-groups within *Torymoides*. I retain the generic level for several reasons. The genus *Torymoides* has species known throughout the major zoogeographic regions. To my knowledge only *Platykula*, confined to the New World, has the condition of "spine-like" spurs. The implication, based on known taxa, is that the condition has arisen only once. If such spurs are discovered in Old World taxa (note that *Aloomba*, from Australia, has long spurs which are not homologous with the spine-like spurs of *Platykula*) then the implication would be that the character is homoplasious and capable of arising multiple times within *Torymoides*. This, then, would not be a suitable character on which to base generic categories. Additionally, little taxonomic work has been done on New World species of *Torymoides*, of which only 2 are now described (*T. sulcius*, *T. smithi*). Retention of the name *Platykula* serves as a convenient recognition tool until proven otherwise.

DISCUSSION. - *Platykula* is more widespread than currently reported (e.g., Grissell 1979). I have included new state records above which considerably expand the distribution of the single described species (*albihirta*), and I published recently on synonymy involved with this species (Grissell 1992a). The presence of several undescribed species in the Neotropics indicates a much greater distribution, and perhaps species diversity, than is currently suspected.

#### *Aloomba* Girault

Figs. 37(E), 38(C), 150, 157, 184

*Aloomba* Girault 1921/358:2. Type-species: *Aloomba calcaris* Girault (monotypic, QM, examined).

NUMBER OF SPECIES (catalog p. 179). - 1.

DISTRIBUTION. - AUSTRALIAN (Australia).

HOST. - Unknown.

KEYS TO SPECIES. - None.

RECOGNITION. - Within Torymoidini, *Aloomba* is recognized by having 2 anelli, the propodeum with longitudinal ridges (Fig. 184), and elongated, preapical hind-tibial spurs (Fig. 157).

## PHYLOGENY . -

Working Hypothesis (Fig. 37E): *Aloomba* is known only from the poorly preserved type specimen from Australia. *Aloomba* arises at node 23 with the Neotropical genus *Perissocentrus*, with which it shares the synapomorphies of elongated and preapical hind-tibial spurs. It is placed in this position based on 3 presumptive synapomorphies: the “modified” propodeum (node 21), the monodontomerine-type structure of the metasternum (node 20) and the monodontomerine-type wing venation (node 19). Of these, the latter was a mistake in wing venation coding, and the metasternal structure was coded as “unknown,” because it cannot be seen on the only known specimen of *Aloomba*. Its inclusion at node 20 is merely a “calculated” probability based on other putative parsimonious states. The state of “modified propodeum” appears correctly coded, because it comes phenetically close in structure to that of *Perissocentrus* in which the propodeum has parallel, longitudinal carinae and a central median carina.

In reexamining *Aloomba* immediately after creating the working hypothesis, and in examining specimens of the clade formed at node 21, I discovered several problems that arose with respect to the genus. Firstly, the hind femur of *Aloomba* has only a small, dentiform angle as commonly found in *Pseudotorymus* or *Torymoides*, but not as found in members of the clade created at node 21, which all have a strongly developed tooth or series of teeth on an expanded hind femur. Secondly, I discovered that my interpretation of the occipital carina was too simple. These characters are discussed under the “Phylogenetic Analyses” section (p. 42 and 32 respectively).

Ending Hypothesis (Fig. 38C): In the ending hypothesis *Aloomba* arises at node 10 as part of a quadrifurcation involving *Platykula*, *Torymoides*, and *Torymoidellus*. The node is defined by the change from 1 anellus to 2 and by the loss of setae from the hind coxa. This latter character is homoplasious and more than likely a species or species-group character. *Aloomba* is defined by 3 synapomorphies: elongated hind-tibial spurs (Fig. 157), preapical hind-tibial spurs, and longitudinally carinate propodeum (Fig. 184). *Platykula* also has a derived form of the hind-tibial spurs, but they are spine-like and not particularly elongated. *Torymoidellus* has a derived propodeum (Fig. 183), which is autapomorphic for the family. *Torymoides* would appear to be the least derived member of the group having simple hind-tibial spurs and a simple, non-modified propodeum. Because of the multifurcation, exact relationships between the taxa are not readily forthcoming.

DISCUSSION . - *Aloomba* was placed with the monodontomerine clade in my working hypothesis but with the torymoidine clade in my ending hypothesis. It is a slightly anomalous taxon. It shares the elongated hind-tibial spurs inserted preapically and the modified propodeum found in *Perissocentrus* (Monodontomerini). Alternatively, it shares 4 synapomorphies associated with members of the Torymoidini and not the Monodontomerini: 2 anelli, elongated marginal vein and shortened stigmal vein, dorsally arched occipital carina closer to the hind ocelli than the occipital foramen, and hind femur angulate rather than distinctively toothed. This evidence is more supportive of a phylogenetic placement within the Torymoidini than the Monodontomerini. *Aloomba* is an endemic Australian genus and the fact that Australia appears to be the center of diversity for *Torymoides* also suggests a stronger phylogenetic association. Members of Monodontomerini are scarce in Australia, with only 2 known species in the single genus *Amoturoides*.

### Tribe Monodontomerini

Monodontomerini is composed of 59 valid species (plus 29 synonyms) in the following genera: *Amoturoides*, *Anneckaida*, *Chrysochalcissa*, *Monodontomerus*, *Oopristus*, *Perissocentrus*, *Pradontomerus*, *Rhynchodontomerus*, *Rhynchoticida*, and *Zdenekius*. The tribe is widespread but not particularly speciose. About half of its species are Holarctic, with the remainder divided between the other zoogeographic regions.

Species of Monodontomerini parasitize predominantly Lepidoptera, aculeate wasps and bees, and sawflies (far more so than all other torymid taxa). This is the only torymid group with species that attack tachinid flies, ichneumonids, and eggs of coreiids, pentatomids, and tettigoniids. Species have not been reared from mantid eggs nor are Coleoptera-feeding species known. Some species are facultatively hyperparasitic, and no species are phytophagous. Only 26 percent of its species are without known hosts (Table 3).

Bouček (1978) was the first to recognize Monodontomerini as a tribe based on the angle of the propodeum (i.e., its steepness), its sculpture, the usual presence of a median carina, and one anellus. He recognized the new tribe Chrysochalcissini (1978), with 2 included genera, again based primarily on the propodeum. Based on my analysis the genera included in Chrysochalcissini (i.e., *Oopristus* and *Chrysochalcissa*, Fig. 38, node 18) arise as part of the monodontomerine-clade not apart from it. The recognition of the tribe Monodontomerini, itself, strains the phylogenetic interpretation of my ending hypothesis (Fig. 38E, node 14). In recognizing a tribal category, I do so purely for practical purposes. The positions of *Exopristus* and *Cryptopristus* (Fig. 38D, node 11) and *Thaumatorymus* and *Stenotorymus* (Fig. 38D, node 13) are discussed under *incertae sedis* (p. 165). Technically, these 4 taxa should be treated as two separate groups of unplaced taxa, one at node 11 and the other at node 13. This belies the inexactitude of my study. It is more valuable in my opinion to recognize major groupings, realizing the shortfalls of the cladistic method, than to nomenclaturally codify a series of ever-compounded, humanly generated interpretations of potential character state evolution. Below I discuss my reasons for recognizing only the single tribe as I do.

The tribe is formed of taxa of relative simple (Figs. 64, 65, 68) to complex appearance (Figs. 66-67). Most members are 4 to 5 mm, excluding the ovipositor, which is rarely longer than the body. Species are often dull olive green in color, but there are metallic blue and green species. Its members share derived characters associated with the hind femur, the propodeum, and the metasternum.

**DIAGNOSIS.** - Monodontomerini is defined by the *marginal vein 4 to 6.5 times the length of the stigmal vein and 1.5 to 3 times the length of the postmarginal vein* (Fig. 242-248) and the *occipital carina dorsally flat* (Figs. 231, 405), *nearer to the occipital foramen than to the hind ocelli and touching or nearly touching the hypostomal carina at its median point*. Additional characters that aid in recognition are metasomal terga without emarginations (except *Oopristus*); hind femur with modifications — a single large tooth or lobe (Figs. 213-215, 226, 228-230) or 1 row of teeth with inner teeth or bumps (Figs. 216, 219, 221, 224); the propodeum with sublateral foveae on either side of a median carina (Figs. 238-240, 394), though foveae poorly developed in

*Oopristus* and *Rhynchodontomerus* (Fig. 241) and absent from *Chrysochalcissa*.

DESCRIPTION . - Occipital carina dorsally flat (Figs. 231, 405), nearer occipital foramen than hind ocelli (autapomorphic for clade except in *Oopristus* where carina is lost entirely), reaching or nearly reaching hypostomal carina at its median point (approximately) except in *Rhynchodontomerus* (Fig. 234) where carina falls far short; antennal club formed of 3 flagellomeres indicated by distinct annulations that completely encircle club, without ventral micropilosity; propodeum with spiracular sulcus evident and reaching (or curved towards) nucha, callus convex and setose; anterior metapleural margin straight; metasternum variable (Figs. 199, 201, 203, 205, 207, 209) with anterior edge of propodeal foramen placed nearer posterior edge of hind-coxal foramen than anterior edge, metasternal area longitudinally narrowed and subequal in length (anterior to posterior) to diameter of propodeal foramen, without metasternal shelf (Fig. 426); shortened marginal vein 4 to 6.5 times longer than stigmal vein, 1.5 to 3 times longer than postmarginal vein, stigma width much less than stigmal vein length (Figs. 242-248); hind femur with single, abruptly produced subapical tooth (Figs. 213-215, 228-230), or medially placed tooth (Figs. 226-227) with or without additional femoral modifications, or enlarged and with 1 or 2 rows of teeth (Figs. 216-217, 219-220, 221-222, 224-225); hind tibia straight (Figs. 228-230) or curved (Figs. 217, 220, 222, 227), with apex truncate at right angles and with 2 spurs at ventral corner; metasomal terga not laterally emarginate, dorsomedially entire (except *Oopristus*).

#### PHYLOGENY . -

Working Hypothesis (Fig. 38): Although the working hypothesis proved to be rather contradictory, its analysis provided a better basis for understanding the ending hypothesis and provided a fairly convincing synapomorphy to define the group. In the working hypothesis (Fig. 37), after considering various interpretations of the tree topology, the most parsimonious way to resolve the tree at nodes 18, 19, 20, and 21 was to take the following steps as explained below: condense node 18, recognize *Stenotorymus* (node 19) and *Zaglyptonotus* (node 20) as *incertae sedis*, and recognize Monodontomerini (node 21) based on character states as discussed next.

Node 18 (condensed): This node was diagnosed in the final working tree by the synapomorphy of the developed hind-femoral tooth. It includes *Pseudotorymus* and, indirectly, Toryminae of authors (= Torymini *sensu* Grissell) which was coded with a question mark for the tooth state because within this large and speciose group the states of *Simple*, *Angle*, *Toothed*, *2teeth*, and possibly *Serrate* are known. Because of this questionable character and several others, the taxon "Toryminae" (of authors) contributed greatly to the instability of the final calculated trees. *Pseudotorymus*, I determined, was miscoded. It does not have the true state of *Toothed* hind femur, but is a slight modification of *Simple* or *Angle*, both states which should have been combined. Therefore, the coding for a "toothed" hind femur would condense to the next node (19).

Node 19: This node would then be diagnosed by 3 synapomorphies, the toothed, or modified, hind femur (a result of altering the definition of at node 18), a purported reversal from the "torymine-type" of wing vein back to the "monodontomerine-type," and a putative reversal from 4 tergal emarginations back to 0 (i.e., unemarginate).

The toothed hind femur is noted for its abruptly produced, single tooth (Figs. 213-215) with the transformation to a swollen or lobed ventral margin (node 25, Figs. 227), and then to a double row of teeth (node 26, Figs. 216, 219, 221, 224). *Zaglyptonotus* (node 20) is the only exception to this and it was removed from this node to an *incertae sedis* as explained on page 173. The wing veins are diagnosed as "monodontomerine" based on the shortened marginal vein 3 to 6 times as long as the stigmal vein, 1.5 to 3 times as long as the postmarginal vein, and the stigma subequal in width to the stigmal vein. *Stenotorymus*, however, is an exception to this (see p. 170). The absence of tergal emarginations is a somewhat more problematic state to elucidate, especially as a number of tergal changes take place at node 29. The character is homoplasious and is discussed here only as it affects node 21, where it might be considered as a synapomorphy for members of the clade (i.e., Monodontomerini). All members of Monodontomerini, except *Oopristus* (see below), have terga without emarginations and they are more sclerotized than most other torymids. Metasomal tergum 2 is especially rigid and "shell-like" and is never laterally compressed or folded medially. The condition occurs sporadically in a few basal taxa including *Glyphomerus* and *Erimerus* (though here it is relatively thinner and prone to lateral compression), and in more derived taxa, including *Chalcimerus* and *Propalachia*. Because this was judged to be the plesiomorphic state as a result of transformation series analysis (see p. 52), possibly little should be made of the point. On the other hand, the tergal condition as found in Monodontomerini is basically not the same as found in the majority of basal taxa such as Microdontomerini. In the latter tribe the terga are weak and often folded medially, the emarginations are difficult to see because of the folding and thinness of the terga, and often there is a slight indication of an emargination but nothing substantial. Under these circumstances it becomes subjective whether or not to call the terga emarginate. Often if the terga are laterally compressed they appear emarginate, if not then they appear entire. In Monodontomerini the terga are entire, and I believe this can be used as a synapomorphy to define the clade. *Oopristus*, with a single Palearctic species, has Mt 2 slightly emarginate and weakly sclerotized. As *Oopristus* arises at the top of this clade (node 28), the state would appear to be a reversal. The taxon has so many apomorphic and autapomorphic states that its position is open to conjecture.

From node 19 arise *Stenotorymus*, node 20, and node 29 (discussed further on p. 165):

*Stenotorymus* is an autapomorphic clade that arises as part of the trifurcation at node 19. It is discussed as part of *incertae sedis* (p. 170).

Node 20: This node is based on the single, putatively autapomorphic state of the metasternum called "mono," in which the propodeal foramen is positioned posteriorly with respect to the hind-coxal foramen, resulting in a longer median plate and distance between the anterior of the propodeal foramen and the anterior margin of the metasternum (Figs. 199, 210, 205, 209). A reversal to the primitive condition occurs at node 24 and some problems of interpretation arise at node 20, so this character needs to be discussed in some detail.

First of all, to dismiss node 20, *Zaglyptonotus* is placed here as the sister taxon to the remaining taxa, but the condition of the metasternum could easily have been coded as an autapomorphic state for *Zaglyptonotus*. Additionally, the hind femur coding at node 18 was a calculated parsimony because the genus was coded as "?" for this state

due to variation in the form of the femur. Therefore, the placement of *Zaglyptonotus* at node 20 is speculative, and I remove it to *incertae sedis* (see discussion, p. 173). I tried above to categorize the groundplan nature of the metasternal character for Monodontomerini. There are variations on the typical structure, but these are difficult to categorize and not readily visible. The most difficult variations to categorize arise at node 24 for *Rhynchodontomerus* (Fig. 207) and *Zdenekius* (Fig. 203) where the state was coded as the plesiomorphic one (*Crypto*), even though these taxa differed somewhat from the state as found in the true primitive condition. These states could possibly be reversals or subtle modifications of the primitive state (*Crypto*) and could be hypothesized as slightly derived. Although the metasternal area in *Rhynchodontomerus* (Fig. 207) appears to be as wide as that found in the primitive state *Crypto*, it is actually as narrow as *Monodontomerus* (Fig. 199). This is because the two submedian carinae, which delimit the central area, are somewhat difficult to see. *Rhynchodontomerus* has the posterior margin of the metapleuron enlarged and lamelliform (Fig. 208), as found in *Monodontomerus*, *Pradontomerus*, and *Amoturoides*, thus bolstering the argument for a derived state. *Zdenekius* is more difficult to assess. It is more heavily sclerotized than typical *Crypto* (a relative comparison at best).

In some genera (e.g., *Monodontomerus*, *Pradontomerus*, and *Amoturoides*) the metasternal area is narrowly longitudinal and not well sclerotized (except for the median carina, Fig. 199). In *Perissocentrus* and *Zdenekius* the area is wide and sclerotized (Figs. 203, 211), whereas in *Rhynchotocida* the metasternal area is narrow and a strong median carina projects from its surface (Fig. 201) and in *Anneckaida* (Fig. 205) it is extremely narrow and the propodeal foramen is far removed from the anterior margin of the metasternum and there is no median carina. *Oopristus* (Fig. 209) has the metasternal area narrowed similar to *Anneckaida*, where it is essentially reduced to a lamelliform carina. These modifications make phylogenetic assessment difficult based solely on the metasternum.

Node 21: This node defines the clade Monodontomerini based on the unique synapomorphy of the "modified" propodeum. In general, a moderate to strong median carina is present and subtending this are depressions (Figs. 238-241, 394). In *Oopristus* only very faint depressions are present, and the median carina is present only dorsally. In *Chrysochalcissa* the propodeum is simple. The highly derived position in which these 2 taxa are placed (node 28) argues for a reversal. *Rhynchodontomerus* is somewhat modified in that the median carina is vaguely developed and begins ventrally as a wide continuation of the nucha which then narrows dorsally. There are foveae on either side dorsally, but these are obscure (Fig. 241).

I did not discover what I consider to be the most likely synapomorphy that unites the Monodontomerini until after the working hypothesis was finished, i.e., that the occipital carina is well developed, closer to the occipital foramen than the hind ocelli, and usually reaches at least to the median point of the hypostomal carinae (Figs. 231, 405). In all torymids from the primitive Megastigminae to the advanced Podagrionini, the occipital carina is always nearer to the hind ocelli, or at least midway, than to the occipital foramen. Therefore, the isolated state found in Monodontomerini would appear to be derived, and this was tested in the ending hypothesis.

Ending Hypothesis (Fig. 38E): As a result of the above study, the position of *Rhynchodontomerus* + *Zdenekius* (node 14) was reversed with respect to *Amoturoides* (node 15). This is discussed in detail below under the generic phylogeny.

*Rhynchodontomerus* + *Zdenekius* are now hypothesized as primitive relative to the remainder of the clade (not derived as in Fig. 37E, node 24). The clade (Monodontomerini) is defined by three synapomorphies: the relatively low occipital carina (autapomorphic; but lost entirely in *Oopristus*), the presence of a frenal line, and a modified propodeum. The frenal line is a homoplasious character and is of questionable phylogenetic value. Although I am convinced that all of the taxa now recognized at node 14 are closely related, it is only the derived occipital carina and the modified propodeum (as discussed above) that lend credence to this phylogenetic interpretation.

One other major difference between the working hypothesis and the ending hypothesis is the removal of *Aloomba* from the clade. This transfer is discussed under the genus (Torymoidini, p. 115), and was caused by a change in the interpretation of wing venation.

SUMMARY. - The ending hypothesis suggests that Monodontomerini is monophyletic and somewhat more derived than Microdontomerini and Torymini/Torymoidini.

***Zdenekius* Grissell**

Figs. 37(E), 38(E), 64, 203-204, 226, 238, 243

*Zdenekius* Grissell 1993:264-267. Type-species: *Zdenekius smithi* Grissell (orig. desig. and monotypic, USNM).

NUMBER OF SPECIES (catalog p. 290). - 1.

DISTRIBUTION. - NEARCTIC (Widespread in northern U.S. and southeastern Canada).

HOSTS. - Associated with aculeate Hymenoptera and their dipterous and hymenopterous parasites but specific relationships are unknown.

KEY. - None.

RECOGNITION. - Within Monodontomerini, *Zdenekius* is recognized by the presence of a weakly expressed frenal line, a medially enlarged hind femur with a single tooth (Fig. 226), a straight hind tibia with apical, unmodified spurs, and in females by the metasoma, which is dorsoventrally flattened and with sclerotized, broad sterna that are not overlapped by the terga (i.e., the sterna are easily seen as flattened plates in ventral view).

PHYLOGENY. - Within the working hypothesis (Fig. 37E), I treated *Zdenekius* as an unplaced taxon. In most respects it appeared to be a species of *Monodontomerus*. *Zdenekius* arose at node 24 with *Rhynchodontomerus*, where it is placed without apomorphies. The node is defined by the reversal of the metasternum from *Mono* (node 20) to the primitive state *Crypto*. In the ending hypothesis (Fig. 38E), however, *Zdenekius* and *Rhynchodontomerus* are hypothesized to retain the primitive *Crypto* state, which then changes to *Mono* at node 15. *Zdenekius* is defined by the retention of primitive character states relative to all other taxa in the clade, but I did not recognize the structure of the metasoma as unique during my analysis. Having seen innumerable specimens of *Monodontomerus* and other monodontomerines, however, I now believe that the metasoma of this genus is unique. In females, the metasoma



(Fig. 64, inset) is dorsoventrally flattened and has broad, flat, heavily sclerotized sterna that are not entirely covered by the terga, so that they are easily seen in ventral view. This construction also exposes the hypopygium as a broad, chisel-shaped sternum. In all other *Monodontomerini* (e.g., Figs. 65-68), the metasomal terga meet ventrally and conceal the sterna entirely (though rarely the sterna are exposed, then they are V-shaped and weakly sclerotized). If the hypopygium is seen at all (e.g., Fig. 65), it appears as an apically pointed structure, but this is due more to the lack of lateral sclerotization rather than its actual shape.

The metasternum of *Zdenekius* was coded as *Crypto* --a primitive state--relative to other *Monodontomerini*, but it is relatively more heavily sclerotized, as is the metasoma. As with *Rhynchodontomerus*, it is not easy to hypothesize the relationships of this monotypic taxon. *Zdenekius*, based on its metasternum, appears to be primitive relative to *Monodontomerus*, and information from the metasoma, being autapomorphic, is relatively uninformative for phylogenetic purposes. The suspected use of aculeate Hymenoptera as hosts is certainly similar to that of *Monodontomerus*. It is possible that the single known species of *Zdenekius* represents an atypical species of *Monodontomerus*. However, it is as relatively distinct from *Monodontomerus* as is *Rhynchodontomerus*, and both should be treated at the same level until additional species, or intermediates of each, are found.

DISCUSSION. - The host records for this genus are vague but indicate solitary, twig nesting wasps (sphecids and vespids). *Zdenekius smithi* also might be facultatively hyperparasitic on dipterous and hymenopterous parasites of these wasps. Two specimens (collected under U. S. Forest Service Hopkins Numbers) were reared in Oregon from nodes of *Alnus rubra*. These nodes also produced a dipteran (Bombyliidae: *Anthrax irroratus*), which is a known parasite of aculeate wasps. Another specimen (also under Hopkins Numbers) was reared in Virginia from a "dead soft and rather dry willow limb" which "contained a number of yellow larvae." These larvae, which were in cells with aphids, were thought to be crabronine sphecids. Also present were some white larvae thought to be ichneumonids. One specimen of *Zdenekius smithi* and 2 specimens of an unidentified ichneumonid were reared from this material. Two additional specimens were reared in Maryland from a nest of *Odynerus canadensis* (Vespiidae). This is a twig-nesting aculeate with numerous recorded parasites (see Krombein 1979 for summary) so that no definite host can be recognized.

***Rhynchodontomerus* Novicky and De Santis**  
Figs. 37(E), 38(E), 207-208, 234-235, 241, 245

*Rhynchodontomerus* Novicky and De Santis 1961:25-26. Type-species: *Monodontomerus inclusus* Kieffer and Jorgensen (monotypic, depository unknown, not examined).

NUMBER OF SPECIES (catalog p. 261). - 1.

DISTRIBUTION. - NEOTROPICAL (Argentina).

HOST. - Reared from Cecidosidae (Lepidoptera).

KEYS TO SPECIES. - None.

RECOGNITION. - Within *Monodontomerini*, *Rhynchodontomerus* is recognized by the

much produced clypeal apex (Fig. 235). Generally, but not always, the dorsal margin of the occipital carina is slightly produced (arched) dorsomedially (Fig. 234), which is also autapomorphic for this genus.

**PHYLOGENY.** - The working hypothesis (Fig. 37E) placed *Rhynchodontomerus* at node 24 along with *Zdenekius*. The node was defined by the single reversal of the metasternum from *Mono* to the more primitive state as found in Microodontomerini (i.e., *Crypto*). In *Rhynchodontomerus* (Fig. 207), the state is actually somewhat intermediate between that of *Crypto* (as in Fig. 389) and that of *Mono* (Figs. 199, 395), because the metapleural plate appears to be about as wide as that found in *Crypto*, but it is submedially delimited by faint carinae, which create a narrowed median area that is more in proportion with that of *Mono*. In overall appearance, however, I coded the state as *Crypto* rather than create an autapomorphic state, because almost all of the variations within *Mono* are autapomorphic. I attempted to code the states in as broad a sense as I could, but this resulted in a lack of refinement.

In the ending hypothesis (Fig. 38E) *Rhynchodontomerus* also arose at the same node (14) with *Zdenekius*, but this time as part of a trifurcation. Both were considered primitive with respect to the remainder of the clade (node 15). *Rhynchodontomerus* is defined by the enlarged clypeus (Fig. 235), which is autapomorphic, and the hind coxa without setae. This last character is homoplasious and is probably a species or species-group character at best. In this taxon the occipital carina may appear to be about midway between the occipital foramen and the hind ocelli, but this is due to the irregularity of the carina dorsomedially, where it arches slightly dorsally (Fig. 234). This is autapomorphic, and if it were not for this abrupt arching the carina would continue straight across the head much as in the remainder of the Monodontomerini.

Although the taxon arises with *Zdenekius* in both analyses, both have morphological peculiarities that are autapomorphic and present little data to establish relationships. In *Rhynchodontomerus* the autapomorphies, as just stated, are the elongated clypeus and the irregular occipital carina. Neither occur in *Zdenekius*, which is typically monodontomerine for these characters. *Zdenekius* has a highly modified metasoma as well as a distinct hind-femoral construction (see p. 121). The two genera differ also in the structure of the metasternum, although both taxa are coded as *Crypto*. Whereas *Rhynchodontomerus* is arguably intermediate between *Crypto* and *Mono*, in *Zdenekius* the state is essentially identical to *Crypto*.

In *Rhynchodontomerus* the propodeal structure is different than in other Monodontomerini in that the median carina is vaguely developed and begins ventrally as a wide continuation of the nucha and narrows dorsally. Foveae occur on either side dorsally, but these are somewhat obscure (Fig. 241). This structure is a modification of the propodeum as found in *Monodontomerus*, and could either be a precursor of the well developed expression of the foveae, or it could possibly be an effacing of the well developed foveae.

Because of the contradictory nature of the character information it is not easy to hypothesize the most likely relationships of this monotypic taxon. Phenetically it appears to be a highly derived taxon based on its greatly elongated clypeus, but based on its rather undeveloped metasternum and propodeum, it appears to be primitive relative to *Monodontomerus*. Its use of Lepidoptera as hosts is consistent with a relationship

with both *Monodontomerus* and *Perissocentrus* at the next higher node (15, Fig. 38E). These hosts are rarely used by other torymids. It is possible that the single known species of *Rhynchodontomerus* represents an atypical species of *Monodontomerus*. The north-African species *Monodontomerus anthidiorum* also has an elongate clypeus, although it is typical in all other respects for its genus. The expression of the clypeal state in two taxa of Monodontomerini indicates that it has arisen independently in closely related lineages. These lineages might be interpreted as species within the same genus or as genus-grade clades. The interpretation that appears to best fit the character states is that *Rhynchodontomerus* is primitive relative to *Monodontomerus*, and considering our poor knowledge of the neotropical fauna, I retain the former generic name until its use should prove indefensible.

***Amoturoides* Girault**  
Figs. 37(E), 38(E), 229

*Amoturoides* Girault 1932/439:2 (unpaged). Type-species: *Amoturoides breviscapus* Girault (monotypic, QM, examined).

NUMBER OF SPECIES (catalog p. 180). - 2.

DISTRIBUTION. - AUSTRALIAN (Australia), ORIENTAL (India), AFROTROPICAL (Ghana).

HOSTS. - One species has been reared from eggs of Tettigoniidae (Orthoptera) and the other from a nest of Vespidae (Hymenoptera) and from Tachinidae (Diptera) that inhabited the nest. [The association with Vespidae may reflect only a hyperparasitic relationship.]

KEYS TO SPECIES. - Bouček (1978:123).

RECOGNITION. - Within Monodontomerini, *Amoturoides* is recognized by the absence of a frenal line, an unenlarged hind femur (Fig. 229) with a single, ventral tooth, a straight hind tibia with apical, unmodified spurs, and in females by laterally compressed metasomal terga that conceal the sterna.

PHYLOGENY. - In the working hypothesis (Fig. 37E) *Amoturoides* arose as the most basal element of node 21, which is defined by the modified propodeum. The genus has no apomorphies but is defined by the absence of a frenal line (putative derived state), which reverses at node 22.

In the ending hypothesis (Fig. 38E), *Amoturoides* arose one node higher (node 15) than in the working hypothesis and as part of the multifurcation which includes both *Monodontomerus* and *Perissocentrus*. This node is based on the presence of a modified metasternum. *Amoturoides* differs from *Monodontomerus* only in the loss of the frenal line. This character is homoplasious based on my character analysis (see p. 46), and is not of much phylogenetic significance. *Amoturoides* is possibly only a species group of *Monodontomerus*, but because the distribution of *Amoturoides* and *Monodontomerus* only barely overlap in the Oriental Region, and each is widespread in its own area, I treat them as valid taxa until such time as species of intermediate scutellar structure may be found.

***Monodontomerus* Westwood**

Figs. 12, 27, 37(E), 38(E), 59, 65, 199-200, 213-215, 230, 240, 242, 383, 394-395, 405, 426

*Monodontomerus* Westwood 1833:443. Type-species: *Monodontomerus obscurus* Westwood (monotypic, OUM, examined).

*Paroligostenus* Cameron 1913a:94-95. Type-species: *Paroligostenus trichiophthalmus* Cameron (monotypic, BMNH, examined).

NUMBER OF SPECIES (catalog p. 205). - 32.

DISTRIBUTION . - HOLARCTIC (widespread throughout), NEOTROPICAL (Cuba, Mexico, Colombia, Argentina), ORIENTAL (Sri Lanka, India, Pakistan).

HOSTS . - Numerous hosts are known for this genus including families in Diptera, Hymenoptera, and Lepidoptera. The primary hosts are solitary aculeate bees and wasps, sawflies, and moths (including their tachinid and ichneumonid parasites). An authentic record of *Monodontomerus* (undetermined species) attacking social vespid (*Mischocyttarus*; Litte 1979) in Arizona occurs in the literature, but the specimens are now lost (Litte, *in litt.*).

KEYS TO SPECIES . - Nearctic: Gahan 1941. Europe: Hoffmeyer 1930d. Europe and north Africa: Steffan 1952. Commonwealth of Independent States (European area): Nikol'skaya and Zerova 1978. Finland: Palmén 1940. Czechoslovakia: Bouček 1954a. Hungary: Erdős 1960. Japan: Kamijo 1963. Peoples' Republic of China: Lio *et al.* 1987. India: Narendran 1994.

RECOGNITION . - Within Monodontomerini, *Monodontomerus* is recognized by the presence of a frenal line, an unenlarged hind femur (Figs. 213-215, 230) with a single, apicoventral tooth, a straight hind tibia with apical, unmodified spurs (except *M. strobili*), and in females by laterally compressed metasomal terga that conceal the sterna (Fig. 65).

PHYLOGENY . - In both the working and ending hypotheses, *Monodontomerus* arises as part of a 4-node multifurcation. In the former hypothesis the multifurcation is defined by the presence of a frenal line, and in the ending hypothesis by the presence of a derived metasternum. Based on character consistency, the frenal line is an exceptionally homoplasious one whereas the metasternum is highly consistent.

In the working hypothesis (Fig. 37E), *Monodontomerus* arises at node 22, which includes nodes 23 (*Aloomba* + *Perissocentrus*), 24 (*Rhynchodontomerus* + *Zdenekius*), and 25. Within this clade, *Monodontomerus* is "diagnosed" by the absence of the derived characters that define nodes 23 and 25 and by its derived metasternum relative to node 24. Thus, it has a femur with only a single enlarged tooth (Figs. 213-215, 230) and a straight hind tibia but not the much-modified hind femur with a curved hind tibia as at node 25; it has unlengthened, apical hind-tibial spurs (with one exception - *M. strobili*) and not the elongate, preapical hind-tibial spurs as at node 23. However, it does have an apomorphic metasternum relative to the *Crypto*-type metasternum that defines node 24 (*Rhynchodontomerus* + *Zdenekius*).

In the ending hypothesis (Fig. 38E), *Monodontomerus* arises at node 15 along with *Amoturoides*, *Perissocentrus*, and node 16. The difference is that *Amoturoides*

occurs at the same node as *Monodontomerus*, whereas *Rhynchodontomerus* and *Zdenekius* are at the next lower node (14). This arrangement is due entirely to the metasternal construction. In the ending hypothesis, *Monodontomerus* is diagnosed by the absence of derived characters relative to *Perissocentrus* (defined by long, preapical hind-tibial spurs) and node 16 (defined by curved hind tibia). *Monodontomerus* differs from *Amoturoides* by having a frenal line, which is lost in the latter taxon. As presence of a frenal line is homoplasious, its use to define genera is questionable. It is possible that the Australian genus *Amoturoides* simply represents a species group of *Monodontomerus*, which is known from all regions except the Australian and Afrotropical.

DISCUSSION . - Steffan (1952) reviewed the nomenclature of many Old World species, but *Monodontomerus* is still fraught with nomenclatural problems. I have pointed out a few of these in the catalog section. I have in preparation a nearly complete revision of New World species of *Monodontomerus* and although there are a half dozen undescribed species, none are at odds with the traditional concept of the genus.

***Perissocentrus* Crawford**

Figs. 37(E), 38(E), 68, 211-212, 228, 231, 239, 247

*Perissocentrus* Crawford 1910c:235. Type-species: *Perissocentrus chilensis* Crawford (orig. desig., USNM, examined).

NUMBER OF SPECIES (catalog p. 230). - 6.

DISTRIBUTION . - NEOTROPICAL (South America, Ecuador and Brazil, southward).

HOSTS . - Reared from numerous families of Lepidoptera and their ichneumonid parasites.

KEYS TO SPECIES . - Grissell (1992b).

RECOGNITION . - Within Monodontomerini, *Perissocentrus* is recognized by long hind-tibial spurs that are basad of the apex by 1/5 or more the length of the hind tibia (Fig. 228).

PHYLOGENY . - In the working hypothesis (Fig. 37E) *Perissocentrus* arose at node 23 with *Aloomba*. This latter taxon was coded incorrectly for wing venation and is discussed further elsewhere (see p. 115). With *Aloomba* removed, *Perissocentrus* becomes part of the quadrifurcation at node 22. This involves node 24 (*Rhynchodontomerus* + *Anneckeida*), the genus *Monodontomerus*, and node 25. These genera are discussed below in the ending hypothesis. *Perissocentrus* is defined by two apomorphies: the elongate hind-tibial spurs and their placement subapically (Fig. 228). No other taxa at node 22 share these states, although some modifications to spurs are found in *Rhynchotocida* and a few species of *Monodontomerus*.

In the ending hypothesis (Fig. 38E), *Perissocentrus* arises at node 15 as part of a multifurcation. The taxa are similar to those found in the working hypothesis. *Monodontomerus* remains the same, and node 16 is exactly the same as node 25 above. *Rhynchodontomerus* + *Zdenekius* are at the next lower node (14) and replaced by *Amoturoides*. *Perissocentrus* is defined by exactly the same apomorphies listed above

and is phenetically more similar to *Monodontomerus* than to *Amoturoides*, based on the presence of a frenal line. The long tibial spurs of *Perissocentrus* are hypothesized as derived, based on my character analysis and would indicate that the genus is derived with respect to *Monodontomerus*.

In both *Perissocentrus* (Fig. 211) and *Monodontomerus* (Figs. 199, 395) the metasternum is coded as *Mono*, based on a relative comparison to that of the more advanced, *Podagrion*-like metasternum (Fig. 397), in which the coxal foramina are some distance removed from the propodeal foramen and the metasternal area is lengthened. There are some slight differences, however, that may reflect a more derived development in *Perissocentrus*. In *Perissocentrus* (Fig. 211) the hind-coxal foramina are relatively close to the propodeal foramina (as in *Monodontomerus*), but the hind-coxal foramina are separated from the anterior margin of the metasternal area by a broadly sclerotized area (absent in *Monodontomerus*, Fig. 199). This sclerotized area in *Perissocentrus* is perhaps the result of a reduction in the size of the hind-coxal (and possibly propodeal) foramina (thus increasing the relative size of the metasternal area) or it could be the result of an elongation of the entire metasternal area. At least the lengthening of the metasternal area would be a derived condition relative to *Monodontomerus* (based on the lengthening of the area in advanced groups such as *Podagrion*). In *Perissocentrus* the foramina still remain relatively close together at the posterior margin of the metasternum, whereas in *Podagrion* the hind-coxal foramina appear to have shifted noticeably forward.

DISCUSSION . - *Perissocentrus* might be considered a derived Neotropical taxon of *Monodontomerus*, just as *Amoturoides* might be a derived Indo-Australian/Afrotropical taxon. The center of diversity for *Monodontomerus* appears to be Holarctic and perhaps both other taxa are geographic variants.

***Pradontomerus* Bouček**

Figs. 37(E), 38(E), 66, 227, 246

*Pradontomerus* Bouček 1978:120-121. Type-species: *Pradontomerus hyper* Bouček (orig. desig. and monotypic, BMNH, examined).

NUMBER OF SPECIES (catalog p. 250). - 1.

DISTRIBUTION . - AFROTROPICAL (Tanzania, Zimbabwe).

HOST . - Reared from Ichneumonidae (Hymenoptera) cocoons.

KEYS TO SPECIES . - None.

RECOGNITION . - Within Monodontomerini, *Pradontomerus* is recognized by the presence of a frenal line, a hind femur that has a large median tooth and is markedly sinuate to its distal apex (Fig. 227), and a curved hind tibia with unmodified spurs.

PHYLOGENY . - In both the working (Fig. 37E) and ending hypothesis (Fig. 38E) *Pradontomerus* arises as the sister group to *Oopristus* + *Chrysochalcissa* and *Rhynchoticida* + *Anneckaida*. Therefore, the remainder of this section treats only the ending hypothesis. *Pradontomerus* arises at node 16, which is defined by a curved hind tibia, and is defined solely by the lobed hind femur (Fig. 227). In this autapomorphic

state, instead of a distinct subapical tooth, the femur has a median tooth and then is markedly sinuate to its apex. *Pradontomerus* differs from other of node 17 by lacking the double or nearly double rows of ventral teeth.

Relative to taxa at node 17, *Pradontomerus* does not have the derived double-row of teeth on the hind femur, nor the derived clypeal apex. It does share the derived, curved hind tibia with members of the clade and is considered the primitive sister group to the remainder of its taxa. *Pradontomerus* has the metasternum structurally similar to *Monodontomerus* (Fig. 199), but the median carina between the hind coxae is more strongly developed (nearly as in *Rhynchotocida*, Fig. 201). *Oopristus* (Fig. 209) and *Anneckeida* (Fig. 205) differ from *Pradontomerus* (as in *Monodontomerus*, Fig. 199) by having the metasternum much narrowed between the coxal foramina and essentially lacking a median carina (although in *Oopristus* the metasternal area is so narrow it becomes essentially a ridge or carina). This character is unknown for *Chrysochalcissa*.

As *Pradontomerus* is represented by a single, autapomorphic species that is somewhat intermediate between *Monodontomerus* and node 17, it seems most expedient to accept its placement as a valid taxon. Additional information based on biology also suggests this placement. *Pradontomerus* was reared as a hyperparasite of *Gelis* (Ichneumonidae) cocoons possibly associated with *Dasychira* (Lymantriidae) and of *Meteorus* cocoons (Braconidae), a habit more associated with *Monodontomerus* than with taxa of node 16 in which species of 3 of the 4 genera are parasites of heteropterous eggs (host of *Anneckeida* unknown).

***Chrysochalcissa* Girault**  
Figs. 37(E), 38(E), 216-218, 244

*Chrysochalcissa* Girault 1915/245:327. Type-species: *Chrysochalcissa olivacea* Girault (orig. desig. and monotypic, QM, examined).

NUMBER OF SPECIES (catalog p. 181). - 5.

DISTRIBUTION. - AFROTROPICAL (Uganda, Nigeria), AUSTRALIAN (Papua New Guinea), ORIENTAL (Burma, Malaysia, India).

HOST. - Reared from eggs of Coreidae (Heteroptera).

KEYS TO SPECIES. - Narendran (1994) modified the key of Bouček (1978) to include a new Indian species.

RECOGNITION. - Within Monodontomerini, *Chrysochalcissa* is recognized by the absence of a frenal line, the enlarged hind femur having an outer row of small teeth and an inner row of nearly equally developed teeth (Figs. 216-217), the curved hind tibia (Fig. 217) that is apically subpointed (Fig. 218), the emarginate clypeus (Fig. 41, Character 6, Emarg), and 2 anelli.

PHYLOGENY. - In both the working (Fig. 37E) and ending hypotheses (Fig. 38E) *Chrysochalcissa* arises in the same position relative to *Oopristus* and *Rhynchotocida* + *Anneckeida*. Therefore, the remainder of this section treats only the ending hypothesis. *Chrysochalcissa* arises at node 18 along with *Oopristus*. The node is diagnosed by the putative loss of both the frenal line and the hind-coxal setae. Both of these

characters are homoplasious and not much emphasis should be placed on them. *Chrysochalcissa* is defined by 6 synapomorphies, of which the emarginate clypeus (Fig. 41, Character 6, Emarg) is autapomorphic. The subpointed hind-tibial apex (Fig. 271-218) is found only at node 24. The wing venation (*Tory*), notauli (*Faint*), and anelli (2) are all homoplasious whereas the propodeum (*Nocarin*) is a reversal to the primitive state.

The relationship of *Chrysochalcissa* to *Oopristus* is not entirely evident based on morphology. *Chrysochalcissa* differs from *Oopristus* by having the hind tibia sub-pointed (Figs. 217-218) rather than truncate (Fig. 225), having 2 anelli instead of 1, having an occipital carina, having the metasomal terga without emarginations rather than slightly emarginate, and in having the clypeus emarginate (Fig. 41, Character 6, Emarg) rather than recessed (Fig. 232). *Oopristus* also has some autapomorphic characters not used in the analysis, which are discussed further under the recognition section of that genus. *Chrysochalcissa* is reared from coreid eggs whereas *Oopristus* is known only from pentatomid eggs.

Bouček (1978) placed the two genera together as a tribe, based on the “steep” propodeum, with deep reticulation and no median carina, and the condition of the hind femur. I did not use steepness of the propodeum as a character. In my analysis *Chrysochalcissa* and *Oopristus* also arise together, although their differences appear to be greater than their similarities. Bouček (1978) pointed out that species of *Chrysochalcissa* are “very similar” to *Anneckeida* and have a “relatively close affinity to *Monodontomerus*.” I agree with his assessment. In my analysis *Rhynchotocida* + *Anneckeida* (node 19) are sister taxa to *Oopristus* + *Chrysochalcissa* (node 18). All of these taxa, except *Anneckeida*, for which no host is known, attack heteropterous eggs. It is possible that all are placed together due to convergence.

The wing venation of *Chrysochalcissa* differs from typical venation for the Monodontomerini in that the marginal vein is 8 to 10 times longer than the stigmal vein which is the condition found in Torymini, Torymoidini, Podagrionini, and Palachiini. As a relatively long marginal vein is hypothesized to be apomorphic, it could be argued that the wing venation of *Chrysochalcissa* is further indication of its relatively derived position within the Monodontomerini.

### *Oopristus* Steffan

Figs. 37(E), 38(E), 67, 209-210, 224-225, 232-233

*Oopristus* Steffan 1968:212. Type-species: *Oopristus safavii* Steffan (orig. desig. and monotypic, MHNG, MNHN, examined).

NUMBER OF SPECIES (catalog p. 225). - 1.

DISTRIBUTION. - PALEARCTIC (Uzbekistan, Iraq, Iran), ORIENTAL (Pakistan).

HOST. - Reared from eggs of Pentatomidae (Heteroptera).

KEYS TO SPECIES. - None.

RECOGNITION. - Within Monodontomerini, *Oopristus* is recognized by the absence of a frenal line, the enlarged hind femur having an outer row of small teeth and an inner row of small bumps (Fig. 224-225), the curved hind tibia that is apically truncate, the recessed clypeus (Fig. 232), and the absence of an occipital carina. Additionally,



there are several autapomorphies that define the only known species: basal end of scape protuberant and bearing a tuft of setae (Figs. 232-233), either side of clypeus with projecting tubercles (Figs. 232-233), a fringe of setae projecting downward from ventral edge of clypeus, and the prepectus extremely small and scarcely visible. These characters are more pronounced in females than males.

**PHYLOGENY.** - In both the working (Fig. 37E) and ending hypothesis (Fig. 38E) *Oopristus* arises in the same position relative to *Chrysochalcissa* and *Rhynchotricida* + *Anneckeida*. Therefore, the remainder of this section treats only the ending hypothesis. *Oopristus* arises at node 18 along with *Chrysochalcissa*. The node is diagnosed by the putative loss of both the frenal line and the hind-coxal setae. Both of these characters are homoplasious, and not much emphasis should be placed on them. *Oopristus* is defined by 3 synapomorphies, of which the recessed clypeus (Fig. 232) is autapomorphic. The loss of the occipital carina is considered derived (though it does occur at stem 4 and in *Stenotorymus*), and the slightly emarginate metasomal terga 1 and 2 are considered homoplasious.

The relationship of *Oopristus* to *Chrysochalcissa* might be questioned, based on numerous differences in morphology. *Oopristus* differs in having the hind tibia truncate (Fig. 225) rather than subpointed (Figs. 217-218), 1 anellus instead of 2, the occipital carina absent rather than present, the clypeus autapomorphically recessed (Fig. 232) rather than emarginate (Fig. 41, Character 6, *Emarg*), and the first two metasomal terga slightly emarginate rather than entire. *Oopristus* also has several autapomorphic characters not used in the analysis that are discussed above in the recognition section. These may be species characters, because only a single species is known. Both *Oopristus* and *Chrysochalcissa* are reared from pentatomid eggs and *Chrysochalcissa* is also reared from coreid eggs. It may be that these taxa bear an overall resemblance due to convergence.

### *Anneckeida* Bouček

Figs. 37(E), 38(E), 205-206, 219-220

*Anneckeida* Bouček 1978:111. Type-species: *Anneckeida watshami* Bouček (orig. desig., BMNH, examined).

**NUMBER OF SPECIES** (catalog p. 180). - 5.

**DISTRIBUTION.** - ORIENTAL (Thailand, Laos, Malaysia (Peninsular Malaysia, Sabah), AFROTROPICAL (Zimbabwe).

**HOST.** - Unknown.

**KEYS TO SPECIES.** - Bouček (1978:112).

**RECOGNITION.** - Within Monodontomerini, *Anneckeida* is recognized by the presence of a frenal groove, the enlarged hind femur having an outer row of regular, saw-like teeth and an inner row of similar, but much reduced, teeth (Figs. 219-220), the curved hind tibia that is apically truncate, the convex clypeus (as in Fig. 236), and a malar keel (as in Fig. 237).

**PHYLOGENY.** - In working (Fig. 37E) and ending hypotheses (Fig. 38E) *Anneckeida*

arises in the same position relative to *Rhynchotricida* and *Oopristus* + *Chrysochalcissa*. Therefore, the remainder of this section treats only the ending hypothesis. *Anneckeida* arises at node 19 (Fig. 38E), along with *Rhynchotricida*, based on the presence of a malar keel. This is a synapomorphy for the two taxa. The keel appears as a raised ridge along the posterior margin of the malar groove. Anterior to the groove the area is slightly sunken. Relative to *Rhynchotricida*, *Anneckeida* is defined by no apomorphies, but retains the presumptive primitive *2Rows* state of the hind femur (node 17) whereas *Rhynchotricida* has the derived *2Rows\** state in which the inner row of teeth is reduced to scattered bumps with a single, enlarged inner tooth basally. *Anneckeida* also retains the primitive hind-tibial spurs (Fig. 220) rather than the derived *Thick* state (Figs. 223-224). Based on these states *Anneckeida*, is hypothesized as the more primitive of the two taxa.

An additional indication of possible relationship concerns the metapleural area. This was not realized until after the analyses were completed. Both taxa have a small ventral projection that extends slightly in front of the hind coxa (Figs. 202, 206), though this is extremely difficult to see without removing a coxa (it is possible, albeit difficult, to see in lateral view). Although both taxa have the *Mono* type of metasternum (i.e., the placement of the metasomal foramen is far posterior of the coxal foramina) the structure differs in the two taxa. In *Anneckeida* (Fig. 205) the median plate is extremely narrow and medially sunken (i.e., arched in cross section), whereas in *Rhynchotricida* the plate is flat with a deep median carina that separates the hind coxae (Fig. 201).

Assessment of the number of anelli is difficult for *Anneckeida*, because all of the flagellomeres are transverse and somewhat reduced. It appears that only 1 anellus is present (Bouček 1978 stated 1 anellus or none), but I coded the state as "?". As all Monodontomerini except *Chrysochalcissa* have 1 anellus, this does not conflict with the groundplan condition of the clade.

### *Rhynchotricida* Bouček

Figs. 37(E), 38(E), 201-202, 221-223, 236-237, 245

*Rhynchotricida* Bouček 1978:116. Type-species: *Rhynchotricida ovivora* Bouček (orig. desig., BMNH, examined).

NUMBER OF SPECIES (catalog p. 262). - 5.

DISTRIBUTION. - ORIENTAL (India, Philippines, Laos, Malaysia (Sarawak, Sabah), Vietnam), AUSTRALIAN (Indonesia (Irian Jaya), Papua New Guinea).

HOST. - One species has been reared from heteropterous eggs.

KEYS TO SPECIES. - Bouček (1978:117).

RECOGNITION. - Within Monodontomerini, *Rhynchotricida* is recognized by the presence of a frenal area (although the frenal line is indistinct), an enlarged hind femur having an outer row of irregular teeth, an inner array of irregular, bump-like protuberances and a single inner enlarged basal tooth (Fig. 221), a curved hind tibia that is apically truncate with thick spurs (Figs. 222, 223; though outer spur extremely short and easily overlooked), a convex clypeus (Fig. 236), and a malar keel (Fig. 237).

PHYLOGENY. - In both the working (Fig. 37E) and ending hypotheses (Fig. 38E) *Rhynchotricida* arises at the same position relative to *Anneckeida* and *Oopristus* + *Chrysochalcissa*. The remainder of this section treats only the ending hypothesis. *Rhynchotricida* arises at node 19 along with *Anneckeida* based on the presence of a malar keel. This is a synapomorphy for the two taxa. The keel is a raised ridge along the posterior margin of the malar groove. Anterior to the groove the area is slightly sunken. *Rhynchotricida* is diagnosed by 2 autapomorphies: the 2Rows\* state of the hind femur in which the inner row of teeth is reduced to bumps with a single, enlarged inner tooth basally, and the Thick state (Fig. 223) of the hind-tibial spurs. Based on these states, *Rhynchotricida* is hypothesized as the more advanced of the two taxa.

*Rhynchotricida* + *Anneckeida* are the hypothetical sister taxa to *Oopristus* + *Chrysochalcissa* (node 18), based on the shared character of the hind femur having 2 rows of teeth and supposedly the convex clypeus from which, according to transformation series analysis, the recessed state of *Oopristus* and the emarginate state of *Chrysochalcissa* were each derived. Each of these states is autapomorphic and would seem intuitively difficult to be derived from a convex clypeus. On the other hand, the double row of hind-femoral teeth has not arisen in any other group of torymids and this provides some evidence that *Rhynchotricida*, *Anneckeida*, *Oopristus*, and *Chrysochalcissa* form a natural group. With the exception of *Anneckeida*, in which the host is unknown, all are parasites of heteropterous eggs, which is another indication of potential phylogenetic association.

### Tribe Palachiini

The tribe Palachiini consists of 16 valid species (no synonyms) in the following 4 genera: *Gummilumpus* (newly described), *Neopalachia*, *Palachia*, and *Propalachia*. Two species are Neotropical (of which 1 is an amber inclusion), and the remainder are largely Afrotropical and Oriental. A single Palearctic species is known.

Only a single species of the tribe has a known host, being reared from a mantid egg case (Table 3).

The tribe was established by Bouček (1976a) and placed in the subfamily Podagrioninae. At the time it included only a single species in the genus *Palachia*. Later Bouček (1978) added 5 more species of *Palachia* and 2 new genera, redefined the tribe, and placed both Palachiini and Podagrionini as tribes of the subfamily Monodontomerinae. He also gave a key to the 6 known world genera and species. Narendra and Sureshan (1989) gave a key to 4 additional species of *Palachia* described from India since Bouček (1978).

Both my working and ending hypotheses substantiate the recognition of this clade although the tribe is based on three rather weak factors: a synapomorphy associated with the structure of the occipital carina, states of the hind femur, and combinations of derived characters, many of which are autapomorphic for the group. It is fairly difficult to define Palachiini, because individual genera have a number of autapomorphies that are shared between pairs of genera in different combinations. I discuss these problems further under the generic sections below. Some years ago I described an amber fossil species of *Neopalachia* (Grissell 1980), which is herein transferred to the new genus *Gummilumpus*.

Palachiini is formed of taxa of relatively modified appearance (Fig. 70). Most

members of the tribe are 2-3 mm in length excluding the ovipositor, which is rarely longer than the meso- and metasoma combined. Species are often brightly metallic in coloration. Its members share derived conditions associated with the hind femur, propodeum, metasternum, occipital carina, antennae, and wing veins.

**DIAGNOSIS.** - Palachiini is defined by *the narrow hind femur with 2 or more prominent teeth* (Figs. 252-254, 256-258) or *enlarged with a row of teeth* (Fig. 255); *hind tibia slightly* (Fig. 252) to *noticeably* (Fig. 255) *curved and with 2 apical spurs (one of which may be extremely difficult to see); hind-tibial apex truncate* (Figs. 252-253) or *diagonal* (Fig. 255); *propodeum without spiracular sulcus or, if present, oriented towards the lateral corner (not nucha)* (Fig. 276-277); *metasternal shelf present* (Figs. 251, 273, 275); *metasomal terga not laterally emarginate*. An additional character aiding in recognition is that the occipital carina appears to connect to the hypostomal carina in its upper half, but abruptly turns downward toward the base of the mandible and that the occipital carina is ventrolaterally expanded (Fig. 249).

**DESCRIPTION.** - Occipital carina developed, appearing to connect to hypostomal carina in upper half, but abruptly turned downward toward base of mandible and ventrolaterally expanded, with dorsum of carina arched, nearer to hind ocelli than to occipital foramen (Fig. 249) (not confirmed for *Gummilumpus*); antennal club either formed of 3 flagellomeres indicated by distinct annulations that completely encircle club (Fig. 271; sometimes faintly so, Fig. 270) and without ventral micropilosity or club apparently formed of one segment with no visible annulations and with an area of micropilosity ventrally (Figs. 268-269; micropilosity obvious in females, but less so in males); propodeum without spiracular sulcus or, if present, oriented towards the lateral corner, and callus absent (Figs. 276-277); anterior metapleural margin straight; metasternum variable, either with propodeal foramen adjacent to hind-coxal foramina (and connected by two carinae, Fig. 272) or propodeal foramen placed well beyond bases of hind coxae (Fig. 274), with metasternal shelf (Figs. 251, 273, 275); wing veins variable, marginal vein 3 to 11 times longer than stigmal vein and 2 to 4 times longer than postmarginal vein (Figs 259-264); hind femur narrow, with 2 or more prominent teeth (Figs. 252-254, 256-258) or enlarged with row of teeth (Fig. 255); hind tibia slightly (Fig. 252) to noticeably (Fig. 255) curved and with 2 apical spurs, one of which may be extremely difficult to see; hind-tibial apex truncate (Fig. 252-253) or diagonal (Fig. 255); metasomal terga not laterally emarginate, dorsomedially entire or emarginate.

**PHYLOGENY.** - As both the working hypothesis (Fig. 37F, node 33) and ending hypothesis (Fig. 38D, node 21) recognize Palachiini as a clade, I discuss here only the ending hypothesis. The genus *Gummilumpus* was recognized as valid during the ending hypothesis based on a single fossil species in Dominican amber previously placed in *Neopalachia*. The reason for recognizing *Gummilumpus* is given in its generic discussion.

Although the tribe was diagnosed above in part by the occipital carina, the state for this character is unknown in *Gummilumpus*. This fossil is embedded in amber and is difficult to see in any but a lateral view. I coded the genus with a question mark for the state, and the state that defines Palachiini arises one step above *Gummilumpus* at

node 22. It remains to be seen whether the occipital carina is a true synapomorphy for *Gummilumpus* + node 22.

Node 21 (which defines the tribe) is defined by 3 synapomorphies: the hind femur, which has 2 or more well defined, irregular wide-spaced teeth (Fig. 252-254, 256-258: *Propalachia*, *Palachia*, *Gummilumpus*) or a "comb" of small, regular teeth (Fig. 255; autapomorphic in *Neopalachia*); the hind tibia which is partially curved (Fig. 252-253); and the hind coxa without setae (medially slightly setose in *Gummilumpus*, which was coded as question mark). Of these characters, the hind-tibial state is found in one other clade (*Exopristus*, node 11), and the hind-coxal state is homoplasious. The shape of the hind femur appears to be autapomorphic, but a similar shape is sometimes found in *Physothorax* (Torymini, Figs. 196-197). The similarity in shape appears to result from convergence, because the Torymini are almost certainly monophyletic and independently derived.

As hypothesized by the tree, Palachiini is considered the sister group to Chalcimerini + Podagrionini based on node 20 where the hind femur is hypothesized to have arisen from the *Bigteeth* state found in all *Chalcimerus* + Podagrionini. In Palachiini the hind femur changes to the *2Teeth* state (node 21) and then to the *Neo* state at *Neopalachia*. Intuitively this transformation seems to be backwards. The most direct transformation would seem to be from the *2Teeth* state with the femur relatively unmodified, to the *Neo* state with femur swollen and half rimmed with numerous small teeth to *Bigteeth* with the femur greatly swollen and completely rimmed with teeth. Palachiini retains the primitive 2 hind-tibial spur state, which changes to 1 spur in Chalcimerini + Podagrionini, and it retains the primitive apically truncate hind tibia, or has the apex slightly modified into a diagonal truncation (Fig. 255), whereas in Chalcimerini + Podagrionini the apex is apomorphically prolonged and sharply sub-pointed (Figs. 327-328).

The biology of only a single species of Palachiini is known (*Palachia mangalae*). This was purportedly reared from a mantid egg case (Narendran 1984a). If this is true, then the relationship of Palachiini and Podagrionini is further supported from biological evidence. Bouček (1978) stated that *Propalachia beaveri* was reared from a log infested by several different kinds of beetles. It will be interesting from a phylogenetic perspective to eventually discover what the true host range for Palachiini might be.

The relationship of Palachiini to Podagrionini is further suggested by the overall structure of the propodeum and metasternum, although specific parts of these structures are dissimilar in many respects. In the propodea of both Palachiini (Figs. 276-277) and Podagrionini (Figs. 319-320, 396), the spiracular sulcus is absent or, if present, is oriented towards the lateral corner, and the callus is undifferentiated (a flattened, aetose area rarely may be present). In Chalcimerini (Fig. 377) and all other Toryminae (Fig. 386, 388, 390, 392, 394), the spiracular sulcus is evident and reaching (or curved towards) the nucha and the callus is convex and setose. In both Palachiini and Podagrionini the metasternum in lateral view forms a shelf above the midcoxae. In Chalcimerini and all other Toryminae a metasternal shelf is absent.

DISCUSSION. - Palachiini is widespread, being found in the south Palearctic, Oriental, Afrotropical, and Neotropical Regions. Individuals are rarely encountered, and all species have been described only since 1976. I have seen at least 6 species that appear

to be undescribed. Relationships of Palachiini are not entirely clear, but it seems to be more closely related to Podagrionini than to any other group. The tribe is diverse in morphological characters, containing many autapomorphic states. Its host relations are essentially unknown. Obviously there is much opportunity for investigation in the tribe.

***Gummilumpus* Grissell, new genus**

Figs. 38(D), 250-251, 256, 271

Type-species: *Neopalachia bouceki* Grissell, present designation.

NUMBER OF SPECIES (catalog p. 194). - 1.

DISTRIBUTION . - NEOTROPICAL: Dominican Republic.

HOST . - Unknown.

AGE . - Tertiary, Oligocene amber.

DESCRIPTION . - Occipital carina present dorsally (lateral areas of head cannot be seen), 1 anellus, antennal club 3-segmented (filiform, Fig. 271), head in dorsal view somewhat squarish, but in lateral view obviously ridge-like or narrowed (Fig. 250-251), clypeal apex not visible, malar keel absent, submarginal vein with normal, weakly developed bristles that are shorter than tegula, marginal vein 5.5 times as long as stigmal vein, 3.3 times as long as postmarginal vein, stigmal vein longer than stigma, hind femur with 2 sets of double large teeth (Fig. 256), hind tibia slightly curved, apically truncate, with 2 normal spurs inserted apically, frenal line distinct, notauli distinct and meeting transcutal articulation laterad of scutoscutellar suture, propodeum without carinae, propodeal foramen adjacent to hind-coxal foramina, hind coxa without dorsal setae, metasternum not visible, metasternal shelf indicated in side view (Fig. 251), anterior metapleural margin straight, metasomal terga appearing entire (but this character cannot be seen clearly).

ETYMOLOGY . - From *gummi* (Latin for resin) and *lompe* (Dutch for lump), in reference to the amber in which this genus is encased; masculine gender.

RECOGNITION . - Among Palachiini, *Gummilumpus* is recognized by the following combination of characters: dorsum of head narrowed in lateral view (Fig. 250), antennal club distinctly 3 segmented (Fig. 271), notauli and frenal line well defined, apical half of the ventral surface of hind femur with several distinct, widely spaced teeth (Fig. 256), hind tibia apically truncate (Fig. 256), propodeal foramen adjacent to the hind-coxal foramina (i.e., propodeum not elongated much beyond base of hind coxa) (Fig. ), marginal vein 5.5 times length of stigmal vein and 3.3 times length of post-marginal vein (based on single known specimen, stigma width unknown), and metasomal terga appearing unemarginate medially (though this cannot be seen distinctly through the amber).

PHYLOGENY . -

Working Hypothesis (Fig. 37): In my original work I did not include *Gummilumpus* (i.e., *Neopalachia bouceki*) in my analysis. I included *Neopalachia* based on its type-species only (*N. noyesi*). After establishing the working hypothesis (Fig. 37F,

node 33), I reexamined *Neopalachia bouceki* with reference to the type-species. Based on that examination, I discovered the following: *N. bouceki* shares with *Propalachia* and *Palachia* the state of the truncate hind-tibial apex, whereas *N. noyesi* has the hind tibia diagonally truncate; and *N. bouceki* has the ventral surface of the hind femur with several distinct teeth (Figs. 252, 253, 256), whereas *N. noyesi* has a comb of fine, regular teeth (Fig. 255). *Neopalachia bouceki* shares with *Palachia* the dorsum of the head being narrowed in lateral view (Fig. 250), and the metasternum (in side view, Fig. 251) with the propodeal foramen adjacent to the hind-coxal foramina (*Neopalachia noyesi* and *Propalachia* have the metasternum (and propodeum) elongated and the foramen much removed from hind-coxal foramina, Figs. 273, 275). *Neopalachia bouceki* share with *Propalachia* and *Neopalachia* the shortened marginal vein, which is between 3 to 6 times the stigmal vein (*Palachia* with marginal vein 9 or more times length of stigmal vein), but it does not have the elongate submarginal bristles of *Propalachia* and *N. noyesi*. *Neopalachia bouceki* shares with *N. noyesi* a New World, Neotropical distribution. *Neopalachia bouceki* differs from all other Palachiini genera in having the antennal club distinctly 3-segmented (Fig. 217), not indistinctly 3-segmented as in *N. noyesi* (Fig. 270) or 1-segmented as in *Propalachia* and *Palachia* (Figs. 268-269). Based on these findings, I decided to code *N. bouceki* as a separate taxon for the ending hypothesis.

Ending Hypothesis (Fig. 38D): In this hypothesis, *Neopalachia bouceki* (= *Gummilumpus*) arises at node 21 as the basal element of the clade. The genus is defined by the presence of a frenal line (absent in *Neopalachia* and *Propalachia*; questionable in *Palachia*). *Gummilumpus* is placed as the most primitive member, based on the following characters and their primitive states in the transformation series analyses: antennal club 3-segmented, apex of hind tibia truncate, propodeum with propodeal foramen not projecting much beyond hind-coxal foramina, and elongated stigmal vein.

DISCUSSION. - *Gummilumpus bouceki* was originally described in the genus *Neopalachia* from a single Dominican amber specimen (Grissell 1980). In that description I stated that *bouceki* was somewhat intermediate between the 3 known genera of the tribe, but based on its New World distribution and my knowledge of the world Palachiini, it seemed most conservative to place *bouceki* in the available genus *Neopalachia*. In reassessing character states for the genera of Palachiini during the current study, I found that *Neopalachia bouceki* was not defined by those states considered to be valid for *Neopalachia*. Neither was it defined by the states used for *Propalachia* or *Palachia*. Based on this observation, the fact that it is an amber inclusion, and that it appears to have more primitive states relative to *Neopalachia*, I have placed *bouceki* in the new genus *Gummilumpus*.

In *Gummilumpus*, I coded the wing venation as a question mark. Its structure appeared to be autapomorphic for the taxon, and I did not add it to the data. This should not make a difference in its phylogenetic position. Within the amber inclusion it is not possible to see some character states with precision. This applies to the occipital carina, clypeal apex, propodeum, metasternal area, and metasoma. I coded these states as question marks for the data but comments may be made about several of them. I believe that the metasoma is unemarginate but decided to omit this possible source of error in the data. Although the propodeum is not entirely visible (Fig. 251) it is obvious that it is more nearly like that of *Palachia* than *Neopalachia* + *Propalachia* (Figs.

273, 275), it is not elongated and in side view it appears that the hind coxae are relatively closely placed to the metasomal insertion, i.e., the propodeal foramina. The ventral metasomal region also cannot be seen, but in side view (Fig. 251) a prominent metasternal shelf is present, and this indicates that *Gummilumpus* should be placed either with Palachiini or Podagrionini as only these 2 clades exhibit the shelf. The structure of the hind femur argues convincingly for placement with Palachiini.

***Palachia* Bouček**

Figs. 37(F), 38(D), 70, 249, 253-254, 257-258, 261-269, 272-273, 276

*Palachia* Bouček 1970:39-40. Type-species: *Palachia pulchra* Bouček (orig. desig. and monotypic, BMNH, examined).

NUMBER OF SPECIES (catalog p. 225). - 11.

DISTRIBUTION . - PALEARCTIC (Yugoslavia), AFROTROPICAL (Zimbabwe, Nigeria, Malawi, South Africa), ORIENTAL (India).

HOST . - The only published host is for *P. mangalae*, reared from a mantid egg case (Mantodea).

KEYS TO SPECIES . - Bouček (1978) gave a key to the 6 species then known, and later Narendran and Sureshan (1989) added 4 Oriental species and gave a key to them. Farooqi *et al.* (1990) gave a key to world species of the *oculata*-group. Narendran (1994) gave a key to Indian species.

RECOGNITION . - Within Palachiini, *Palachia* is defined by 5 autapomorphies: clypeal apex medially toothed and with its lateral edges slightly angulate (Fig. 267), notauli posteriorly meeting the scutoscuteellar sutures at the transscutal articulation (Fig. 265), metasternum with propodeal foramen adjacent to the hind-coxal foramina (and connected by two carinae, but this is difficult to see, Fig. 272), propodeum (Figs. 265, 276) without carina, slightly elongated in axis of body, spiracular sulcus and callus absent or difficult to discern, and metasoma laterally compressed with metasomal tergum 1 petiolate and at least metasomal tergum 2 emarginate. Additional synapomorphies which aid in recognition are: dorsum of head narrowed in lateral view (Fig. 266) although squarish in dorsal view, antennal club appearing 1-segmented (i.e., without annulations; Fig. 268-269), notauli well-defined, frenal groove faintly indicated or absent, hind tibia apically truncate (Fig. 253), ventral surface of hind femur with 2 or more distinct, irregular teeth (Figs. 253-254, 257-258), marginal vein 9 to 11 times the length of the stigmal vein and 1.5 to 4 times the length of the postmarginal vein, and stigmal vein equal to stigma width (Figs. 261-263).

PHYLOGENY . - In the working hypothesis (Fig. 37F), *Palachia* arose at node 34 as the sister genus to *Propalachia*. The node is defined by the antennal club appearing solid (its 3 segments presumably fused) and with ventral micropilosity, and by the hind femur having at least 2 large teeth (Figs. 253-254, 257-258), but often also with several other irregular teeth. With respect to *Neopalachia*, *Palachia* also retains the plesiomorphic truncate apex of the hind tibia. According to this hypothesis, *Palachia* is defined further by 4 autapomorphies (clypeal tooth, notauli meeting scutoscuteellar sutures, metasternum, metasomal terga, described above under recognition) and 1



synapomorphy shared with *Propalachia* that is a reversal to the wing venation found in most Torymini + Torymoidini (and all Podagrionini), in which the stigmal vein is shorter than the stigma width and the marginal vein is 9 times or greater the length of the nearly sessile stigmal vein.

In the ending hypothesis (Fig. 38D), *Palachia* arises at node 22 as the sister to *Propalachia* + *Neopalachia* (node 23). *Palachia* differs from node 23 in the 5 autapomorphies described above under recognition, and in 2 additional characters: it retains the primitive wing vein state of *Tory* (node 23 changes to the autapomorphic state *Neopal*), and it has a 1-segmented club (found only in *Propalachia* at the next node).

The working and ending hypotheses differ in placement of *Palachia* as a sister taxon either to *Propalachia* (working hypothesis) or *Propalachia* + *Neopalachia* (ending hypothesis). Based on relatively stable mesosomal structure (i.e., propodeum, metasternum), the latter case seems to be more supported than the former, in which a close relationship was based on the more homoplasious characters of antennal club and hind tibia, with the hind femur being the only stable, derived character.

DISCUSSION.- With the exception of *Palachia pulchra*, all *Palachia* are reported from the Afrotropical and Oriental regions. They have not yet been found in Australasia. I have seen a number of Afrotropical species that are apparently undescribed.

### *Propalachia* Bouček

Figs. 37(F), 38(D), 252, 259, 274-275

*Propalachia* Bouček 1978:101. Type-species: *Propalachia infumata* Bouček (orig. desig., BMNH, examined).

NUMBER OF SPECIES (catalog p. 251). - 3.

DISTRIBUTION . - ORIENTAL (Malaysia, Thailand, India), AFROTROPICAL (Zimbabwe, South Africa).

HOST. - Unknown.

KEYS TO SPECIES . - Bouček (1978), later modified by Narendran (1994).

RECOGNITION . - Within Palachiini, *Propalachia* is defined by the apically truncate hind tibia (Fig. 252), apical half of ventral surface of hind femur with at least 2 large teeth (Fig. 252), and often with several other irregular teeth, antennal club appearing 1-segmented and with ventral micropilosity, notauli absent or weakly defined, frenal line absent, propodeum projecting posteriorly as a curved neck (Fig. 275), propodeal foramen placed well beyond the bases of the hind coxae (as in Fig. 274), submarginal vein with enlarged black bristles that are longer than the tegula, marginal vein 3 to 4 times as long as stigmal vein and 2 to 3 times as long as postmarginal vein, stigmal vein 2 to 3 times as long as stigma width (Fig. 259), and all metasomal terga shell-like and posteriorly unemarginate.

PHYLOGENY . - In both the working (Fig. 37F) and ending (Fig. 38D) hypotheses *Propalachia* arises at the most apical part of the clade. The only difference is in the working hypothesis the genus is placed with *Palachia* and in the ending hypothesis it is placed with *Neopalachia*. My discussion here is based on its placement in the ending hypothesis.

*Propalachia* arises at node 23 with *Neopalachia*. The node is defined by the notauli, which are faint (a homoplasious character), and the propodeum (Figs. 275, 277), which has no carinae, is elongated in the axis of the body and projects posteriorly as a narrowed neck, and has the callus and spiracular sulcus absent, or, if the sulcus is present, it is oriented to the lateral corner of the propodeum. The propodeum is autapomorphic for the node. Two apomorphies arise at node 22, which includes *Palachia*, but they change immediately for *Palachia*, so that they are autapomorphies for *Propalachia* + *Neopalachia*. The first is the metasternal state of *Neopal* (changing to *Palachia* for *Palachia*), and the second is the wing vein state of *Neopal* (changing to *Tory* for *Palachia*).

*Propalachia* and *Neopalachia* are structurally similar in derived states related to wing venation, propodeum, and metasternum. Alternatively, *Propalachia* and *Palachia* are structurally similar in derived states related to the hind femur, hind-tibial curvature, and antennal club. Based on the consistency and transformation of character states, the former characters are less prone to homoplasy and thus *Propalachia* would appear to be derived with respect to *Palachia*. Unraveling the relationships between all three is complicated by the numbers of autapomorphies shared by *Propalachia* with one or other of *Palachia* or *Neopalachia*, but *Propalachia* itself has no uniquely derived character state. Its position on the tree reflects this ambiguity. *Propalachia* differs from *Palachia* and *Neopalachia* only in the metasomal terga being entire, a homoplasious synapomorphy. The abdomen is much like that found in *Monodontomerini*, in which the terga are especially rigid and never laterally compressed or folded medially. *Propalachia* is the only member of the Palachiini with a shell-like metasoma with unemarginate terga. Although it appears unemarginate in the fossil *Gummilumpus*, this cannot be seen with certainty, and the terga do not appear to be rigid in *Gummilumpus*.

DISCUSSION. - *Propalachia* is rarely collected, and its relationship to other Palachiini remains somewhat of a mystery. Bouček (1978) suggested that the genus is more primitive than *Palachia*. My analyses suggest that it is likely to be derived with respect to *Palachia*.

### *Neopalachia* Bouček

Figs. 37(F), 38(D), 255, 260, 270, 277

*Neopalachia* Bouček 1978:104. Type-species: *Neopalachia noyesi* Bouček (orig. desig. and monotypic, BMNH, examined).

NUMBER OF SPECIES (catalog p. 224). - 1.

DISTRIBUTION. - NEOTROPICAL (Tobago Island).

HOST. - Unknown.

KEYS TO SPECIES. - None.

RECOGNITION. - Within Palachiini, *Neopalachia* is recognized by the following autapomorphies: hind tibia apically diagonally truncate (Fig. 255), and apical half of ventral surface of hind femur with minute, regular teeth. Additional characters that aid in recognition include: antennal club with 3 segments barely indicated by weak dorsal

annulations and no ventral micropilosity (Fig. 270), notauli absent or weakly defined, frenal line barely perceptible as a change in sculpture, propodeum projecting posteriorly as a curved neck (Fig. 277) with propodeal foramen placed well beyond the bases of the hind coxae, submarginal vein with strong bristles that are longer than tegula (Fig. 260), marginal vein about 4 times as long as stigmal vein and 1 to 1.5 times as long as postmarginal vein, stigmal vein about 4 times as long as stigma width (the stigma, however, is poorly defined making the stigmal vein appear as a linear vein with little or no stigma), and at least metasomal tergum 2 obviously incised medially.

**PHYLOGENY** . - In the working hypothesis (Fig. 37F) *Neopalachia* arose as the basal taxon of the clade (node 33) that includes *Propalachia* and *Palachia*. It was defined by the hind tibia being apically diagonally truncate, the apical half of the ventral surface of the hind femur with minute, regular teeth (Fig. 255; from node 33), and the antennal club with 3 segments barely indicated by weak dorsal annulations. Additionally, the curved hind tibia and faint notauli define *Neopalachia*, but these are homoplasious character states.

In the ending hypothesis (Fig. 38D), *Neopalachia* arises with *Propalachia* (node 23) as one of the most derived taxa of the clade. The node is defined by 2 characters: 1) the notauli, which are faint (a homoplasious character), and 2) the propodeum (Fig. 277), which has no carinae, is elongate in the axis of the body and projects posteriorly as a narrowed neck, and has the callus and spiracular sulcus absent or, if present, is oriented to the lateral corner of the propodeum. The second character is autapomorphic for the node. Two apomorphies arise at node 22, which includes *Palachia*, but they change immediately for *Palachia*, so that they are autapomorphies for *Neopalachia* + *Propalachia*. The first is the metasternal state of *Neopal* (Fig. 47, Character 20) changing to *Palachia* for *Palachia*, which appears to be a reversal. The second is the wing vein state of *Neopal* (Fig. 42, Character 8) reversing to *Tory* for *Palachia*.

*Neopalachia* and *Propalachia* are structurally similar in derived states related to wing venation, propodeum, and metasternum (all autapomorphic). They differ as follows: *Neopalachia* with the antennal club indistinctly 3-segmented (3Seg\*) versus 1-segmented (1Seg) in *Propalachia* (both states are derived from distinctly 3-segmented); *Neopalachia* with hind tibia curved (*Curved*) vs. slightly curved (*Curved\**) in *Propalachia* (both states are derived from straight); *Neopalachia* with the hind-tibial apex diagonally truncate (*Diagonal*) vs. truncate (*Trun*) in *Propalachia* (diagonal is derived with respect to truncate); *Neopalachia* with the hind femur having numerous small teeth ventrally (*Neo*) vs. 2 teeth (*2Teeth*) in *Propalachia* (*Neo* state derived relative to *2Teeth*); and *Neopalachia* with metasomal terga 1 and 2 slightly emarginate (*1/2*) vs. no emarginations (*0*) in *Propalachia* (emarginate state derived relative to no emarginations). Based on this enumeration, *Neopalachia* has three more derived states than *Propalachia* and is most likely derived with respect to this genus.

**DISCUSSION** . - *Neopalachia* is known only from Tobago, but I have seen a specimen from Peru as well. Although I originally placed *bouceki* as a *Neopalachia*, I transfer it here to the new genus *Gummilumpus* and explain my reasons for doing so under that genus. Based on geographic limits, the Neotropical genus *Neopalachia* would appear

to have no direct, modern link with either of the Old World genera (*Propalachia*, *Palachia*) included in the tribe. A presumptive ancestral taxon to *Gummilumpus boučeki* (from Dominican amber and placed as the most primitive member of the tribe), might represent a member of a primitive, widespread taxon that gave rise in the New World to one lineage and in the Old World to another.

### Tribe Chalcimerini

Chalcimerini is based on a single genus and species found so far only in the Palearctic Region. It is associated with cynipid wasps in poppy seed capsules. Bouček (1978) first proposed the tribal name.

The single species is derived in habitus (Fig. 69). It is dull metallic blue and about 5 mm, excluding the ovipositor, which is shorter than the body. I am not convinced that the placement of Chalcimerini on the tree is due to anything more than an inflated emphasis on the hind leg, but in this paper I treat the placement of the tribe as hypothesized by the tree.

**DIAGNOSIS.** - Chalcimerini is defined by the *shortened marginal vein subequal in length to the stigmal vein and 0.5 times as long as the postmarginal vein* (Fig. 381) and the *hind femur enlarged* (Fig. 69) *with a single row of ventral teeth, and hind tibia greatly curved with apex diagonally truncate and ventrally prolonged into spine* (Fig. 379-380), *with 1 thickened and truncate spur*. Additional characters that aid in recognition are the heavily carinate propodeum with an evident spiracular sulcus reaching (or curving toward) the nucha, the presence of a convex and setose callus, the absence of a metasternal shelf (Fig. 378), and the unemarginate metasomal terga.

**DESCRIPTION.** - Occipital carina dorsally arched (as in Fig. 361), nearer hind ocelli than occipital foramen or midway between both and lateral margins not nearly reaching upper half of hypostomal carina; antennal club formed of 3 flagellomeres indicated by distinct annulations that completely encircle club, without ventral micropilosity; propodeum (Fig. 377) heavily carinate, with spiracular sulcus reaching or curved towards nucha, callus convex and setose; anterior metapleural margin straight; metasternum (Fig. 376) with forward edge of propodeal foramen closer to posterior edge of hind-coxal foramina than anterior, metasternal area relatively wide, fully as long (anterior to posterior) as diameter of propodeal foramen, a short carina connecting propodeal and hind-coxal foramina, without metasternal shelf; shortened marginal vein subequal in length to stigmal vein and 0.5 times as long as postmarginal vein, stigma width much less than stigmal vein length (Fig. 281); hind femur enlarged (Fig. 69) with single row of ventral teeth; hind tibia greatly curved, with apex diagonally truncate and ventrally prolonged into spine (Fig. 379), with 1 thickened and truncate spur (Fig. 380); metasomal terga without lateral or apicomedian emarginations.

**PHYLOGENY.** - Chalcimerini arose at the same relative position as the sister group to the Podagrionini in both the working hypothesis (Fig. 37F) and ending hypothesis (Fig. 38F), and I discuss its phylogeny with respect to the ending hypothesis only. Chalcimerini arises at node 24, which is defined by 4 synapomorphies: curved hind tibia (Fig. 69), subpointed hind-tibial apex, single hind-tibial spur, hind femur inflated

and ventrally toothed (i.e., *Bigteeth* state) (*n.b.*, although node 20 was a change from a toothed hind femur to *Bigteeth*, the immediate change at node 21 to modifications of this condition retain the state solely for members of node 24). All of these states, however, are found throughout the clade. *Chalcimerini* is defined by three autapomorphies: a thickened, truncate hind-tibial spur (i.e., *Wide* state, Fig. 380), a modified propodeum (state *Chalci*), and a modified metasternum (state *Chalci*); as well as a homoplasious apomorphy, the presence of a frenal line.

Opposing these relatively derived characters are the primitive states of wing venation (*Ptero*; Fig. 381), the absence of tergal emarginations (*O*), a primitive occipital carina (state *I*), the spiracular sulcus evident and reaching or curved towards the nucha, and the callus convex and setose. There is no doubt that the single species taxon *Chalcimerini* is unique and primitive relative to *Podagrionini*. Its placement as the sister taxon of *Podagrionini*, however, is subject to debate, because only in the single complex of states associated with the hind femur is *Chalcimerini* placed so highly in the tree (its other character states being autapomorphic, lend little support for placement). Such hind-femoral states define several families (e.g., *Leucospidae*, *Chalcididae*) or genera in families (e.g., *Pteromalidae*, *Eulophidae*) but may not be completely adequate for formulating hypotheses of relationships given the absence of additional characters to reinforce them.

In its host relationship with *Cynipidae*, *Chalcimerini* again has more in common with the primitive groups of *Toryminae* — especially *Glyphomerus*, *Microdon-tomerini*, and *Torymini* — and nothing in common with its purported sister group *Podagrionini*, which all attack mantid egg cases.

For now there is little alternative but to accept the hypothesized position of *Chalcimerini* and its sister relationship to *Podagrionini*. I discuss the relationships of *Chalcimerini*, *Palachiini*, and *Podagrionini* further under *Podagrionini*.

***Chalcimerus*** Steffan and Andriescu  
Figs. 37(F), 38(F), 69, 376-381

*Chalcimerus* Steffan and Andriescu 1962:225-226. Type-species: *Chalcimerus borceai* Steffan and Andriescu (orig. desig. and monotypic, MHNB).

NUMBER OF SPECIES (catalog p. 181). - 1.

DISTRIBUTION . - PALEARCTIC (Romania, Israel, Spain).

HOST. - Reared from *Cynipidae* (Hymenoptera) in seed capsules of *Papaver* (*Papaveraceae*).

KEYS TO SPECIES. - None.

RECOGNITION and PHYLOGENY are the same for the genus as for the tribe (see above).

DISCUSSION . - *Chalcimerus* is a rarely collected group. I have seen only 4 specimens. I have not seen the type but have examined a specimen labeled paratype sent to me by Steffan (MNHN). It is a male specimen, but since no males were described in the original description, the specimen cannot be a paratype. The specimen has no locality data but may be from male material described by Andriescu after the original description (1963).

In overall structure (Fig. 69) the genus appears to be built from parts of primitive lineages and advanced ones. The wings are definitely primitive in venation, appearing essentially as those for a pteromalid; the metasoma is typical of Monodontomerini; the occipital carina is primitive, as in *Glyphomerus*; and the mesosoma, as in Monodontomerini and *Glyphomerus*, lacks a metasternal shelf. The apparently derived state of the metasternum, however, could be correlated with the derived hind leg (like that of Podagrionini), perhaps as a functional complex. In its host relationship with Cynipidae, *Chalcimerus* would again appear to have more in common with the primitive taxa than with the advanced ones (e.g., Podagrionini). Cynipid parasites are all confined to *Glyphomerus*, Microdontomerini, and Torymini.

The combination of primitive occipital carina, wing venation, metasoma, and host association suggests to me that the heavy weighting of the hind-femoral (and perhaps metasternal) characters is unwarranted in this case. It is possible that *Chalcimerus* should be placed as a primitive genus in the subfamily, possibly even associated with *Glyphomerus*. I have left it at the position given to it in my analysis, but in all respects it would best be flagged as an *incertae sedis* which needs further study.

### Tribe Podagrionini

The tribe Podagrionini is composed of 135 valid species (plus 11 synonyms) in the following genera: *Mantiphaga*, *Micropodagrion*, *Palmon* (new status, with *Pachytomoides* new synonym), *Podagrion*, *Podagrionella* (with *Tarachodiphaga* and *Iridophagoides*, new synonyms), and *Propachytomoides*. Although worldwide in distribution, the majority of its species are pan-tropical occurring in the Neotropical, Afrotropical, Oriental, and Australian Regions. Less than 10 species are Holarctic.

Although 39 species of this tribe are known to attack mantid egg cases, host records for 70 percent of the tribe are unknown (Table 3). The tendency has been to extrapolate data to imply that all species are associated with mantid eggs. In this regard, however, two records are of special interest. *Podagrionella indarbela* was reported by Narendran and Sureshan (1988) to parasitize the eggs of Arbelidae (Lepidoptera). This record is in need of confirmation, however, because cashew bark containing eggs of *Indarbela* was placed in a cage and a male and female podagrionine were collected the next day (Narendran *in litt.*). Attempts to repeat the rearing did not succeed. Additional rearing or collecting efforts are in order.

I have substantiated a record for *Podagrion coeruleoviride* reared from a "hesperiid pupa" collected in Colombia (7 females, 1 male, BMNH). There is no doubt that the specimens emerged from the pupa because the pupal case is with the specimens, and there is still one female parasite inside it. There are 2 complete emergence holes visible in the venter of the pupa and 1 complete hole dorsally. Within the case and surrounding each hole appears to be a brown septa which partitions the case into cells. *Podagrion coeruleoviride* was originally described from specimens reared from a mantid egg case. It is likely that the lepidopterous pupa was an accidental host and that Podagrionini may be sufficiently plastic enough to accept and complete development on an alternate host when the situation arises. This possibility provides endless opportunity for experiment and discussion with regard to host-specificity, alternate hosts, adaptive radiation, and so on.

We know little about the internal community of mantid egg masses, which may be

somewhat gall-like in construction. Several families of Hymenoptera attack mantid eggs, including Eupelmidae and Scelionidae, both of which could serve as possible hosts for podagrionines. The two aberrant records cited above give some reason to be more open-minded in our assessment of biological specificity in the Podagrionini, at least until we accumulate more positive and detailed host records.

The tribe Podagrionini was established by Bouček (1978) and placed along with Palachiini in the subfamily Monodontomerinae. The defining synapomorphies to separate these two tribes were that in Podagrionini the hind tibia was greatly curved, had 1 apical spur, and was elongated into a "spine" (= *Subpoint* or *Pointed* states of this study; Fig. 44, Character 11), while in Palachiini the hind tibia was "less curved," had 2 apical spurs, and was "almost truncate" (= *Trun* or *Diagonal* states of this study; Fig. 44, Character 11). I can confirm these differences and add several more derived states that bolster the monophyly of Podagrionini. The putative synapomorphies are: at least metasomal terga 2-4 with lateral emarginations (Figs. 19, 21) (autapomorphic), occipital carina completely encircling the back of the head, meeting the hypostomal carina slightly above base of mandible, and ventrolaterally expanded (Figs. 3, 410) (state nearly like that found in Palachiini (Fig. 249) and similar, but not identical, to that rarely found in a few Torymini, e.g., *Ecdamua*, *Diomorus* (Fig. 408)), propodeum without a callus (Fig. 16, shared only with Palachiini), metapleuron ventrally (i.e., metasternum) with a widened shelf (in lateral view this is evident by the posterior ventral margin of the mesepimeron not reaching the venter of the metapleuron, Figs. 11, 427) (shared with Palachiini and *Stenotorymus*), and venter of antennal club at least with one clavomere having an area of micropilosity and usually all three (Figs. 308-314; shared only with *Propalachia* and *Palachia*).

Podagrionini is formed of taxa of relatively complex appearance (Fig. 71). Most members of the tribe are 3 to 5 mm excluding the ovipositor, which is often several times longer than the body. Species are often brightly metallic in color. Members share derived conditions associated with the hind femur, propodeum, metasternum, occipital carina, and metasoma.

**DIAGNOSIS.** - Podagrionini is defined by the *enlarged hind femur with numerous ventral teeth, the greatly curved hind tibia with apex diagonally truncate and ventrally prolonged into a spine, and a single hind-tibial spur* (Figs. 323-339); *the long marginal vein 3 to 9 times longer than the stigmal vein and 4 to 9 times longer than the post-marginal vein* (Figs. 287-288, 293); *the venter of the antennal club with an area of micropilosity* (Figs. 308-314, 407, 409); *and metasomal terga 2-4 laterally and dorso-medially emarginate* (Figs. 321-322). Additional characters that aid in recognition are the occipital carina joining the hypostomal carina near the base of the mandible (Figs. 3, 410), the propodeum with spiracular sulcus absent or oriented to lateral corner rather than nucha (Figs. 16, 396), and a long metasternal shelf above midcoxae (Figs. 11, 278B-285B, 427).

**DESCRIPTION.** - Occipital carina ventrolaterally expanded, joining hypostomal carina near base of mandible (Figs. 3, 410); antennal club formed of 3 flagellomeres, sometimes indicated only by indistinct or poorly delimited sutures confined to dorsum of club, an area of micropilosity present ventrally (Figs. 308-313, 407, 409) (in *Mantiphaga* all 3 clavomeres visible ventrally, but area of micropilosity on apical

clavomere, Fig. 314); propodeum (Figs. 16, 319-320, 396) with spiracular sulcus absent or, if present, oriented to lateral corner of propodeum (not nucha), callus absent (a flattened, bare area rarely may be present); anterior metapleural margin straight (Fig. 11, 427); metasternum variable (Figs. 278A-285A), but with propodeal foramen posteriad with respect to hind-coxal foramina (not, or barely, touching an imaginary line drawn across posterior edge of hind-coxal foramina), metasternal area between hind-coxal foramina well developed and sclerotized, and much wider than diameter of hind-coxal foramen, with lateral carina connecting propodeal and hind-coxal foramina, and produced into a long metasternal shelf above midcoxae (Figs. 11, 278B-285B, 427); long marginal vein 3 to 9 times longer than stigmal vein, 4 to 9 times longer than postmarginal vein, stigma width equal to or shorter than stigmal vein length (Figs. 287-288, 293, 296-306); hind femur enlarged with numerous ventral teeth; hind tibia greatly curved, with apex diagonally truncate and ventrally prolonged into a spine, with 1 (Figs. 323-339); metasomal terga 2-5 laterally and dorsomedially emarginate (Figs. 19, 21, 321, 322).

PHYLOGENY . - In both the working hypothesis (Fig. 37G, node 36) and the ending hypothesis (Fig. 38F, node 25) Podagrionini arises at the same position in the tree and with the same genera (though their specific placement varies within the node, and several are synonymized). I discuss here the results based only on the ending hypothesis (Fig. 38F). The node is defined by 5 synapomorphies: 1) metasomal tergum 2 (Figs. 19, 21) laterally emarginate (autapomorphy), 2) metasternum of the *Micropod* and *Podag* types (Fig. 47, Character 20), with forward edge of propodeal foramen placed relatively posteriad with respect to hind-coxal foramina (rarely posterior edge), with the hind-coxal foramina separated from each other by an area much wider than diameter of hind-coxal foramen, with a carina connecting the propodeal and hind-coxal foramina, and with a wide metasternal shelf, 3) propodeum (Fig. 45, Character 18) elongate in the axis of the body, spiracular sulcus absent or, if weakly indicated, then oriented to the lateral corner of propodeum (not the nucha), with or without carinae (if present, carinae oriented diagonally or transversely across propodeum, not longitudinally), callus bare and undifferentiated (or slight flattened area may be present), 4) wing venation of the *Tory* type (Fig. 42, Character 8), with a sessile (or nearly sessile) stigmal vein that is much shorter than the marginal vein, and 5) the occipital carina completely encircling the back of the head, ventrolaterally expanded, and joining the hypostomal carina just above the mandible (Fig. 39, Character 1, state 3).

Although the autapomorphic state *3seg*\* arises at node 26 according to my analysis, it should be noted that the taxon *Mantiphaga* (node 25) is slightly atypical for the state but does have an area of ventral micropilosity. Therefore, ventral micropilosity is another synapomorphy which unites the Podagrionini (but found also in *Propalachia* and *Palachia*).

In both working and ending hypotheses, Podagrionini is placed as a sister group to *Chalcimerus* (= Chalcimerini). Chalcimerini differs in having primitive pteromalid-like wing venation (Fig. 381), a partially developed occipital carina, an autapomorphic propodeum and metasternum (Figs. 376, 377), and a 3-segmented club without ventral micropilosity. Members of both tribes share the single hind-tibial spur, but in *Chalcimerus* the tibia is autapomorphically thickened and apically truncate (Figs. 379-380) (possibly the fusion of two spurs). In essence, *Chalcimerus* has primitive states



for occipital carina, mesosomal structure, wing venation, metasomal structure, and antenna while sharing with Podagrionini the highly derived character states of the hind leg (i.e., enlarged and toothed femur, curved tibia, subpointed tibial apex, single spur).

*Chalcimerus* was placed in its own tribe, Chalcimerini, by Bouček (1978), and there is no doubt that the monotypic taxon is unique and primitive relative to Podagrionini. Its placement as the sister taxon, however, is subject to debate, because only in the single complex of states associated with the hind femur is *Chalcimerus* placed so highly on the tree. Similar hind-femoral states define several families (e.g., Leucospidae, Chalcididae) but arise sporadically in others (e.g., Pteromalidae, Eulophidae). Such states might not be totally convincing in formulating hypotheses of relationships, given the absence of additional characters to reinforce them. For now, there is little alternative but to accept the hypothesized position of *Chalcimerus* and its sister relationship to Podagrionini.

Palachiini is hypothesized as the sister group to *Chalcimerus* + Podagrionini, and this relationship was discussed under the former tribe. Presumably, the ancestor to both groups developed the enlarged hind femur (*Bigteeth* state) (node 20), but Palachiini changed to the *2Teeth* state (node 21) and then to the *Neo* state (i.e., comb-like, *Neopalachia*). That Palachiini and Podagrionini are closely related is not much in doubt. They share the following synapomorphies: callus undifferentiated (though a flattened, asetose area rarely may be present), spiracular sulcus absent or, if weakly indicated, then oriented to the lateral corner of the propodeum (not the nucha), and metasternal shelf developed. Additionally, in both groups the antennal club is either 1-segmented (Palachiini, except *Neopalachia*) or 3-segmented (Podagrionini, though the dorsal sutures are sometimes very difficult to see) in dorsal view (ventral sutures are obscure or interrupted by micropilosity) and has ventral micropilosity (no other torymid has this micropilosity), the hind femur is modified in some manner as are the tibia (curved or partially curved), and the occipital carina completely encircles the back of the head, is ventrolaterally expanded, and reaches the hypostomal carina. In this last state there is a slight difference in that the carina of Palachiini appears nearly to connect to the hypostomal carina in its upper half but actually turns abruptly downward and touches near the base of the mandible (Fig. 249), but in Podagrionini the carina reaches directly to the base of the mandible (Figs. 3, 410). In addition, the only species of Palachiini for which a host is known (*Palachia mangalae*) was reared from mantid egg cases, as are essentially all reared Podagrionini.

Palachiini appears to be the more heterogeneous taxon, comprised of few species that vary widely in character states, whereas Podagrionini is relatively homogeneous with many species that are relatively conservative in character states. In the section on "Biology and Phylogenetics" (p. 59) I mentioned the possibility of explosive radiation within the podagrionines in relation to their apparently singular host association with mantid eggs. This might explain the relatively conservative morphological diversity found within this group.

DISCUSSION. - The following analysis of Podagrionini cannot be considered the last word by any means. For one thing, I was unable to see more than 50% of the 135 species involved. My data matrix is drawn largely from type-species of genera, but I have examined about 4000 specimens from all parts of the world in an attempt to test

the validity of the generic hypotheses. No emphasis was placed on males, because they are relatively uncommon and are unknown for many species. Males can differ from females in the shape of the hind femur (sometimes being dimorphic between themselves) and in the antennal club. In species where females have enlarged clubs, males have filiform antennae. Females have a large area of micropilosity on the venter of the club (except in *Mantiphaga*), but males do not. Finally, I did not formally analyze some character states, as discussed below.

In my initial attempts to define podagrionine groups I examined some characters thought to be of specific value and did not include them in the phylogenetic analyses of higher taxa. These characters included: anellus length, antennal club width (i.e., filiform, greatly swollen), distribution of micropilosity on the ventral surface of the club, wing vein proportions (other than the more general *Tory* state that was used in the analysis), wing surface setal pattern, and mid and hind-tarsal spur construction. Additionally, I found variation within the metasternal structure which was not coded fully (a more general state descriptor was given [i.e., *Micropod*, *Podag*] as defined under Phylogeny).

While the characters listed above apparently are of diagnostic value, their value was not discovered until the research was completed and the manuscript nearly finished. I did not analyze them within a phylogenetic context, and in retrospect these states could have been analyzed for the construction of infratribal phylogeny. The best I can do now is highlight my findings for these characters as possible avenues for further research.

1) Anellus length: The length of the first anellus (there is only 1 in Podagrionini) apparently can be divided into two or possibly three states. The first (Figs. 309, 311-314) anellus wider than long, the second (Figs. 307, 310) anellus cylindrical and longer than wide, and the third (Fig. 318) anellus longer than wide and shaped like the mouthpiece of a trumpet. Only in the genus *Palmon* is the anellus cylindrical and elongate; in *Micropodagrion* it is elongate but in the fashion of a trumpet mouthpiece, and in other Podagrionini the anellus is transverse. A transverse anellus would appear to be plesiomorphic, based on outgroup comparison (other torymids). The mouthpiece shape would seem to be a slight elongation of the plesiomorphic state, whereas the cylindrical shape would seem to be the most derived condition. Intermediate states are known in taxa that are placed in generic rankings based on other characters (e.g., *Podagrionella*).

2) Antennal club: The following discussions pertain only to females. Males either do not exhibit the conditions, or do so only superficially (as noted previously).

A) Size. - The two extreme conditions found in female club size in Podagrionini are filiform (Fig. 312) and greatly swollen (Fig. 307) (males are essentially filiform). In the genus *Palmon* the club is always of gigantic proportions (Figs. 307, 310); in most other genera the flagellum is filiform, and in *Podagrion* both conditions are found (e.g., *P. mantidiphagum*: Fig. 312; *P. crassiclava*: Fig. 313). It is possible that further examination of the character within *Podagrion* will prove useful for establishing phylogenetic groups.

B) Micropilosity on ventral surface of club. - Three potential states exist for this character: apical segment with an area of micropilosity (Fig. 314); apical two segments with an area of micropilosity (Figs. 308, 311, 313); and all three segments with an area of micropilosity (Fig. 310, 312). Because micropilosity is absent from the clade

of all plesiomorphic torymids, the most straightforward transformation series would be *None—One—Two—Three*. But this may not be the case. *Podagrionella* species display both states *Two* and *Three*. All the species of *Podagrion* I have examined exhibit state *Three*, except for *Podagrion koebelei* (with state *Two*), a species which is atypical for *Podagrion* in several other respects (see *Podagrion* section). Further examination should be made of this potential character across all species.

3) Wing vein proportions (other than the more general *Tory* state used in the analysis): although the *Tory* state applies to taxa in Podagrionini (as well as Torymini, Torymoidini, and some Palachiini), there is some variation within the state. In *Torymus* enough variation exists to help define species groups, but the situation is not entirely clear in Podagrionini. In this tribe, the wing veins appear to be of two primary types. In one type (Figs. 294-295), the costal cell is longer (usually about 1.5 times) than the marginal + postmarginal veins and usually the stigmal and postmarginal veins are relatively short. In the other (Figs. 290-291), the costal cell is about equal to the marginal + postmarginal veins and usually the stigmal and postmarginal veins are relatively long. In examining a number of specimens of all genera, I believe the character may eventually help elucidate some pattern, but I have not been able to determine what that pattern might be. It appears that the latter condition is true for all *Palmon* and the former condition for most other Podagrionini, but I have seen a few exceptions (e.g., the Neotropical species *Podagrion echthrus* and *Podagrion mantidiphagum*). Additional study is needed.

4) Wing surface setal pattern: there appear to be two states of setal pattern. In one state (Fig. 293), the basal cell, basal vein, cubital vein, and speculum are clearly visible because the basal cell and speculum lack setae; and the basal vein and cubital veins are each marked by a row of setae. In the other state (Fig. 289), the entire wing surface is covered with setae and the basal cell, basal vein, cubital vein, and speculum cannot be seen. By outgroup comparison the former state is typical of Toryminae and the latter appears to be autapomorphic for the taxon *Palmon*. This character is discussed further under that genus.

5) Tibial spur construction:

A) Midtibia. - The midtibial spur appears to exist as either an extremely fine, thread-like spur (in association with a reduced basitarsus; Fig. 330) or as a thickened, setose barb (in association with an elongate basitarsus; Fig. 329). The former state is found only in the monotypic genus *Micropodagrion* and an undetermined species of the genus *Podagrionella*, whereas the latter state is typical of other Podagrionini. Because this state is apparently rare, its phylogenetic importance will need to be confirmed by discovery of additional taxa and/or characters.

B) Hind tibia. - At 100X magnification, the hind-tibial spur appears as either a setose or asetose spine. At first this was thought to be an additional character that might be used to distinguish *Podagrion* and *Palmon*. At higher magnification (about 500X), however, the distinction is not apparent. In both taxa the spur is seen to have elongate plates, or scales. In *Podagrion*, the tips point more outward than in *Palmon*, thus making the spur in *Podagrion* appear "setose" at lower magnifications. Most taxa of Podagrionini that I have examined (at 100X) appear as for *Podagrion*. While it is possible that some distinctions can eventually be discovered for the use of this character, preliminary examination suggests that more material will have to be studied before its use is warranted.

6) Metasternal area: Although this character was included in my phylogenetic analyses under the states *Micropod* and *Podag*, the recognition of character states does not seem to have been assessed finely enough within the Podagrionini. In this group the metasternal area appears to vary significantly in structure (as in Monodontomerini) when compared, for example, to more plesiomorphic groups such as Microdontomerini, Torymoidini, and Torymini, in which the metasternum is uniform in appearance. Within Podagrionini several types of metasternal construction are apparent, but it is difficult to assess either the importance or evolution of these states, because many species have not been examined and the extent of variation is not known.

Some overview for this character is in order at this point, which includes all of the variants I have discovered. A general description of the states follows. In describing the relative distances between foramina, I use the following convention: "close-spaced" = anterior margin of the propodeal foramen nearly touching an imaginary line across the posterior margins of the hind-coxal foramina (Fig. 278A); "wide-spaced" = anterior margin of the propodeal foramen some distance away from an imaginary line across the posterior margins of the hind-coxal foramina (Fig. 285A).

A state of two submedian carinae with close-spaced foramina (Fig. 280A) is found in *Propachytomoides* (with propodeal neck curved in profile), *Podagrionella*, *Mantiphaga*, and the synonymized genus *Propodagrion* (now placed as *Podagrion*, *teste* Bouček 1988).

A state of two submedian carinae (or at least somewhat parallel broken carinae) with wide-spaced foramina (Figs. 283A, 285A) is found in the genus *Palmon* (previously synonymized with *Podagrion* but recognized in this work as a valid genus with *Pachytomoides* as new synonym).

A state of one median carina with close-spaced foramina (Fig. 278A) is found in *Micropodagrion* (additionally, two small carinae veer off the anteromedian point where the median carina intersects it).

A state of one median carina with wide-spaced foramina (Fig. 279A) is found in *Podagrion*. (This is typical for the majority of species of *Podagrion*, but below I point out some problems of species found within the genus.)

Although Grissell and Goodpasture (1981) stated that the number of carinae was consistent for the taxa *Podagrion* and *Pachytomoides* (now equals *Palmon*), this was based only on the New World fauna. The statement still appears to be correct for this region, based on much additional material examined, but it is not as simple a matter for the Old World fauna, of which the above list of variants is mostly composed, nor is it simply a matter of number of carinae. The relative position of foramina appear to vary as well. During my examination of Old World species assigned to *Podagrion* I have discovered taxa that do not fit the metasternal definition cited above or are like other taxon in this respect. At least the following species differ from the typical form: *Podagrion koebelei* (Australian) is without ventral carinae; *P. abbreviatus* (Australian) and an undetermined species from Nigeria appear as *Palmon*; *P. brasiliense* (Neotropical, Nearctic) as for *Micropodagrion* but with propodeal neck bent at a nearly right angle in profile (Fig. 281B); and *P. worcesteri* (Australian) as described above (type species of the junior synonym *Propodagrion*). None of these taxa, however, belong to *Palmon*, based on its defining synapomorphies (listed under the generic heading).

Bouček (1988) suggested that *Podagrion worcesteri* (and several other taxa) could be placed as a subgenus of *Podagrion* (i.e., *Propodagrion*), but if the metasternal area

is of generic value, then it would appear that *Propodagrion* should be recognized as a genus.

If *P. worcesteri* and *P. abbreviatum* together are recognized as a valid taxon, then *Podagrion koebelei* should also be recognized at the generic level, based on the metasternum and other characters (see additional discussion under *Podagrion*). As the problem taxa are Australian and Afrotropical, wherein typical species of *Podagrion* also occur, it seems appropriate that the species of *Podagrion* from these regions are completely reassessed before generic limits are determined.

Under the taxa discussed in the generic sections below, I discuss further and illustrate the structure of the metasternum in context with other characters. Additionally, under *Palmon* I discuss the phylogenetic implications of the metasternum as it relates to all genera.

Summary of Podagrionini: the genus *Podagrion* represents the largest section of the tribe (92 of 130 species) and is as intransigent in understanding as is *Torymus*. Although most species of *Podagrion* at the world level appear to form a well defined monophyletic group, there are outlying taxa that suggest either plasticity or patchiness in character state evolution and/or the inability of the systematist to decipher character development.

Within *Podagrion* and Podagrionini the addition of more refined statements of character state development will doubtless alter the phylogenetic concepts, as found in the ending hypotheses of my analyses. Because the species of Podagrionini are poorly known by me, and my grasp of the group has changed substantially, based on even a small subset of the known species, I discuss generic phylogeny primarily in terms of the ending hypothesis and then only in a preliminary manner. I have been relatively conservative in nomenclatural matters and explain my reasons for doing so under each generic section below.

***Mantiphaga* Ferrière**  
Figs. 37(G), 38(F), 282, 314

*Mantiphaga* Ferrière 1955:212-213. Type-species: *Podagrion pseudocreobotrae* Risbec (orig. desig. and monotypic, MNHN, examined).

NUMBER OF SPECIES (catalog p. 201). - 6.

DISTRIBUTION. - AFROTROPICAL (Senegal, Madagascar, South Africa).

HOSTS. - Reared from egg cases of Mantidae (Mantodea).

KEYS TO SPECIES. - Ferrière (1958).

RECOGNITION. - Within Podagrionini, *Mantiphaga* is recognized by the diagonally truncated and ventrally produced hind-tibial apex (= subpointed) with a single spur situated at its apex (as in Fig. 327), by the transverse anellus, by the 3-segmented antennal club (clavomeres completely encircled by sutures) with ventral micropilosity only on the apical clavomere (Fig. 314), by the mesepimeron which is not bulged outwardly or raised as a flange above the surface of the metapleuron (Fig. 282B), and by the metasternum (Fig. 282A) which has: 2 submedian carinae, the anterior edge of the propodeal foramen close to an imaginary line connecting the posterior edges of the hind-coxal foramina and with short, curved lateral carinae connecting the two; and

metasomal petiole in lateral view scarcely removed from base of hind coxa.

PHYLOGENY . - In the working hypothesis (Fig. 37G) *Mantiphaga* arises at node 38, where it is placed without apomorphies. The node is based on the absence of a frenal line, a homoplasious character. As the taxon was not altered in character assessment from working to ending hypothesis, I treat here only the ending hypothesis (Fig. 38F; node 25).

*Mantiphaga* arises as the most plesiomorphic member of the Podagrionini. Based on my analyses the genus is without defining apomorphies, but is unique in the clade (node 25) because of the retention of the plesiomorphic 3-segmented antennal club (Fig. 314; clavomeres completely encircled by sutures), whereas all other members have at least one and usually two of the ventral sutures interrupted by an area of micropilosity (Figs. 308, 313). A refinement of the data not appreciated at the time of analysis is that in *Mantiphaga* only the apical clavomere has a ventral patch of micropilosity. A 3-segmented club with a single, apical patch of micropilosity appears to be autapomorphic. It suggests a straight transformation between the plesiomorphic 3seg club state (complete sutures) with no ventral micropilosity and the 3seg\* club (interrupted sutures) with ventral micropilosity found in most podagrionines.

A second apomorphy was not recognized until after the analysis was completed. The metasternum of *Mantiphaga* (Fig. 282A) has two carinae on the wide metasternal area and the anterior of the propodeal foramen is placed nearly on an imaginary line drawn across the posterior border of the hind-coxal foramina. This character state, or slight modifications of it, is found also in *Podagrionella* (Fig. 284A) and *Propachytomoides* (Fig. 280A). Because I did not refine the metasternal character into more states within the Podagrionini, I have no evidence as to its possible effect on the tree.

DISCUSSION . - The recognition of this genus is based on putative synapomorphies found in the type species. I have not examined the other 5 known species of *Mantiphaga* to determine if the antennal club and metasternum is constructed the same as for the type. I have seen about two dozen specimens from various localities in South Africa that agree with the type species in character states, but are not *M. pseudocrebotaerae*.

With the exception of the antenna and metasternum, *Mantiphaga* differs in no other respect from typical *Podagrion*, and it would not be difficult to justify synonymizing the two names. As the generic name tentatively appears to represent a geographically (Afrotropical) and morphologically defined group, I retain its use until intermediate forms are found.

#### *Podagrionella* Girault

Figs. 37(G), 38(F), 284, 286-287, 296-298, 308-309, 315-317, 323-326, 328, 332

*Podagrionella* Girault 1913/159:96-97. Type-species: *Podagrionella bella* Girault (monotypic, QM, examined).

*Iridophaga* Picard 1933:237-239. Type-species: *Iridophaga lichtensteini* Picard (monotypic, MNHN, examined).

*Tarachodiphaga* Ferrière 1955:214-215. Type-species: *Tarachodiphaga senegalensis* Risbec (orig. desig., MNHN, examined). **New synonymy.**

*Iridophagoides* Erdős 1964:93. Type-species: *Iridophagoides petiolatus* Erdős (orig. desig. and monotypic, MNHN, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 249). - 10.

DISTRIBUTION . - PALEARCTIC (France, Spain, Algeria), AFROTROPICAL (Senegal, Malawi), AUSTRALIAN (Australia), ORIENTAL (India).

HOSTS . - Reared from egg cases of Mantidae (Mantodea). (One record from eggs of Arbelidae (Lepidoptera) (Narendran and Sureshan 1988) cannot be ruled out, even though it is highly unusual for the tribe.)

KEYS TO SPECIES . - Ferrière (1958:289-290) gave a key to African *Iridophaga* as understood at that time (4 species).

RECOGNITION . - Within Podagrionini, *Podagrionella* is recognized solely by the elongate hind-tibial apex (= pointed), with its truncation much wider than twice the cross section of the tibia and the spur situated basally near the basitarsus (Figs. 324, 326, 328, 332). An additional aid in recognition is that the hind basitarsus is subequal in length to the hind tibia. (This character was not noted until after the phylogenetic analysis was completed and may prove of some phylogenetic value.)

PHYLOGENY . -

Working Hypothesis (Fig. 37G): In the first set of analyses I treated *Podagrionella*, *Iridophaga*, and *Tarachodiphaga* as valid taxa. I overlooked the genus *Iridophagoides* by mistake, omitting it from my data. Subsequently, I examined the type of *Iridophagoides* and determined that it was a synonym of *Podagrionella* (see discussion of synonyms below). *Podagrionella* + *Tarachodiphaga* arise at node 37, based on the apex of the hind tibia (Figs. 324, 326, 328, 332) being diagonally truncate and ventrally produced into a greatly acute angle, the truncation much wider than twice the cross section of tibia (about as long as hind basitarsus), and the spur inserted at the base near the basitarsus. *Iridophaga* arose as part of a multifurcation one step up (node 38), based on the loss of the frenal line, but then is defined by the same hind-tibial condition as just described for *Podagrionella* + *Tarachodiphaga*. Although *Iridophaga* has no frenal line, the frenal area is indicated by a change in sculpture and, as the frenal line is shown to be homoplasious in any event (see x 46), the use of this character state alone to define higher taxa is suspect. For this reason, *Iridophaga* should at least be placed with *Podagrionella* + *Tarachodiphaga*. It might also be noted that within other genera (e.g., *Podagrion*, *Torymus*) the frenal line is a variable character used to define species, or in some cases species groups (Grissell 1976).

Because the explanation of my decisions to synonymize these names is quite involved, I have detailed my reasons for doing so in a "Synonymy" section following the ending hypothesis.

Ending Hypothesis (Fig. 38F): *Podagrionella* + *Propachytomoides* arise two steps up from *Mantiphaga* (nodes 26, 28). Node 26 (remainder of Podagrionini) is a change from a distinctly 3-segmented antennal club (3Seg) to one that has only poorly defined dorsal sutures (3Seg\*) and the apical 2 segments ventrally covered with micropilosity; and node 28 is defined by the presence of a distinct frenal line. The presence or absence of a frenal line is homoplasious, and as I demonstrate below under synonymy, offers little reliance for establishing taxonomic categories.

*Podagrionella* is defined by 2 synapomorphies: a homoplasious intermediate state of setae on the hind femur (*Yes\**) and an autapomorphy of the elongated and pointed apex of the hind tibia (*Pointed*, Figs. 324, 326, 328, 332). This genus is discussed in relation to *Propachytomoides* under the latter genus, and I next discuss the reasons for synonymizing taxa as I have done.

SYNONYMIES. - For the purposes of establishing synonymy the 4 generic names considered in this section are discussed as they currently appear in the literature. They are: *Podagrionella* with 1 Australian and 1 Oriental species, *Iridophaga* with 4 Afrotropical species, *Tarachodiphaga* with 1 Afrotropical species, and *Iridophagoides* with 1 Afrotropical and 1 Palearctic species. In the following discussion I first refer to these genera in the sense of the *type-species only*, after which I discuss other species, most likely undescribed, that alter current generic concepts. These taxa are placed in Table 5 (p. 345) to help in following the discussion.

The type-species of each of the 4 generic names is unique in its own way. Alone, each is recognized by characters found in the antenna, genal sulcus, wing, scutellum, propodeum, and metasomal petiole. Most of these characters were considered only of species recognition value and were not examined for purposes of phylogenetic reconstruction. It is the existence of undescribed species that show intermediate conditions and leads me to accept that all taxa belong to the same genus. As additional evidence, similar specific variation is found in the speciose genus *Podagrion*, suggesting either that there can be much variation between species of a genus or that we do not yet know how to interpret the data. Under either circumstance, variation must be well understood before recognizing generic-level taxa based on single species.

***Tarachodiphaga*:** In *Tarachodiphaga senegalensis*, the type- and only described species of *Tarachodiphaga*, the primary generic level character has been the presence of a pronounced apical cross-carina on the scutellum (Fig. 315) (e.g., Ferrière 1955, Bouček 1978). The carina has an anterior depression that accentuates it, but both are shifted so far posteriorly that it would not normally be called a frenal line, even though this is what it appears to be. The frenal area is a vertical, sculptured, setose face directly above the dorsellum. This construction is found in no other podagrionine species. In an undescribed species from Somalia (over 60 specimens, USNM), the carina is moved forward causing the nearly vertical face (as found in *senegalensis*) to slope at a 45 degree angle (Figs. 316-317). The face is still covered with setae, but its median area is polished and not sculptured. In this species the transverse carina and depression become simply an extremely well defined frenal line. Both *senegalensis* and the undescribed species otherwise appear identical in other characteristics. Both are small (about 3 mm), have short ovipositors, are similarly sculptured, and have an inner, basal, flattened tooth on the hind femur that has not been previously reported in the literature (Figs. 323-324). The presence of the elongated hind-tibial apex and the inner tooth indicate synapomorphies that unite these 2 species, more so than scutellar modifications which, in this case, are simply part of a continuum and are known to be homoplasious as well. The differences between *Tarachodiphaga* and other taxa discussed in this section may be seen in Table 5 (p. 345). From *Podagrionella* it is distinguished by the distinctly 3-segmented dorsum of the club; by the inner, basal tooth of the hind tibia; by the flattened median area of the propodeum (with even, fine reticulation) with strong, semicircular lateral carinae; and by the sculptured vertical frenal



area.

***Iridophaga*:** In *Iridophaga lichtensteini*, the type species of *Iridophaga*, the primary generic level character has been the absence of a cross carina from the scutellum (e.g., Ferrière 1955, Bouček 1978). The frenal area is indicated by a polished surface (which is covered with setae). Both *Iridophaga* and *Tarachodiphaga* share the flattened median area of the propodeum (with even, fine reticulation) with strong, semi-circular lateral carinae, and the presence of a flattened projection (tooth) on the inner base of the hind femur (newly discovered). If these characters are considered, rather than the presence or absence of a frenal line or cross carina, then *Iridophaga* and *Tarachodiphaga* are indicated as monophyletic taxon. It therefore becomes a matter of how one sorts character states as to how taxa are defined. The differences between *Iridophaga* and other taxa discussed in this section may be seen in the tabular comparison (Table 5, p. 345). From *Podagrionella* it is distinguished by the distinctly 3-segmented dorsum of the club; by the inner, basal hind-tibial tooth; by the absence of a frenal groove and presence of a setose frenal area; and by the flattened median area of the propodeum (with even, fine reticulation) with strong, semicircular lateral carinae.

***Podagrionella*:** In *Podagrionella bella*, the type-species of *Podagrionella*, generic level characters have never been firmly established except on a regional basis (e.g., Bouček 1988). Based on my study it is defined by the indistinctly 3-segmented antennal club (appearing 1-segmented at first examination). It differs from *Tarachodiphaga* in having a finely delimited frenal line with a polished frenal area, and it differs from *Iridophaga*, which has no frenal line but does have a polished frenal area. From both *Tarachodiphaga* and *Iridophaga*, *Podagrionella* differs by having the dorsum of the antennal club indistinctly 3-segmented (appearing 1-segmented at first examination); having no inner hind-femoral tooth; and the propodeum with a transverse carina midway between the anterior and posterior margins. Based on this information, alone, theoretically it is easier to justify the recognition of *Podagrionella* as a distinct genus and not to synonymize *Iridophaga* with it as was done by Bouček (1988). The differences between *Podagrionella* and other taxa discussed in this section may be seen in the tabular comparison (Table 5, p. 345).

***Iridophagoides*:** *Iridophagoides petiolatus*, the type-species of *Iridophagoides*, was accorded generic level status based on metasomal tergum 1 (petiole) much longer than wide, the propodeum lacking carinae, and the forewing with a spot posterior to the marginal vein. (The genus was also originally based on having the genal sulcus essentially absent, but I have not found this to be a reliable generic character and have found at least one intermediate species as discussed below.) A second species added by Bouček (1976a: *I. tatianae*) differed in that the metasomal petiole was scarcely as long as broad so that this character is variable at best and would not appear to be the basis for establishing or recognizing genera. The differences between *Iridophagoides* and other taxa discussed in this section may be seen in the tabular comparison (Table 5, p. 345). From *Podagrionella* it differs by the distinctly 3-segmented dorsum of the club; by the absence of a genal groove; by the presence of a wing spot; by the absence of propodeal carinae; and by the petiolate first metasomal tergum.

**Other species examined:** After defining taxa based on the type-species, it becomes necessary to assess other known species and to place undescribed species into a generic hierarchy. If the definitions are based on well defined synapomorphies this

should not be a problem. I have seen a number of Afrotropical specimens representing several undescribed species that require either the description of new generic taxa, or the reevaluation of definitions of the genera as outlined above.

A species from Somalia (2 females, USNM) has the antennal club fused (and with nearly complete ventral micropilosity and a polished, aetose frenal area set off by a groove, as in the type of *Podagrionella* (Australian), but the hind femur has an inner, basal tooth as found in the type-species of *Tarachodiphaga* and *Iridophaga* (Afrotropical). The propodeum is intermediate in structure between the two groups.

A species from Mozambique (1 female, USNM) has the antenna and inner basal hind-femoral tooth as in *Tarachodiphaga* and *Iridophaga* and the scutellum and propodeum as for *Iridophagoides*. (It also has the midtibial spur and basitarsus as found otherwise only in *Micropodagrion* but differs from that taxon by the elongated hind-tibial apex.)

A species from Botswana (10 females, USNM) that would be placed as *Iridophagoides*, based on the absence of an inner, basal hind-femoral tooth and presence of a spotted forewing, differs from that genus in having a short metasomal petiole (as found in *I. tatarica*), a carinate propodeum (similar to *Podagrionella*), and a distinct genal sulcus (found in all other taxa).

In all these taxa I also compared metasterna, wing venation, and metasomal construction in an attempt to reconcile my decision to unite all of the above taxa. Wing venation varies only slightly in that *Podagrionella bella* has a slightly longer stigmal vein than *Iridophaga* + *Tarachodiphaga*. *Iridophagoides* has a slightly shorter marginal vein (relative to the stigmal vein). These slight differences might be quantifiable but would require much more material than is presently available. Metasternal morphology is consistent for all the taxa (Fig. 284). Metasomal construction is somewhat atypical for *Tarachodiphaga* in that Mt5 is by far the longest segment, it is somewhat carapace-like, extending to the base of the ovipositor, and is covered with reticulations and setae. In *Podagrionella*, *Iridophagoides*, and *Iridophaga* Mt5 differs only in being highly polished and without setae. The elongation of Mt1 (metasomal petiole) is found only in a single species of *Iridophagoides*.

*Podagrionella indarbela*, the only known Oriental species, does not agree entirely with any of the taxa diagnosed above (see tabular comparison, Table 5, p. 345). It agrees with *Podagrionella* in most respects but has no frenal line (groove) and its propodeal carina is apical rather than median.

DISCUSSION. - The generic name *Podagrionella* was used by Girault in 1913/159 (September) with the described new species *Podagrionella bella*. He did not describe the genus, but the name was validated in the sense of Article 12(b)(5) of the ICZN (1985) and *P. bella* becomes the type by monotypy. The generic name was described again as new in 1914/201 (May) with *P. fasciatipennis* n. sp. as the type of the genus and again in 1915/243:286 (January) with *P. fasciatipennis* as the "genotype." These latter two designations are invalid.

Bouček (1988) synonymized *Iridophaga* under *Podagrionella*, and as discussed above, I propose that *Tarachodiphaga* and *Iridophagoides* also belong here. At first I thought it might be possible at least to recognize *Iridophaga* + *Tarachodiphaga* as a genus distinct from *Podagrionella* based on a combination of the dorsally distinctly 3-segmented, filiform antennal club, inner, hind-femoral tooth, and propodeal structure in the former, and the indistinctly segmented, enlarged club, absence of hind-femoral

tooth, and propodeal structure in the latter. As was noted above, however, I have seen an undescribed species from Somalia that has the club as in *Podagrionella*, but an inner, basal hind-femoral tooth as in *Iridophaga* and *Tarachodiphaga*. [Attempts to define these taxa in terms of overall similarity have failed to work any better than has the strict analysis of characters. For example, the species from Somalia is identical in overall habitus to *Tarachodiphaga* but has the unique antennae of *Podagrionella*.]

To unambiguously define each of the above taxa as monophyletic generic units would require that each genus be defined by a unique set of character states. This would result in recognizing at least 8 genera. In essence it would be stating that every newly discovered taxon with an elongate hind-tibial apex should be placed in its own genus. I am reluctant to do this until additional taxa indicate this to be the more reasonable approach.

### ***Propachytomoides* Girault**

Figs. 37(G), 38(F), 280

*Podagrionella* Girault 1914/201:47. Type-species: *Podagrionella fasciatipennis* Girault (orig. desig. and monotypic, QM, examined). Preoc. by *Podagrionella* Girault 1913/159.

*Propachytomoides* Girault 1917/334:152. Type-species: *Propachytomoides semialbiclavus* Girault (= *fasciatipennis* Girault) (orig. desig. and monotypic, USNM, examined).

NUMBER OF SPECIES (catalog p. 251). - 3.

DISTRIBUTION. - AUSTRALIAN (Australia). (I have seen a single specimen from Papua New Guinea in BPBM.)

HOSTS. - Unknown.

KEY TO SPECIES. - None.

RECOGNITION. - Within Podagrionini, *Propachytomoides* is recognized by the diagonally truncated and ventrally produced hind-tibial apex (= subpointed) with a single spur situated at its apex (as in Fig. 327), by the mesepimeron (Fig. 280B) which is bulged outwardly and is raised as a flange above the surface of the metapleuron, overhanging the metasternal shelf as a lamelliform plate, and by the metasternum with 2 submedian carinae, the anterior edge of the propodeal foramen situated less than its own diameter from the posterior edges of the hind-coxal foramina (Fig. 280A; in lateral view metasomal petiole scarcely removed from base of hind coxa, Fig. 280B), and with short, curved lateral carinae connecting the propodeal and hind-coxal foramina. Also of recognition value, is that the forewing has a darkened spot beneath the marginal vein.

PHYLOGENY. - In the working hypothesis (Fig. 37G, node 36), *Propachytomoides* arises without apomorphies as the most plesiomorphic member of the clade. As the taxon was not altered in character assessment from working to ending hypothesis, I treat here only the ending hypotheses.

In the ending hypothesis (Fig. 38F), *Propachytomoides* arises with *Podagrionella* at node 28, which is defined by the presence of a distinct frenal line. The presence or absence of a frenal line is a homoplasious synapomorphy that is variable in other taxa (e.g., *Podagrion*), and would not, as determined for the genus *Podagrionella*, define a

taxon with any phylogenetic certainty. *Propachytomoides* is defined in the ending hypothesis only by the absence of setae from the hind coxa, but this is a homoplasious character as well, and is not a reliable character on which to base relationships.

After additional study, I discovered that I had overlooked an autapomorphy that I did not code in my analyses. This is the condition of the hind margin of the mesepimeron, which is bulged outwardly and is raised as a flange above the surface of the metapleuron and overlaps the metasternal shelf as a lamelliform plate (Fig. 280B). This is often best observed from a ventral view.

Because the only defining characters of both *Propachytomoides* and *Podagrionella* are autapomorphies, the establishment of relationship between these two taxa is tenuous at best. They may simply be highly derived species (or species groups) of *Podagrion*.

DISCUSSION . - Ferrière (1955) placed *Propachytomoides* in *Podagrion*, but Bouček (1988) recognized it as valid and transferred 3 species to it. *Propachytomoides* is structurally the most distinct podagrionine by virtue of the lamelliform ventral plate of the mesepimeron. This would appear to be an autapomorphically derived state and is seen in no other torymids to my knowledge (though *Thaumatorymus* is vaguely similar). If this state occurs in other chalcidoids, it is quite rare.

### *Micropodagrion* Ferrière

Figs. 37(G), 38(F), 278, 318, 330, 336-337

*Micropodagrion* Ferrière 1955:210-211. Type-species: *Micropodagrion pauliani* Ferrière (orig. design. and monotypic, MNHN, examined).

NUMBER OF SPECIES (catalog p. 205). - 1.

DISTRIBUTION . - AFROTROPICAL (Ivory Coast).

HOSTS . - Reared from egg cases of Mantidae (Mantodea).

KEYS TO SPECIES . - None.

RECOGNITION . - Within Podagrionini, *Micropodagrion* is recognized by the diagonally truncate and ventrally produced hind-tibial apex (= subpointed) with a single spur situated at its apex (as in Fig. 327), by the midtibial spur which is thread-like and longer than the basitarsus (Fig. 330), by the anellus which is about as long as wide and mouth-piece shaped in profile (Fig. 318), by the mesepimeron which is not bulged outwardly or raised as a flange above the surface of the metapleuron (Fig. 278B), and by the metasternum with 1 median carina, the anterior edge of the propodeal foramen situated at imaginary line drawn across the posterior edges of the hind-coxal foramina (Fig. 278A; in lateral view metasomal petiole scarcely removed from base of hind coxa, Fig. 278B), with short, curved lateral carinae connecting the propodeal and hind-coxal foramina, and with two small carinae that veer off from where the median carina intersects the anteromedian margin.

PHYLOGENY . - In both the working hypothesis (Fig. 37G; node 39) and the ending hypothesis (Fig. 38F; node 27) *Micropodagrion* arises in close proximity to *Podagrion* + *Palmon* (*Palmon* of ending hypothesis = *Pachytomoides* of working hypothesis). In

the former hypothesis it arises as the sister group and in the latter as part of a trifurcation. The trifurcation is defined by the notauli changing from the *Yes* state to *Faint*. This is a homoplasious condition and is worthy of little emphasis (see p. 46). This leaves *Micropodagrion* defined by the autapomorphy of the metasternum (*Micropod*), which is essentially like that found in *Podagrion* (*Podag*, a single median carina), except that it has the propodeal foramen relatively closer to the hind-coxal foramina and connected to them by a short, curved carina (Fig. 278A) rather than having a relatively long, straight carina as found in *Podagrion* (Fig. 279A), and also two small carinae that veer off from where the median carina intersects the anteromedian margin. I discuss the relationships of *Micropodagrion* further under *Palmon*.

DISCUSSION . - The distinction between *Podagrion* and *Micropodagrion* is not great, and *Micropodagrion* would most likely be considered a synonym of *Podagrion* were it not for the peculiar anellus (Fig. 318), structure of the midtibial spur and basitarsus (Fig. 330), and the slightly different construction of the metasternum (Fig. 278A). In typical *Podagrion* the anellus is clearly transverse, the midtibial spur is short and setose, the basitarsus is long (Fig. 329), and the metasternum is as described above (Fig. 279A). As discussed in the introductory section, the shape of the anellus and the condition of the midtibial spur were not realized until late in the research and have not been checked against all species of the tribe. This should be done before placing *Micropodagrion* in synonymy.

*Palmon* Dalman, revised status

Figs. 37(G), 38(F), 283, 285, 288-291, 299-302, 307, 310, 320, 329, 334-335

*Palmon* Dalman 1825:388-390. Type-species: *Palmon bellator* Dalman (desig. by Gahan and Fagan 1923:103, SMNH, examined, gum copal).

*Pachytomoides* Girault 1913/140:143. Type-species: *Pachytomoides mirus* Girault (orig. desig., QM, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 227). - 18.

DISTRIBUTION . - NEARCTIC (USA: Florida), NEOTROPICAL (Argentina and also widespread, based on undescribed species), ORIENTAL (India, Philippine Islands, Sri Lanka, Taiwan), AUSTRALIAN (Australia), AFROTROPICAL (Madagascar, Senegal, Ivory Coast, South Africa, Republic of the Congo).

HOSTS . - Reared from egg cases of Mantidae (Mantodea).

KEY TO SPECIES . - Ferrière (1958) provided a key to the known species (as *Pachytomoides*) and Narendran to the Oriental species (as *Pachytomoides*).

RECOGNITION . - Within *Podagrionini*, *Palmon* is recognized by the diagonally truncated and ventrally produced hind-tibial apex (= subpointed) with a single spur situated at its apex (as in Fig. 327), by the mesepimeron which is not bulged outwardly or raised as a flange above the surface of the metapleuron (Fig. 285B), by the anellus which is cylindrical and longer than wide (Figs. 307, 310), by the forewing surface that is evenly covered with setae from base to apex (Fig. 289), and by the metasternum with 2 submedian carinae, the anterior edge of the propodeal foramen nearly its own diameter from the posterior edges of the hind-coxal foramina (Figs. 283, 285A; in lateral

view metasomal petiole removed from base of hind coxa, Fig. 285B), and with long, curved lateral carinae connecting the propodeal and hind-coxal foramina. In *Palmon* the antennal club is always massively enlarged with the venter almost entirely covered with micropilosity, but this is homoplasious and is found in a few species of *Podagrion*.

PHYLOGENY . - In both the working (Fig. 37G) and ending hypotheses (Fig. 38F) *Palmon* (called *Pachytomoides* in the working hypothesis) is placed as the sister taxon to *Podagrion*. In the latter hypothesis it is placed as part of a trifurcation, including *Micropodagrion*, that is defined by the notauli changing from the *Yes* state to *Faint*. This is a homoplasious condition, and little emphasis should be placed on it. *Palmon* is defined in the ending hypothesis by the state of the head being somewhat square in dorsal view (*Square\**). Again, this is a homoplasious character and would not seem to be of much importance. I dismissed several characters thought to be of species rank, and the following discussion is based on additional work with these characters following completion of the ending hypothesis (these characters were described and discussed in introduction to tribe).

*Palmon* is autapomorphic in its complete wing setation (Fig. 289) and elongated anellus (Figs. 307, 310). Members have two metasternal carinae and wide-spaced foramina, although sometimes the carinae are somewhat irregular (Fig. 283, 285A). I did not include the states of 1 versus 2 carinae in my analyses. Based on my analysis of the spacing of foramina in all taxa, wide-spaced foramina is considered apomorphic relative to narrow-spaced foramina. The 2-carinae state occurs in taxa with both narrow (e.g., *Mantiphaga*) and wide-spaced foramina (e.g., *Palmon*) as does the 1-carina state (i.e., *Micropodagrion* — narrow and *Podagrion* — wide). Therefore, number of carinae and foramina spacing are independent characters.

Based on foramina spacing alone, *Mantiphaga*, *Propachytomoides*, *Podagrionella*, and *Micropodagrion* (all narrow) would be primitive relative to *Palmon* and *Podagrion* (all wide). This does not dispute the finding of the ending hypothesis (poor though it may be) which is based on other characters. As *Mantiphaga* is hypothesized as the sister group to the rest of the Podagrionini, a 2-carina, narrow metasternum would appear to be plesiomorphic. A 1-carina, wide metasternum could be hypothesized as the apomorphic condition. Only *Podagrion* would fit that description (Fig. 279A). *Palmon* is plesiomorphic for carinae but apomorphic for foramina (Figs. 283, 285A). *Micropodagrion* is plesiomorphic for foramina and somewhat intermediate for carinae (Fig. 278A) because, although it has a single median carina, it also has two short apicomedian carinae that veer off from the median carina in the position where the double carina of other genera is found (e.g., *Podagrionella*, *Mantiphaga*). It could be argued that the transformation is: 2-carina/narrow foramina (e.g., *Mantiphaga*, *Propachytomoides*, *Podagrionella*) to 2-carinae/wide foramina (*Palmon*) to 1-carina/wide foramina (*Podagrion*). In this case the 1- (or intermediate) carina/narrow foramina (*Micropodagrion*) might represent a nearly complete loss of the 2 submedian carinae and formation of a single median carina. I am certain that other scenarios could be hypothesized, but at least this one is compatible with the ending hypothesis tree. A more rigorous examination of all *Podagrion* and Podagrionini is in order.

SYNONYMY . - *Palmon* has long been considered a synonym of *Podagrion*. Gahan and Fagan (1923:103) incorrectly attributed this synonymy to Walker (1871a:28). Walker

synonymized "*Palmon pachymerus*" with *Podagrion splendens*, but as *pachymerus* is the type of *Priomerus* (by monotypy) and is not the type of *Palmon*, this does not create generic synonymy of *Palmon* with *Podagrion*. Mayr (1874:63) was the first, as far as I can tell, to place *Palmon* as a synonym of *Podagrion*, and I presume that this must be cited as authority for the action.

Gahan and Fagan (1923) designated *Palmon bellator* as the type-species of the genus *Palmon*. I examined the type specimen of *Palmon bellator* and do not agree with its current synonymy with *Podagrion*. It has the elongate anellus, enlarged club, and uniformly setose forewing that are synapomorphies of *Pachytomoides*. Therefore, I place *Pachytomoides* Girault 1913/140 as a junior subjective synonym of *Palmon* Dalman 1825.

*Palmon bellator* is a copal inclusion of unknown origin. Apparently Dalman (1825) hoped to determine the origin of the copal from the identity of the specimen. He thought perhaps it had come from "Amerika" or "Afrika" (Dalman 1825:382). Although Dalla Torre (1898) listed France as the locality for *P. bellator*, Picard (1933) pointed out that a term of measurement given by Dalman (1825: *lineae Parisiensis*) had been shortened by Westwood (1847) to "lin. Paris." Apparently Dalla Torre (1898) concluded that France was the origin of the copal.

We still do not know the origin of the copal, but I have examined specimens from Nigeria (Ibadan), Botswana (Serowe), and Republic of South Africa (Natal) (all USNM) that are comparable in every respect with *Palmon bellator* except that the propodeum is more carinately sculptured. In these specimens the metasternum is as found in *Pachytomoides*, and although I cannot see the metasternum in *Palmon bellator*, I am convinced that based on the synapomorphies listed above, it is closely related to the Nigerian species. As one-third of known species of *Palmon* (*sensu* Grissell) are from Africa, it seems likely that Dalman's copal might have come from that area.

DISCUSSION . - Although *Palmon* and *Podagrion* are both geographically widespread, the former genus is uncommonly encountered. I have seen fewer than 100 specimens compared to nearly 3000 specimens of *Podagrion*.

Within *Palmon* the metasternum always has 2 submedian carinae, or at least multiple incomplete or broken carinae, but the relative width of the area between the hind-coxal foramina appears to vary from narrow to wide. This apparent difference is related more to degree of sclerotization than to change in actual proportion. Thus, the narrowed appearance is the result of a lack of sclerotization laterad of the submedian carinae, which makes the chitin appear translucent rather than solid. In those species in which the metasternum appears wider, this translucent area is heavily sclerotized. I have seen an undescribed species from Ecuador (based on the elongate anellus, wing setation, and greatly expanded club, USNM) in which the metasternum is as relatively wide, flat, and heavily sclerotized as in *Podagrion*, but 2 narrow-spaced submedian carinae are present (Fig. 283). At low power, these carinae appear to form a single, thick carina, but at 100X it is apparent that two separate carinae are present. These specimens suggest that the relative width and sclerotization of the metasternum is not necessarily of diagnostic value. Rather, it is the presence of single (*Podagrion*) or multiple (*Palmon*) carinae that is apparently of phylogenetic significance. This would need to be tested further with a study of all species of *Podagrion*.

I discovered several diagnostic characters near the conclusion of writing this paper

that might also prove of phylogenetic importance, though this was not tested. First, the entire forewing surface of *Palmon* is covered with setae and the basal cell, basal vein, cubital vein, and speculum cannot be seen (Fig. 289). This is autapomorphic for the genus and is unlike other genera of Podagrionini, in which distinct veins (as indicated by setal tracts) and bare areas are present (Figs. 287, 293). Also, the wing veins of *Palmon* are more elongate than found in *Podagrion* (*sensu stricto*). Together the marginal + postmarginal veins are about equal in length to the anterior edge of the costal cell (Figs. 290-291; less in *Podagrion*: Figs. 294-295) and the stigmal and postmarginal veins are relatively long (Figs. 299-302) compared to those of *Podagrion* (Figs. 303-306). Although this does define *Palmon*, it will be necessary to survey the entire genus *Podagrion* to determine variation that might be found in this character.

### *Podagrion* Spinola

Figs. 11, 16, 19, 21, 29, 37(G), 38(F), 61, 71, 279, 281, 292-295, 303-306, 311-313, 319, 321-322, 327, 331, 333, 338-339, 396-397, 407, 409, 410, 421, 427

*Podagrion* Spinola 1811:147. Type-species: *Podagrion splendens* Spinola (monotypic, type apparently lost, see below).

*Priomerus* Walker 1833:116, 118. Type-species: *Priomerus pachymerus* Walker (monotypic, BMNH, examined).

*Pachytomus* Westwood 1847:260 (as subgenus). Type-species: *Palmon* (*Pachytomus*) *klugianus* Westwood (monotypic, OUM, examined).

*Bactyrishchion* Costa 1857:223-225. Type-species: *Bactyrishchion bicoloratum* Costa (= *Podagrion splendens* Spinola) (monotypic, Universita Degli Studi di Napoli, not examined, presence confirmed by Gennaro Tomasetta, Curator). Isogenotypic through synonymy.

*Blephonira* Holmgren 1869:438. Type-species: *Blephonira fulvipes* Holmgren (monotypic, SMNH, examined).

*Cleptimorpha* Walker 1872b:85. Type-species: *Cleptimorpha binotata* Walker (monotypic, type lost, see Graham 1981).

*Cyanostola* Saussure 1890:Pl. 15 Fig. 30 (no description). Type-species: *Cyanostola coerulea* Saussure (monotypic, illustration only, no type).

*Coquerelia* Saussure 1890:Pl. 20, Fig. 7 (no description). Type-species: *Coquerelia insidiosa* Saussure (monotypic, illustration only, no type).

*Podagrion* Schulz 1906:150. Unjustified emendation.

*Pachytomoidella* Girault 1913/172:40. Type-species: *Pachytomoidella magniclavus* Girault (orig. desig. and monotypic, type lost).

*Propodagrion* Girault 1915/243:287. Type-species: *Podagrion worcesteri* Girault (orig. desig. and monotypic, QM, examined).

*Coquereliana* Gahan and Fagan 1923:39. Objective replacement name for *Coquerelia* Saussure nec Kraatz.

NUMBER OF SPECIES (catalog p. 234). - 97.

DISTRIBUTION. - Worldwide.

HOSTS. - All reared species have been associated with the egg cases of praying mantids (Mantodea).

KEYS TO SPECIES. - There are few keys available to species of this genus. The following may be useful for the region specified: AFROTROPICAL: Africa:



Bakkendorf 1960 (a list of African species and how they differ from each other). North West Africa: Risbec 1951a. Africa and Madagascar: Risbec 1956. Somalia: Masi 1940. PALEARCTIC: Europe: Hoffmeyer 1931. Commonwealth of Independent States (European part): Nikol'skaya and Zerova 1978. Hungary: Erdős 1960. Japan: Habu 1962. ORIENTAL: India: Mani 1989; Narendran 1994. Taiwan: Masi 1926a. Philippine Islands: Gahan 1925. Korea: Paik 1978 (list only). NEARCTIC: Grissell and Goodpasture 1981.

RECOGNITION . - Within Podagrionini, *Podagrion* is recognized by the diagonally truncated and ventrally produced hind-tibial apex (= subpointed) with a single spur situated at its apex (Fig. 327), by the mesepimeron which is not bulged outwardly or raised as a flange above the surface of the metapleuron (Fig. 279B), by the anellus which is much wider than long (and sometimes difficult to see), and by the metasternum with 1 median carina (Fig. 279A), the propodeal foramen greatly separated from the hind-coxal foramina (Fig. 279B; in lateral view metasomal petiole scarcely removed from base of hind coxa), and with straight lateral carinae connecting the propodeal and hind-coxal foramina. (Several species that do not fit this diagnosis are discussed below, under Discussion.)

PHYLOGENY . - In both the working (Fig. 37G, node 40) and ending hypotheses (Fig. 38F, node 27) *Podagrion* is placed as the sister taxon to *Palmon*. In the latter tree it is placed as part of a trifurcation, including *Micropodagrion*, the clade defined by the notauli changing from the *Yes* state to *Faint*. This is a homoplasious condition. *Podagrion* is defined by no apomorphies in either hypothesis, but my reevaluation of the metasternal structure suggests that the single, median carina and wide-spaced foramina (Fig. 279A) provide a valid apomorphy. I discussed the interrelationships of *Podagrion* to *Micropodagrion* and *Palmon* under the latter two generic names.

SYNONYMS AND TYPE MATERIAL. - I summarized the type information above with each of the names, but some additional information may be useful.

*Podagrion splendens* Spinola: The type of *Podagrion splendens* should reside in the Spinola collection in Turin. Through correspondence with personnel at the Università di Torino I have been told that this name is not listed in the catalog of Spinola material. Dr. Marcus Graham (in *litt.*) informed me that he had also inquired about the material but that none was there.

*Palmon (Pachytomus) klugianus* Westwood: According to Dalla Torre (1898:369) and Gahan and Fagan (1923:103), Walker (1871a:28) synonymized *Pachytomus* with *Podagrion*. This is incorrect. Walker synonymized *Palmon pachymerus* with *Podagrion splendens*. All *Palmon* were not synonymized (the type species, *Palmon bellator*, was not selected until 1923 by Gahan and Fagan), nor was *Pachytomus klugianus* (the type species of *Pachytomus* by monotypy) mentioned. As far as I can tell, Mayr (1874:63) was the first to place *Pachytomus* as a synonym of *Podagrion*, but Williams (1914) also synonymized *Pachytomus* stating that the two were based on opposite sexes.

*Bactyrischion bicoloratum* Costa: The type of *Bactyrischion bicoloratum* is in Università Degli Studi di Napoli (as confirmed by Gennaro Tomasetta, Curator) but could not be loaned for study.

*Cleptimorpha binotata* Walker: Graham (1981:5-6) synonymized this genus, although the type has not been found.

*Cyanostola coerulea* Saussure and *Coquerelia insidiosa* Saussure: Only a figure was published for each species, which is considered valid under Art. 12(b)(7) (ICZN 1985). I wrote to MHNG, thinking I might find specimens of these species but none were located. Gérard Delvare (in *litt.*) pointed out to me that *Coquerelia* Saussure and *Coquereliana* Gahan and Fagan had been overlooked in the literature as synonyms of *Podagrion*.

*Pachytomoidella magniclavus* Girault: Dahms (1984:785) could not find the type of this species in the Queensland Museum, where it was supposedly deposited. I also checked the South Australia Museum, and it is not there, nor is it in the USNM. The greatly enlarged club of this species, as discussed in the original description (Girault 1913/172), suggests that this genus might be placed in *Palmon*. There is no additional information in the description to help in this respect. However, in 1915/243 Girault redescribed *P. magniclavus* and also discussed species of *Pachytomoides* (= *Palmon*), pointing out that *Pachytomoides* was lacking "a ring-joint" (i.e., the anellus was elongate as for a typical funicular). The fact that he stated this for *Pachytomoides* and not for *Pachytomoidella magniclavus* suggests that the anellus was typically transverse for this species and it is, therefore, most likely properly placed in *Podagrion*.

*Notopodion* Dahlbom (1857:295), also spelled *Notopodium* Schulz (1906:144), with no described species, has long been considered a synonym of *Podagrion* (e.g., Ashmead 1904a:382, Gahan and Fagan 1923:41, Habu 1962:182-183, Grissell 1979:767-768, Bouček 1988:140). Gahan and Fagan (1923:98) chose *Podagrion splendens* Spinola as the type-species of *Notopodion*, thus making *Notopodion* isogenotypic with *Podagrion*. Graham (1990:199-200), however, in studying the Dahlbom collection, discovered that *Notopodion* is actually a synonym of *Asaphes* in the Pteromalidae. The name is thus removed from synonymy in the Torymidae.

DISCUSSION. - I have made no attempt to examine every described species of *Podagrion* to determine if, indeed, the taxon actually belongs in this genus. I have seen about half of the described species (i.e., approximately 45 identified species), as well as over 3000 specimens which can be assigned to *Podagrion* without doubt. Although only 12 species are reported from the Neotropical Region, I have seen numerous undescribed species from that region. I have no doubt that the number of world species will double or triple when the group is studied in depth.

Although the diagnosis outlined above applies to the majority of specimens examined and appears to characterize the genus in its strict sense, a few taxa pose problems, as I shall discuss next (and as I discussed in the introductory material to the tribe).

In *Podagrion koebelei* from Australia (type material, USNM), the metasternum is as found in typical *Palmon* except that no carinae are present (extremely vague, irregular carinae may be seen with fluorescent light). However, the reduced forewing setation and transverse anellus is as found in *Podagrion*. The species appears to be much like typical *Podagrion* except that the pronotal collar is sharply margined (reported also for *Podagrion obscurum* by Bouček 1988, but not seen by me). In *P. koebelei* the club is filiform with only a narrow line of micropilosity on apical clavomeres 2 and 3 (condition unknown in *P. obscurum*). This is unlike either *Palmon* or *Podagrion*,

both of which have a large region of micropilosity on the entire ventral surface of the club. If *Mantiphaga* is recognized based on the two metasternal carinae and apical micropilosity of the club, then *koebelei* and perhaps *obscurum* will require a similar treatment.

In *Podagrion worcesteri*, the type-species of the junior subjective synonym *Propodagrion* (proposed by Baltazar 1966), the metasternum has two carinae and closely spaced foramina (as in Fig. 284 for *Podagrionella*). In this state *Propodagrion* is identical to *Podagrionella* (they differ in the short apical hind-tibial apex in the former and the elongated apex in the latter). The type of the genus, and other specimens, have been characterized by the presence of a polished frenal area, but I have seen specimens from Olokemeji, Nigeria (USNM), that appear to be *Propodagrion* (based on the metasternum) except that they do not have a polished frenal area but have a frenal area that is slightly indicated by a change in sculpture. *Podagrion abbreviatum* from Australia (type series, USNM) would also fit into this group, and its frenal area is intermediate between the two. Bouček (1988:140) suggested that *Propodagrion* eventually might be separated as a subgenus based on the polished frenal area. The frenal area is homoplasious and if a genus-level taxon is recognized at all, it probably should be based on the metasternal carinae. This should, most likely, be reelevated to the genus level.

In *Podagrion brasiliense* and several undescribed species from areas in Brazil (Mato Grosso, Pernambuco), Argentina (Santa Fe), and Venezuela (Aragua, Guarico) (all specimens USNM), specimens have a single median metasternal carina with the metasternum curved at nearly a 45 degree angle in profile from anterior to posterior (Fig. 281B; i.e., not essentially flat as in typical *Podagrion*, Fig. 279B). The metasternum is well sclerotized as in typical *Podagrion*, and the propodeal foramen is as relatively distant from the hind-coxal foramina, but because of the metasternal curvature (Fig. 281A), in ventral view its anterior margin appears to be on an imaginary line drawn across the posterior margins of the hind-coxal foramina. All specimens of this group are about 3 mm or less (usually about 2 mm). Additionally, females have an enlarged antennal club, the anellus slightly elongate, and an elongate metasomal petiole (all found in *Palmon*). It is possible to place these taxa as an atypical species group of *Podagrion*, but they might also be classified as a distinct genus based solely on the metasternum. I point this out as an avenue for future study.

The recognition of genera should be based on the establishment of their monophyly. Eventually, if metasternal construction is considered to represent some indication of monophyly, then more genera will have to be recognized. For example, *Podagrion koebelei*, *Propodagrion*, and a group of species based on *brasiliense* would each be recognized as genera.

It sometimes appears as if species groups or subgenera of *Podagrion* might be recognized (see also Bouček 1988:140), but based on current knowledge, character states appear to sort in checkerboard rather than transformational patterns (see also, as an example, the tabular comparison of taxa in *Podagrionella*). In all likelihood, the above taxa should be removed from *Podagrion* and placed in generic-level categories. I hesitate to do so, however, because I believe a thorough study of the Old World species is necessary to better assess characters and their importance in *Podagrion*.

*Incertae Sedis*

In attempting to interpret the ending hypothesis tree (Fig. 38) in nomenclatural rather than phylogenetic terms, several taxa could not be placed by unambiguous set-soft synapomorphies into a simple nomenclatural scheme. These are treated below as "unplaced taxa" with an explanation of their relevant problems of association. In each case the taxa are placed as part of a multifurcation: node 2 includes *Glyphomerus* and *Zaglyptonotus*, node 11 includes *Exopristus* and *Cryptopristus*, and node 13 includes *Stenotorymus* and *Thaumatorymus*. In addition, the genus *Echthrodape* is treated here, because it was diagnosed as a torymid after the first draft of this paper was completed. Taxa are treated alphabetically below.

*Cryptopristus* Förster

Figs. 37(F), 38(D), 351, 353, 359, 365-366, 369

*Cryptopristus* Förster 1856:43. Type-species: *Torymus caliginosus* Walker (monotypic, BMNH, examined).

*Websterellus* Ashmead 1893a:164. Type-species: *Websterellus tritici* Ashmead (monotypic, USNM, examined).

NUMBER OF SPECIES (catalog p. 182). - 2.

DISTRIBUTION . - NEARCTIC (widespread throughout eastern USA, possibly introduced), PALEARCTIC (Czechoslovakia, France, Great Britain, Germany, Commonwealth of Independent States).

HOST. - Reared from Eurytomidae (Hymenoptera) in grass nodes (Poaceae).

KEYS TO SPECIES. - None.

RECOGNITION . - *Cryptopristus* is recognized by a minimum combination of pteromalid-like wing venation (Figs. 351, 359), toothed hind femur (Fig. 353), straight hind tibia, and elongate, emarginate metasomal terga 2 and 3 in females (Fig. 365).

PHYLOGENY . - There was a large discrepancy between the working hypothesis and ending hypothesis in the placement of *Cryptopristus*, and I discuss this as an indication of the difficulty of placing this genus in a hierarchical system. In the working hypothesis (Fig. 37F), *Cryptopristus* arises at node 29, based on a reversal to a pteromalid-like wing venation and is there defined by the metasoma, which has terga 2 and 3 greatly elongate and distinctly emarginate on their posterior margins. *Cryptopristus* arises 8 steps distant from *Glyphomerus* (node 5, base of tree), but it differs only in two states: the hind femur has a tooth and metasomal tergal emarginations as just mentioned. Considering metasomal terga, the reason for the large number of steps to reach node 29 resides in the homoplasious nature of the character which requires state 2A to arise once from state 2 at node 11 (*Idarnotorymus*) and once from state 0 at node 29. This latter hypothesis requires a reversal (node 15 from 0 to 4 and then node 19 from 4 to 0) and then the appearance of 2A (*Cryptopristus*).

The metasoma of these two taxa are certainly distinctive. In *Glyphomerus* (Fig. 363) the metasoma is short, squat, and without emarginations. The terga are heavily

sclerotized and evenly and heavily reticulate. In *Cryptopristus* (Fig. 365) the metasoma is laterally narrowed and elongated with Mt2 ligulate and deeply incised, and Mt3 shallowly emarginate but with an elongated median fold. The terga are weakly sclerotized and weakly reticulate. The males of both taxa are constructed like *Glyphomerus*, with the terga entire, although there is still some slight difference in intensity of sculpture.

In the ending hypothesis (Fig. 38D) *Cryptopristus* (node 11) arises with *Exopristus*. Its relationship to that genus is discussed under *Exopristus* (p. 167). In this hypothesis *Cryptopristus* arises only 1 step up from *Glyphomerus* (node 2) based on a single derived character, namely the development of a tooth on the hind femur. The hind femur of *Glyphomerus* (Fig. 356) is slightly angulate in the region where the tooth of *Cryptopristus* (Fig. 353) arises and the difference between the two is not really very great. The ending hypothesis suggests that state 2A was derived directly from the outgroup state of 1/2 and that *Glyphomerus* is a reversal to the pteromalid-like state of 0. Intuitively this is a much simpler set of steps to envision than the complicated tergal emargination transformation hypothesized by the working hypothesis.

I am not satisfied that the placement of *Cryptopristus* is accurate even with the relatively better results of the ending hypothesis. For one thing, the wing venation is identical in both *Glyphomerus* and *Cryptopristus*. In this case the pteromalid-like venation (*Ptero*) appears to be primitively retained at node 11 from the pteromalid outgroup and its reappearance at node 2. Nodes 3 and 9 are each defined by other states of the wing character. It is my opinion that *Cryptopristus* is incorrectly placed on the tree and that its phylogenetic affinities lie more at the base of the tree (with *Glyphomerus*) than at the apex (sister to node 12). Because of this, I have placed *Cryptopristus* as an *incertae sedis*.

DISCUSSION. - *Cryptopristus* is reported in the Nearctic from 1 species and in the Palearctic from another. It is possible that both are the same species and, if so, that it was introduced into the Nearctic from the Palearctic much as hypothesized for *Glyphomerus*, *Ditropinotus*, and *Eridontomerus*. The Nearctic species was reared from nodes of wheat, an introduced plant. Some attention needs to be given to this matter, but unfortunately the species involved are not often collected. Based on my examination of both Palearctic and Nearctic specimens, the latter do not have the wing stain as well developed as Palearctic ones, and they have yellow hind femora and scapes (dark brown in Palearctic specimens). I can find no differences in facial proportions, wing setation, or hind-femoral shape. My opinion is that *Cryptopristus* is adventive in the Nearctic, but this needs further study of populations from both regions.

### *Echthrodape* Burks

Figs. 30, 371-375

*Echthrodape* Burks 1969:73-75. Type-species: *Echthrodape africana* Burks (monotypic, USNM, examined).

NUMBER OF SPECIES (catalog p. 189). - 2.

DISTRIBUTION. - Afrotropical (Kenya); Australian (Papua New Guinea).

HOST. - Reared from Anthophoridae (Hymenoptera) in dead stems of *Lantana* (Verbenaceae).

KEYS TO SPECIES. - None.

RECOGNITION. - *Echthrodape* is recognized by the relatively short wing venation (Fig. 374) with the postmarginal vein far removed from the apex of the wing, with a widened marginal vein and shortened postmarginal vein (Fig. 373), and with the marginal vein slightly removed from the anterior edge of the wing (Figs. 373-374). Additional characters that help in recognition are the toothed hind femur (Fig. 375), the developed occipital carina that lies midway between the hind ocelli and occipital foramen with ventrolateral edges that do not extend to an imaginary line drawn horizontally across the venter of the occipital foramen (Fig. 372), and the reduced mouth opening (Fig. 371, indicated, in part, by the large malar distance) with reduced mandibles (scarcely visible and obscured by other mouth parts). According to Heraty, (pers. comm.), several undescribed species that he has seen are variable for the size of the mouth opening and the structure of the occipital carina. All species agree, however, in having the characteristic wing venation and reduced mandibles.

PHYLOGENY. - This genus was not included in the phylogenetic analysis because its affiliation with Torymidae was discovered only after completion of the first draft of this paper. (I discussed the inclusion of this genus earlier in the the "Family Systematics" section, p. 18.) Based on the type-species of the genus, *Echthrodape* has two autapomorphies not found in other torymids, including the structure of the wing veins and the reduced mandibles, as just mentioned above. As the wing venation is of importance in establishing phylogeny, its unique state does not contribute much to an elucidation of the problem. *Echthrodape* displays plesiomorphic states in other important characters, including occipital carina, hind-tibial shape and apex, number and length of spurs, and metasternal construction. In overall appearance it would seem to be related to Monodontomerini, but a strict reliance on character states argues a more basal position. The use of bees as host does not offer much corroboration from biological evidence. Bee parasites are found in the Microdontomerini, Torymini, and Monodontomerini. Without further study I do not know where to place this taxon.

### *Exopristus* Ruschka

Figs. 37(F), 38(D), 348, 355, 364

*Exopristus* Ruschka 1923:400. Type-species: *Cryptopristus trigonomerus* Masi (monotypic, MCSN, USNM, examined).

*Exopristoides* Bouček 1982:184-186. Type-species: *Exopristoides dentatus* Bouček (orig. desig. and monotypic, BMNH, examined). **New synonymy.**

NUMBER OF SPECIES (catalog p. 192). - 2.

DISTRIBUTION. - PALEARCTIC (Italy, Romania, Mongolia, Turkey, Tunisia).

HOST. - Associated with gall-formers on *Papaver* sp. (Papaveraceae), *Verbascum* sp. (Scrophulariaceae), and *Centaurea* (Asteraceae).

KEYS TO SPECIES. - None.

RECOGNITION . - *Exopristus* is recognized by the autapomorphic hind femur (Fig. 355), which has rounded lobes from midpoint to apex, by the slightly curved hind tibia (Fig. 355), and by the pteromalid-like wing venation (Fig. 348).

PHYLOGENY . - Working hypothesis (Fig. 37F): *Exopristus* and *Exopristoides* arise at node 31, which is defined by the change to an autapomorphic hind femur (*Toothout*, Fig. 355) and slightly curved hind tibia (Fig. 355, *Curved\**). As explained below in the discussion section, I consider both taxa synonyms and therefore refer only to *Exopristus* herein. This genus, as with *Cryptopristus*, was a puzzle arising as it did near the apex of the tree (node 31), yet differing little from *Glyphomerus* at the base (node 4). It has primitive, pteromalid-like wing venation, yet the autapomorphic hind femur was hypothesized to be derived from the *Bigteeth* state, and the partially curved hind tibia was considered a reversal rather than an intermediate state. In both characters, the states for *Exopristus* would intuitively appear to be intermediate rather than derived. Thus, *Toothout* would seem to be a condition between the *Simple* or *Tooth* state and the *Bigteeth* state in the case of the hind femur, and *Curved\** would seem to be intermediate between *Straight* and *Curved* in the case of the tibia. As the hind femur is autapomorphic, its further analysis was not of much relevance. That left the defining character of the degree of curvature in the hind tibia with which to make phylogenetic inferences, and I did not believe this was adequate.

Ending hypothesis (Fig. 38D): In the final analysis *Exopristus* is placed as part of a trifurcation with *Cryptopristus* (node 11) only 1 step removed from *Glyphomerus* (node 2), and is still defined by the hind femur and partially curved hind tibia. In this case, however, the *Toothout* state is derived directly from the *Tooth* state not via *Bigteeth* and the hind-tibial shape (*Curved\**) is derived directly from the *Straight* state not indirectly through *Curved*. Intuitively this makes more sense than the alternative given in the working hypothesis.

*Exopristus* differs from *Cryptopristus* based on the two apomorphies given above, i.e., hind femur and hind tibia (cf. Figs. 355, 353), as well as the metasomal terga. In *Exopristus* the terga are of the plesiomorphic *1/2* state (Fig. 363) whereas in *Cryptopristus* they are of the modified state of *2A* (Fig. 365), hypothetically derived from the *1/2* state. Interestingly, the males of both genera have pedicellate antenna, a character found in no other genera, to my knowledge. This character was not included in the data matrix, but it does seem to unite the two taxa.

*Exopristus* is a problematic taxon in that it shares characters of both basal and apical taxa. It is not much different from *Chalcimerus* (node 24), a torymid with highly apomorphic legs but plesiomorphic wings (i.e., pteromalid-like) and metasternal structure. Also, both taxa attack cynipid gall-formers in Papaveraceae. This is a totally different host niche than all the remaining taxa at node 25, which feed within the egg chambers of praying mantid oothecae. But neither is *Exopristus* remarkably different from *Glyphomerus* (node 4), a plesiomorphic genus that also attacks cynipids but in different host plants. The morphological differences between all three of these taxa are associated with the hind femur and hind tibia, while all three retain most other characters in the plesiomorphic state. It is possible that the taxa are totally misplaced, based solely on the hind legs. In this case does one accept the calculated hypothesis or the intuitive one? Intuitively, I would place *Exopristus*, *Chalcimerus*, and *Glyphomerus* in close phylogenetic proximity at the base of the tree, but this argues

against the importance placed on leg structure in the ending hypothesis.

DISCUSSION. - *Exopristoides* differs from *Exopristus* only in having a slightly more produced clypeal apex, slightly different facial and antennal proportions, a weak frenal line, and Mt2 and Mt3 entire. The facial (including clypeal) and antennal proportions are used as species defining characters in many genera of Torymidae (e.g., *Monodontomerus*, *Torymus*) and should not, in my opinion, be used to define 2 genera each based on a single species. The weak frenal line in *Exopristoides* is only slightly more pronounced than in *Exopristus*, in which a change in sculpture occurs at the point corresponding to a sulcus. In general, the frenal line is extremely homoplasious, as I demonstrated earlier (see p. 46), and, again, is not a good character on which to define 2 genera. Metasomal terga 2 and 3 of *Exopristus* are so minutely emarginate that they scarcely differ at all from those of *Exopristoides*.

Bouček (1982) stated that *Exopristoides* differed from *Exopristus* in the male having pedunculate flagellomeres, but both have such flagellomeres. It is just more difficult to see the condition in *Exopristus*, because they are more transverse and closely appressed. He also stated that the stigmal vein of *Exopristoides* was relatively longer than that of *Exopristus*, but direct measurement shows no difference. For these reasons I synonymize *Exopristoides* as a junior subjective synonym of *Exopristus*.

### *Glyphomerus* Förster

Figs. 18, 37(A), 38(A), 56, 349 356, 361, 363

*Glyphomerus* Förster 1856:43, 44, 145. Type-species: *Ichneumon stigma* Fabricius (orig. design., syntypes ZMC, examined).

*Oligostenus* Förster 1856:145. Unnecessary new name.

NUMBER OF SPECIES (catalog p. 193). - 5.

DISTRIBUTION. - NEARCTIC (USA: 1 species, widespread and transcontinental, probably introduced in association with the mossy rose gall, *Diplolepis rosae*, introduced from Europe); PALEARCTIC (widespread in Commonwealth of Independent States, Western Europe, Japan).

HOST. - Species of *Glyphomerus* are reared from Cynipidae (Hymenoptera) that form galls on Rosaceae and Asteraceae, and from Eurytomidae (Hymenoptera) that form galls on Poaceae.

KEYS TO SPECIES. - Erdős (1960) published a key to the species of Hungary, and Bouček (1970) published a key to the then known species.

RECOGNITION. - *Glyphomerus* is defined only by a combination of primitive character states which include at a minimum the following: wing venation pteromalid-like (Figs. 56, 349); occipital carina present, nearer to dorsum of head than occipital foramen or midway between, and with ventrolateral edges extending nearly to imaginary line drawn horizontally across venter of occipital foramen (Fig. 361); hind femur simple (Fig. 356) and hind tibia with 2 apical, unmodified spurs. Additional characters that aid in recognition are antenna with 1 anellus and metasomal terga without emarginations (Fig. 363).



PHYLOGENY . - In both the working (Fig. 37A, node 4) and ending (Fig. 38A, node 2) hypotheses, *Glyphomerus* is placed as part of a basal multifurcation. It would appear to be the most primitive genus of Toryminae but is without apomorphies and is "defined" by retention of the primitive pteromalid-like wing venation, a character that changes states or defines nodes above *Glyphomerus*. It differs from the derived wing vein of Megastigminae. *Glyphomerus* combines all of the primitive states for characters within the subfamily, and members of the genus are consequently generalized in appearance.

Within the ending hypothesis (Fig. 38A) it takes little imagination to derive either the Microdontomerini (node 3, Fig. 38B) or the Monodontomerini (node 14, Fig. 38E) from ancestors that approached *Glyphomerus* in appearance. *Glyphomerus* would seem to represent a relictual phenotype for the subfamily and is currently placed as an *incertae sedis* with relation to other genera.

DISCUSSION . - I believe that *Glyphomerus* is an adventive genus in the Nearctic. The only species recorded from the Nearctic, *G. stigma*, is parasitic on the mossy rose gall (*Diplolepis rosae*) which is, itself, considered to be an introduction from Europe (Burks 1979).

### *Stenotorymus* Masi

Figs. 37(D), 38(D), 340-347

*Stenotorymus* Masi 1938:207. Type-species: *Stenotorymus linearis* Masi (monotypic, MCSN, examined).

NUMBER OF SPECIES (catalog p. 262). - 1.

DISTRIBUTION . - AFROTROPICAL (Somalia) (and ORIENTAL based on undescribed species, see Discussion, below).

HOST . - Unknown.

KEYS TO SPECIES . - None.

RECOGNITION . - *Stenotorymus* is recognized by the "square" head when seen in dorsal view (Fig. 341), the presence of a metasternal shelf (Fig. 346), the propodeum (Fig. 346) without carina and horizontally elongated in the axis of body and with the spiracular sulcus either obscure or reaching to hind margin of propodeum about mid-way between nucha and lateral corner, the absence of an occipital carina, and the unemarginate metasomal terga (with abdomen laterally flattened) (these states based on single known species and 2 undescribed species from Borneo and India).

PHYLOGENY . - In my working hypothesis (Fig. 37D), *Stenotorymus* arose from the trifurcation at node 19. The node was diagnosed by unemarginate metasomal terga (0) and the *Mono* wing venation (Fig. 42, Character 8). The wing venation is different (Figs. 343-344) than typically defined as monodontomerine (as in Fig. 42, Character 8), however, in that the stigmal and postmarginal veins of *Stenotorymus* are relatively longer. I could not define the wing vein unambiguously, however, and since the ratios of its components fell within the *Mono* state, I assigned it to that state. Additionally the metasomal terga are constructed differently than those found in the 0 state,

even though neither is emarginate. In *Stenotorymus* the terga are extremely laterally flattened, whereas in the *O* state, the terga are at most slightly dorsoventrally flattened. Although *Stenotorymus* was diagnosed by the autapomorphy of the square head (*Square*), the states of this character are relative and homoplastic. The state *Square*\* occurs at nodes 33 and 40 and is only somewhat less square than *Square*. I could not place *Stenotorymus* with respect to other taxa and so reexamined it for the ending hypothesis.

Ending hypothesis (Fig. 38D): In this analysis the propodeal state was changed from *Nocarin* to the autapomorphic state *Steno* (Fig. 346) because it is intermediate between the primitive *Nocarin* state and the derived *Multi* state. The propodeum lacks a spiracular sulcus or has a weakly developed sulcus that reaches midway between the nucha and lateral propodeal corner, and the callus is poorly developed, flattened, and with few setae. In the *Nocarin* state the sulcus is developed and reaches (or is curved towards) the nucha and there is a convex callus with setae. In the *Multi* state the spiracular sulcus is absent or oriented towards the lateral corner of the propodeum, the callus is absent, and no setae are present. The metasternal state, it now turns out, should have been coded as autapomorphic as well, but I could not see it with any assurance when coding the ending hypothesis states (I discuss this further below in the discussion section.)

*Stenotorymus* arises at node 13 with *Thaumatorymus* and Monodontomerini (node 14) based on the hind-femoral tooth (node 11), the unemarginate metasomal terga (node 12) and the *Mono* wing venation (node 13). This is essentially the same as found in the working hypothesis and the same comments about structure apply. In my opinion, the placement of *Stenotorymus* here does not indicate true relationship as much as an inability to code character states as precisely as possible. Not only is the wing venation of *Stenotorymus* different than typical Monodontomerini, but the character, itself, is homoplasious so it is perhaps doubly misleading as an indication of phylogeny. The same can be said for the metasomal tergal structure. Only the hind femur is arguably coded correctly. In addition to the metasternum, *Stenotorymus* is defined by 4 apomorphies including the loss of the occipital carina, the square head, the autapomorphic propodeum, and the hind coxa without dorsal setae. Of these apomorphies only the propodeum is non-homoplasious (and perhaps the metasternum as well, see discussion, below).

In general appearance, *Stenotorymus* would seem to have no relationship to *Thaumatorymus*. Their position together at node 13 is based on the hind femur and tergal emarginations, but they differ in occipital carina, head shape, wing venation, propodeum, hind-coxal setae, and mesepimeral margin (as well as superficial aspects such as size and color). Even relative to Monodontomerini there is no obvious overall similarity. Because there appear to be no defining synapomorphies which unite taxa at node 13, and because *Stenotorymus* and *Thaumatorymus* do not appear to form a natural group, I have placed both as *incertae sedis* until the problem is resolved.

DISCUSSION. - My final concept of *Stenotorymus* is somewhat broadened from the ending hypothesis based on 5 specimens representing possibly 3 undescribed species from Thailand, India, and Malaysia (Borneo and Peninsular Malaysia). These specimens differ from *Stenotorymus linearis*, the type-species, only in proportions of wing venation, completeness of spiracular sulcus, slope of propodeum, facial proportions,

and size of hind-femoral tooth. These species do not help with phylogenetic placement, but they do reinforce several of the autapomorphic aspects of this taxon. The species also suggest that *Stenotorymus* is a validly defined, widespread taxon in the Afrotropical and Oriental Regions. They share several characters that I did not code for phylogenetic analysis, but which may prove to be of some value in determining relationships. These include a single anellus, which is elongated and somewhat trumpet-shaped (Fig. 342), a relatively large prepectus, and a narrowed face (perhaps resulting also in the dorsally squared head).

Species of *Stenotorymus* share the structure of the metasternum, which I did not fully realize at the time of the ending analysis. Its structure (Fig. 345) is intermediate (as in the case of the propodeum) between the more primitive *Crypto* state (Fig. 47, Character 20) and the more derived *Podag* state (Fig. 47, Character 20). In *Stenotorymus* the metasternum is developed into a shelf in front of the hind coxae (as in the *Podag* state) but the propodeal foramen is oriented between the hind-coxal foramina as in the *Crypto* state, not removed from it as in the *Podag* state.

*Stenotorymus* appears to be correctly placed on the tree as an advanced taxon, but its precise relationship to the Monodontomerini and the Podagrionini is not clarified by the hypothesized tree. It should possibly be placed as a tribe of its own, but its position as part of a trifurcation suggests that problems still remain in assigning its correct position within a hierarchy. Until that time I treat it as an *incertae sedis*.

### *Thaumatorymus* Ferrière and Novicky

Figs. 38(D), 352, 354, 360, 368

*Thaumatorymus* Ferrière and Novicky 1954:34. Type-species: *Thaumatorymus notanisoides* Ferrière and Novicky (orig. desig. and monotypic).

NUMBER OF SPECIES (catalog p. 262). - 1.

DISTRIBUTION . - PALEARCTIC (Tunisia, Yugoslavia).

HOST. - The only known species is associated with cynipid galls on *Hypochoeris* spp. (Asteraceae).

KEYS TO SPECIES. - None.

RECOGNITION . - *Thaumatorymus* is recognized by the reduced wing venation (Fig. 360), of which the postmarginal vein is far removed from the apex of the wing, and by the mesepimeron (Fig. 368), which is slightly sinuate and raised above the anterior margin of the metapleuron. Additional characters that help in recognition are the occipital carina developed in the upper half of the head, the toothed hind femur (Fig. 354), and the metasomal terga, which are unemarginate. (The propodeal spiracles are elevated onto projections, but this is considered a species character in *Adontomerus nesterovi*, and I did not include it in my analysis.)

PHYLOGENY . - In the working hypothesis I considered *Thaumatorymus* part of the Torymini clade and did not analyze it separately. After reexamination I decided that it should be coded as a distinct taxon. The synapomorphy that defines all Torymini is the forward projecting metapleuron (Figs. 10, 425). In *Thaumatorymus* the metapleuron appears slightly sinuate (Fig. 368) but not markedly so. Actually the posterior

margin of the mesepimeron is sinuate and is raised above the anterior margin of the metapleuron which lies partially hidden underneath. Superficially this mimics the condition found in Torymini, but in *Thaumatorymus* the anterior margin of the metapleuron is essentially straight. This condition is similar to that found in *Propachytomoides* (Podagrionini) (Fig. 280B), in which the lower margin of the mesepimeron is developed as a sinuate lamella that projects over the lower metapleuron, giving the appearance that the upper metapleuron projects slightly forward.

In the ending hypothesis (Fig. 38D) *Thaumatorymus* arises at node 13 with *Stenotorymus* and Monodontomerini (node 14), based on the hind-femoral tooth (node 11), the unemarginate metasomal terga (node 12), and the *Mono* wing venation (node 13), which changes to the autapomorphic state of *Thaumat* for *Thaumatorymus*. It is defined by this wing state and by the intermediate condition of the mesepimeral margin. Although the propodeum might be considered an autapomorphic state, because the spiracles are situated on projections, I coded it as *Nocarini* (i.e., primitive). In *Adontomerus nesterovi* the propodeal spiracles are elevated, and the condition appears to be a species-level character. I concluded that to be the case with *Thaumatorymus* as well.

As I discussed previously, *Stenotorymus* and *Thaumatorymus* do not appear to be closely related to each other or to the Monodontomerini. They are placed together based on the femur and metasomal terga but differ in many characters, as noted under *Stenotorymus*. Both taxa are somewhat autapomorphic in morphology and their placement, in my opinion, is open to speculation. I am not convinced that their hypothesized relationships are correct in my analysis, and for that reason I treat both as *incertae sedis*.

DISCUSSION . - This monotypic genus formed the basis of Bouček's proposal for the subfamily Thaumatoryminae (in Peck *et al.* 1964). I treated the taxonomy of the subfamily earlier in this paper (see p. 24). It would be possible to place *Thaumatorymus* as its own tribe, but this would require also placing *Stenotorymus* as a tribe. In the case of taxa involved with node 13, a multifurcation, the resolution is relatively poor, and I do not see the need to codify the unresolved relationships with nomenclature. The point is not that single taxa should be excluded from hierarchical nomenclature (*Chalcimerus*, Fig. 38F, node 24, is placed as a tribe) but that unresolved problems should be recognized, not necessarily formalized, until better understood. The relationship of *Thaumatorymus* remains a problem which needs better resolution.

### *Zaglyptonotus* Crawford

Figs. 37(E), 38(A), 350, 357-358, 362, 367, 370

*Zaglyptonotus* Crawford 1914:125-126. Type-species: *Zaglyptonotus schwarzi* Crawford (orig. design. and monotypic, USNM, examined).

*Perissocentroides* Blanchard 1938:44. *Nomen nudum*.

NUMBER OF SPECIES (catalog p. 290). - 3.

DISTRIBUTION . - NEARCTIC (USA: Mississippi, Alabama, but more widespread than current records indicate), NEOTROPICAL (Argentina, and see discussion below).

HOSTS. - Reared from Tephritidae (Diptera) associated with Asteraceae and from

Gelechiidae (Lepidoptera) and Curculionidae (Coleoptera).

KEYS TO SPECIES. - None.

RECOGNITION. - *Zaglyptonotus* is recognized by its greatly elongate, apically placed hind-tibial spurs (Figs. 357-358; note that the hind basitarsus is also elongate).

PHYLOGENY. -

Working Hypothesis (Fig. 37E): *Zaglyptonotus* is an autapomorphically unique, New World clade. In my working analysis this taxon arose at node 20 as the sister taxon to Monodontomerini. This was due, in part, to its "toothed" hind femur and the structure of the metasternal area. The hind-femoral condition was coded "?," because species varied from simple to angle to almost toothed (Figs. 357-358). Thus the inclusion of *Zaglyptonotus* among the "toothed" forms of torymids is a calculation based on other parsimonious character states. The hind femur is not toothed but is constructed about as in *Pseudotorymus* and *Torymoides* (Torymoidini), each of which vary similarly for this state. In addition, the metasternal area was coded as *Mono* but is actually autapomorphic in its design, being the only state in which the interior coxal carinae join medially and continue to the anterior margin of the plate (Fig. 367). At the time of coding I could not assess its structure with any certainty and even placed it, for a few analyses, as its own autapomorphic state. In my opinion this is now the correct interpretation.

*Zaglyptonotus* did not appear to belong with the clade at node 20 for the following reasons (mostly derived from further analysis after the working hypothesis was finished) The occipital carina is well developed with its dorsum closer to the posterior ocelli than to the occipital foramen (Fig. 362). In this respect it is more allied to members of nodes 16 and 17 than to either the basal nodes (e.g., 5, 8) in which the carina is essentially weakly developed or absent, or node 21 in which the carina is strong but much closer to the occipital foramen (Fig. 231). Alternatively, however, the wing venation of *Zaglyptonotus* is more nearly like that of most members of node 21 than other groups. In *Zaglyptonotus* the marginal vein is about 4.5 to 6.0 times the length of the stigmal vein which overlaps the range for node 21 at 3 to 6.5 times (excluding *Chrysochalcissa*). In wing venation, both *Zaglyptonotus* and node 21 are somewhat intermediate between the lower nodes such as 5 or 8 (marginal vein 2.0 to 4.5 times the stigmal vein) and nodes 16 or 17 (marginal vein from 6.5 to 11 or more times the stigmal vein). An additional reason to believe that *Zaglyptonotus* is not a member of node 20 is that metasomal tergum 2 is medially emarginate (all node 20 members except *Oopristus* have entire Mt2).

I recoded *Zaglyptonotus* for several states to determine their effect on the ending hypothesis. The occipital carina, hind femur, and metasomal terga were recoded in accordance with my reevaluation of these characters. I coded wing venation as a question mark because of its intermediate condition, and the metasternum similarly because of its putative autapomorphic state.

Ending Hypothesis (Fig. 38A): In this hypothesis, *Zaglyptonotus* arises at node 2 as part of the basal multifurcation. This node is defined by the change to a straight clypeus and the reversal to a pteromalid-type wing venation. Because *Zaglyptonotus* was coded as questionable for wing veins, and because the majority of its other character states are primitive, it is placed basally in this analysis as opposed to apically as in the working hypothesis. The genus is defined by the elongate hind-tibial spurs

(Figs. 357-358) (placed apically, a plesiomorphic state, see node 1) and by the propodeum, which is variable for the presence or absence of a median carina (state *One\**). The presence of elongated hind-tibial spurs alone does not offer much help in determining phylogenetic placement because such spurs are found in Monodontomerini (*Perissocentrus*) and Torymini (*Aloomba*). Additionally, variously modified hind-tibial spurs are found in other Torymini (*Platykula*) and Monodontomerini (*Monodontomerus*, *Rhynchotocida*) indicating that spurs are capable of independent modification. It might be noted that the hind basitarsus is elongate, but this appears to be directly related to the length of the hind-tibial spurs. It is probably a functional complex that allows for better movement of the hindtarsi relative to the spur. In *Perissocentrus*, although the spurs are equally as long as those found in *Zaglyptonotus*, they are some distance removed from the apex and the basitarsus is not unusually long. The *One\** state for propodeal structure indicates some variability for the propodeal carina, from completely plesiomorphic (*Nocarina*) to slightly apomorphic (*One*). This still does not help in placing the taxon phylogenetically.

Based on both the working and ending hypotheses, *Zaglyptonotus* appears problematic in establishment of relationships, and for that reason I treat it as an *incertae sedis*.

DISCUSSION. - The name *Perissocentroides* Blanchard was cited as a "MS" name by De Santis (1967:185). I have not seen the original publication, but I have seen examples of Blanchard's other works that appeared in "Boletín Informativo de la Dirección de Sanidad Vegetal" and they are simply mimeographed lists of species and their hosts. No descriptive material is given. In spite of the absence of a description and specimens, I am convinced this genus is the same as *Zaglyptonotus* for the following reasons: the formation of the name *Perissocentroides* refers to "resembling or having the form" (Brown 1978) of *Perissocentrus* ("-oides"); therefore, the specimens must have borne some resemblance to this genus but not enough to be placed in it; the generic name *Perissocentrus* was derived from the Greek for "large spur" (*-periosios* and *-centoro*) in reference to the enlarged hind-tibial spurs, so clearly the specimens must have looked like *Perissocentrus* in respect to the characteristically enlarged hind-tibial spurs; only one other genus, *Zaglyptonotus*, fits this description, and this genus also has greatly enlarged spurs.

In addition to the similarity of appearance, both species of "*Perissocentroides*" were reared from Bruchidae in Argentina, and there is at least one undescribed new species of *Zaglyptonotus* in the USNM reared from Bruchidae in Argentina. There is no doubt that the name *Perissocentroides* was used by Blanchard in the same meaning as *Zaglyptonotus*. Although a *nomen nudum* has no nomenclatural standing, it is preferable to know what concept it stands for and to be able to dismiss the name completely rather than place it in a list of *nomina nuda*.

Recently, I transferred the species *Perissocentrus bruchi* to *Zaglyptonotus* (Grissell 1992b). The single type specimen is presumably from the Neotropical Region but the label data is cryptic, reading only "from Bruchi P. C. 55/5." Neither Spanish, Portuguese, nor Italian speaking entomologists can make sense of this label, and I cannot locate this topotypic locality. I have, however, seen specimens from Argentina which are referable to this species. I have also seen material of this genus (some undescribed) from Brazil, Colombia, and Chile.

### ANNOTATED WORLD CATALOG OF TORYMINAE

The following section is an annotated catalog for the subfamily Toryminae as defined by this work and is complete through 1994. As explained earlier in the introduction (p. 3), this catalog is meant to be used in conjunction with the reclassification proposed in this paper, and it duplicates only the generic listings given in that section and does not repeat the overview of each genus given earlier. Therefore, information summarizing the genus as a whole, i.e., number of species, taxonomy, distribution, hosts, etc., will be found in the phylogeny section, whereas information concerning the species will be found in the catalog. Each generic heading in the catalog refers the reader back to the revision by page number.

All genera of the subfamily are included herein except *Torymus*, which is presented as a "preliminary" check-list. This was done because *Torymus* represents a large group of species names (483 including synonyms) and is somewhat of an unresolved nomenclatural quagmire. The inclusion of *Torymus* in my study was an unexpected result of the phylogenetic reorganization of the subfamily and doubled the size of my original project. For *Torymus* I give a list of current valid species names, synonyms, and zoogeographic regions as a simple beginning to a project that will involve much additional effort. This is especially true first in understanding the synonymies involved in the Palearctic fauna, and then in reconciling these names with the Nearctic fauna.

A nearly complete accounting of the world fauna of Torymidae (excluding the sycophagines now placed in Agaonidae, *sensu* Bouček 1988) may be approximated by adding the Megastigminae found in Milliron's (1949) catalog and in Bouček (1988).

The catalog format is fairly straightforward, but a few comments should be made as follows:

**Arrangement:** All taxa are alphabetic, first by genus then by species. In this manner, the catalog will not become so quickly obsolete with further changes in higher classification. The page number following the genus name refers the reader to the main systematic entry in the classification, and there will be found summary statements about the genus (i.e., number of species, distribution, hosts, keys, etc.). The original description and generic combination is cited below the species name, followed by synonyms, if any. Where I have been able to trace synonymies, I cite the authority for them. Little attempt has been made to rediscover the authorities for many of the synonyms that have existed since long before the turn of the century. Generic transfers are not given under synonymy, but are traced, where necessary, in the taxonomic discussion. There is no certainty that all species are assigned to their correct genera, because I have not seen every single species and determined its correct placement. This will be necessary, of course, to provide a completely accurate catalog, but it will be many years before anyone sees all of the species in this family

**Distribution:** Distribution follows the species name and is listed by zoogeographic region. After the region, the general distribution may be broadly summarized for a few common species, but for most I give the known distribution by country. In a few of the larger countries (e.g., Australia, Commonwealth of Independent States [CIS in catalog], India, Brazil, United States of America [USA in catalog]; Canada), the state or province is also given in parentheses. Authorities for distribution are cited in the distribution section, but if no authority is cited it may be assumed that the locali-

ty is associated with the type specimens in the original description, the citation for which is the author of the species. In many species the type locality remains the only known site of collection. In cases where synonyms are involved the type locality country is given for each. In almost all cases, the country of the type locality of each species (and its synonyms, if any) is listed first, followed by a semicolon. Distribution after the semicolon is followed by the author who first cited it. In the text, abbreviations are used for the compass directions north (n), south (s), east (e), and west (w).

**Type material:** For each species I summarize all type information and state the primary type depository from the original description (see methods section for acronyms of museums). If there is more recent information on the type, I cite the location and authority for that. Where I have seen the type, I state "examined" after the depository. If no type information or depository is stated in the original paper, I generally state this or place a question mark in front of a likely depository.

**Other:** Citations to references covering the topics of taxonomy, morphology, biology, and host are straightforward and are mentioned only if something is known. For example, I do not state "HOST. - Unknown." I have attempted to be as complete as possible in reviewing all literature pertaining to world species, but in the case of a very few, common species I have selected only the major papers to cite.

In the case of some common New World species, I *summarize* the information given in the catalogs of Peck (1963), Grissell (1979), and De Santis (1967, 1979, 1980, 1983, 1989). Peck's catalog was so complete that I soon gave up any attempt to review the hundreds of papers he cites but accept them at face value. Typically an early paper simply mentioned a locality or a host and then was cited many additional times without new information. Thus, many (if not most) papers add nothing to the knowledge of a taxon. Where a paper is fairly detailed (and useful), I cite it for the species being treated.

In the host-text for each species, I cite the host record as it appeared in the literature and in its currently valid form. Thus, for example, the host citation for *Pseudotoxymus medicaginis* reads "*Cecidomyia* (now = *Contarinia*) *loti*." If the difference in the two is simply gender agreement, I use the presumably correct endings without referring to the original spelling of the name. In each host record in the text, I indicate its family name, but not the author of the name or the order. Authors' names and orders are given in the host-parasite list which is arranged alphabetically first by order and then by family (see page 292). There is also an alphabetical index to all host names (see page 309). In both these lists, host names as originally cited in the literature and their currently recognized names are listed. In this manner, access to the older literature is maintained while still using the most current nomenclature.



***Adontomerus* Nikol'skaya (text, p. 76)**

*Adontomerus* Nikol'skaya 1955:339. Type-species: *Adontomerus eriogasteris* Nikol'skaya (orig. desig. and monotypic).

*Mellitotorymus* Steffan 1964:101-102. Type-species: *Mellitotorymus gregalis* Steffan (monotypic). [Synonymized earlier in the present work.]

***amygdali* (Bouček). PALEARCTIC: Jordan.**

*Plastotorymus amygdali* Bouček 1958:583-585 (Figs. A-C). Holotype ♀, Nablus-District, Jordan (NMP); 1 ♂ paratype same as holotype, 2 ♀ paratypes Tulharm (= Tulkarm), Jordan.

TAXONOMY. - Earlier in this paper I transferred this species to *Adontomerus* based upon its partially developed occipital carina, single anellus, and wing venation. Bouček (1976b) transferred it to *Antistrophoplex* which is now considered a synonym of *Microdontomerus*.

HOST. - The type series was reared from fallen fruit of *Prunus communis* (Rosaceae) infested with *Eurytoma amygdali* (Eurytomidae).

***crassipes* (Bouček). PALEARCTIC: Spain, Algeria.**

*Microdontomerus crassipes* Bouček 1982:188-189 (Figs. 8-9). Holotype ♀, nr. Totana, Spain (BMNH, examined); 2 ♂ paratypes, Calella d. Costa, Spain; 1 ♂ paratype, Balears Island, Spain; 1 ♂ paratype Oran, Algeria.

TAXONOMY. - Earlier in this paper I transferred this species to *Adontomerus* based upon its partially developed occipital carina, single anellus, and wing venation.

HOSTS. - A type male was reared from a gall on *Centaurea sphaerocephala* (Asteraceae) in Algeria. Askew and Nieves (1988) reported the species from *Isocolus tavaresi* (Cynipidae) on *Centaurea conifera* and from *Andricus kollari* (Cynipidae) on *Quercus petraea* and *Q. pubescens* (Fagaceae).

***eriogasteris* (Nicol'skaya). PALEARCTIC: CIS (Tadzhikistan).**

*Adontomerus eriogasteris* Nikol'skaya 1955:339-341. 62 ♀, 71 ♂, "Molotovabad region," Tadzhikistan (ZIAN, paratypes examined, in part).

HOSTS. - The type series was reared from cocoons of *Eriogaster henckei* (Lasiocampidae) on *Calligonum* sp. (Polygonaceae), and later Shchetkin (1965:111) briefly mentioned the same host for this species.

***gregalis* (Steffan). PALEARCTIC: Sardinia. New combination.**

*Mellitotorymus gregalis* Steffan 1964:102-104 (Figs. 1, 2). Holotype ♀, Macomer, Sardinia (MHNG); 3 ♀, 8 ♂ paratypes same as holotype (1 ♀ paratype, MNHN, examined).

TAXONOMY. - According to Besuchet (pers. comm.), the holotype and some paratypes are in MHNG.

HOST. - The type series was reared from *Anthidium* (now = *Paraanthidiellum*) *lituratum* (Megachilidae).

***impolitus* Askew and Nieves. PALEARCTIC: Spain.**

*Microdontomerus impolitus* Askew and Nieves 1988:356 (Figs. 1-4). Holotype ♀, Madrid, Spain (Museo Nacional de Ciencias Naturales, Madrid); 23 ♀, 15 ♂ paratypes same as holotype (some in BMNH, examined).

TAXONOMY. - Although this species was placed in *Microdontomerus* by Askew

and Nieves, I have seen a paratype from the British Museum, and this species should be transferred to *Adontomerus* as I explained earlier in this paper. It is similar to *Adontomerus crassipes* and *A. robustus*, both of which I also transferred from *Microdontomerus*.

HOSTS. - The type series was reared from galls of *Aulacidea tragopogonis* (Cynipidae).

**nesterovi** Zerova. PALEARCTIC: CIS (Turkmenistan).

*Adontomerus nesterovi* Zerova 1985:61-63. Holotype ♀, Badkhyzshy Preserve, Turkmenia (Schmalhausen Institute of Zoology, Academy of Science, Kiev); 16 ♀, 33 ♂ paratypes same data.

TAXONOMY. - Zerova and Romasenko (1986) key and figure this species in a paper on the parasites of megachilid bees in the Commonwealth of Independent States.

HOST. - The type series was reared from cocoons of *Paraanthidiellum lituratum* (Megachilidae).

**robustus** (Bouček). PALEARCTIC: Bulgaria, Yugoslavia; Hungary, Italy, and CIS (Ukraine: Bouček 1982).

*Paraholaspis robusta* Bouček 1970a:34-35. Holotype ♀, Sandanski, Bulgaria (Bouček collection); 1 ♀ paratype same as holotype; 2 ♀ paratypes, Stari Dojran, Yugoslavia; 1 ♀ paratype, Novi Dojran, Yugoslavia.

TAXONOMY. - Bouček (1982) transferred this species to *Microdontomerus*, but earlier in this paper I transferred it to *Adontomerus*. It is similar to *A. crassipes*.

**rosarum** Zerova and Seregina. See *Pseudotorymus rosarum* (Zerova and Seregina).

### *Allotorymus* Huber (text, p. 100)

*Allotorymus* Huber 1927:104. Type-species: *Syntomaspis splendens* Provancher (orig. desig. and monotypic).

**splendens** (Provancher). NEARCTIC: Canada (Ontario; British Columbia: Huber 1927); USA (Colorado: Huber 1927).

*Syntomaspis splendens* Provancher 1887:196-197. Lectotype ♀ [designated by Gahan and Rohwer 1918:197], Ottawa, Canada (CNC, confirmed by Sarazin 1987).

TAXONOMY. - Huber (1927:105-106) stated that only a female "type" specimen was found for this species and Burks (1963:1262) did not mention any other specimens (paralectotypes) in his study. Provancher (1887) cited a male in his description.

### *Aloomba* Girault (text, p. 115)

*Aloomba* Girault 1921/358:2. Type-species: *Aloomba calcaris* Girault (monotypic).

**calcaris** Girault. AUSTRALIAN: Australia (Queensland).

*Aloomba calcaris* Girault 1921/358:2. Holotype ♀, Mangrove, Buruda, Queensland, Australia (QM, examined).

TAXONOMY. - Dahms (1983) demonstrated that the single female specimen is the holotype.

***Amoturoides*** Girault (text, p. 124)

*Amoturoides* Girault 1932/439:2 (unpaged). Type-species: *Amoturoides breviscapus* Girault (monotypic).

***breviscapus*** Girault. AUSTRALIAN: Australia (Queensland; New South Wales: Bouček 1978). ORIENTAL: India (Karnataka: Bouček 1988).

*Amoturoides breviscapus* Girault 1932/439:2. Lectotype ♀ [designated by Bouček 1978:123], Townsville, Queensland, Australia (QM, examined).

TAXONOMY. - Although Bouček (1978) designated a lectotype for this species, it was presumably described from only 1 specimen based upon the original description. Dahms (1983) referred to the specimen as holotype. Bouček (1978) illustrated the hindleg (1978:122, Fig. 55).

HOST. - Reared from nest of *Ropalidia plebeiana* (Vespidae) in Australia, and from *Koralliomysia portentosa* (Tachinidae) in the nests of *R. plebeiana* in India (see Bouček 1988).

***pachymerus*** Bouček. AFROTROPICAL: Ghana.

*Amoturoides pachymerus* Bouček 1978:123-124, Fig. 56. Holotype ♀, Tafo, Ghana (BMNH); 6 ♀, 2 ♂ paratypes same as holotype.

HOST. - Reared from tettigoniid eggs.

***Anneckeida*** Bouček (text, p. 130)

*Anneckeida* Bouček 1978:111. Type-species: *Anneckeida watshami* Bouček (orig. desig.).

***angustifrons*** Bouček. ORIENTAL: Thailand.

*Anneckeida angustifrons* Bouček 1978:114-115 (Fig. 3). Holotype ♀, Chiangdao, Thailand (BPBM).

***laotica*** Bouček. ORIENTAL: Laos.

*Anneckeida laotica* Bouček 1978:115 (Fig. 38). Holotype ♀, Sedone Province, Pakse, Laos (BPBM); 1 ♀ paratype, Savannakhet, Laos.

***latifrons*** Bouček. ORIENTAL: Malaysia (Sabah).

*Anneckeida latifrons* Bouček 1978:115-116 (Figs. 39, 40). Holotype ♀, Sabah, Sandakan, North Borneo, Malaysia (BMNH, examined).

***orientalis*** Bouček. ORIENTAL: Malaysia (Peninsular Malaysia).

*Anneckeida orientalis* Bouček 1978:114 (Fig. 36). Holotype ♀, Gomak Forest Reserve, nr. Kuala Lumpur, Malaysia (BPBM).

**watshami** Bouček. AFROTROPICAL: Zimbabwe.

*Annekeida watshami* Bouček 1978:112-113 (Figs. 34, 35). Holotype ♀, Makumbi Mission, Rhodesia (BMNH, examined); 1 ♀ paratype same data; 2 ♀, 3 ♂ paratypes, Salisbury-Chishawasha, Rhodesia.

***Austorymus*** Bouček (text, p. 100)

*Austorymus* Bouček 1988:145-146. Type-species: *Austorymus nitidus* Bouček (orig. desig. and monotypic).

**nitidus** Bouček. AUSTRALIAN: Australia (Queensland, A.C.T.).

*Austorymus nitidus* Bouček 1988:146 (Fig. 209). Holotype ♀, Canberra, A.C.T., Australia (ANIC); 1 ♂ paratype, Siptons Flat, Queensland, Australia; 2 ♀ paratypes, nr. Brisbane, Queensland, Australia.

***Chalcimerus*** Steffan and Andriescu (text, p. 142)

*Chalcimerus* Steffan and Andriescu 1962:225-226. Type-species: *Chalcimerus borceai* Steffan and Andriescu (orig. desig. and monotypic).

**borceai** Steffan and Andriescu. PALEARCTIC: Romania, Greece (Crete); Israel (Bouček 1978), Spain (Askew and Nieves 1988).

*Chalcimerus borceai* Steffan and Andriescu 1962:226-228 (Figs. 1-9). Holotype ♀, Agigea-Dobrogea, Romania (MHN); 1 ♀ paratype, Bucharest, Romania; 1 ♀ paratype, Herakleion, Crete.

TAXONOMY. - Andriescu (1963) described the male. I have not seen the type but I examined a specimen sent to me by Steffan (MNHN) that is labeled "paratype." This specimen was a male, but because no males were described in the original description, it cannot be a paratype. The specimen has no locality data but may be from males described by Andriescu (1963) after the original description.

HOSTS. - The holotype was collected on *Euphorbia* sp. (Euphorbiaceae). Subsequent material was reared from *Aylax oraniensis* and *Aulacidea nigriceps* (Cynipidae) in seed capsules of *Papaver dubium* and *P. rhoeas* (Papaveraceae) (Andriescu 1971, Bouček 1978, Askew and Nieves 1988).

***Chrysochalcissa*** Girault (text, p. 128)

*Chrysochalcissa* Girault 1915/245:327. Type-species: *Chrysochalcissa olivacea* Girault (orig. desig. and monotypic).

**afra** Bouček. AFROTROPICAL: Uganda, Nigeria.

*Chrysochalcissa afra* Bouček 1978:110 (Figs. 25-27). Holotype ♀, Bugishu, Uganda (BMNH); 4 ♀, 4 ♂ paratypes same as holotype; 2 ♀ paratypes Province Awii, Nigeria; 2 ♀ paratypes Kampala, Uganda.

HOST. - The type series was reared from eggs of several unknown species of Coriidae.

**indica** Narendran. ORIENTAL: India (Tamil Nadu).

*Chrysochalcissa indica* Narendran 1994:55-56 (Figs. 60-62). Holotype ♀, Coimbatore, Tamil Nadu, India (UCK).

**olivacea** Girault. AUSTRALIAN: Australia (Queensland); Papua New Guinea (Bouček 1978, 1988). ORIENTAL: Indonesia (Bouček 1978).

*Chrysochalcissa olivacea* Girault 1915/245:327-328. Holotype (?syntype) ♂, nr. Cairns, Queensland, Australia (QM, examined).

TAXONOMY. - There is some confusion as to the number of specimens in the original type series. In my view Girault's description is based upon the single male he calls "type." Girault referred to another male from Gordonvale following the "type" section. In other species when he had more than 1 specimen in the type series, Girault referred to them as "types." Bouček (1978) referred to the Cairns specimen as holotype, but Dahms (1986:368) believed both males are syntypes.

HOST. - Known only from "bug eggs on tree trunk" (Bouček 1978).

**oviceps** Bouček. ORIENTAL: Burma, Malaysia

*Chrysochalcissa oviceps* Bouček 1978:109 (Figs. 31-33). Holotype ♀, Taungyi, Burma (BMNH); 2 ♀ paratypes same as holotype; 1 ♀ paratype, Selangor, Malaysia.

HOST. - The type material was reared from coreid eggs on *Euphorbia* (Euphorbiaceae).

**physomeri** Bouček. ORIENTAL: Malaysia; ?India (West Bengal: Bouček 1978).

*Chrysochalcissa physomeri* Bouček 1978:109-110 (Figs. 28-30). Holotype ♀, Selangor, Malaysia (BMNH); 5 ♀, 3 ♂ paratypes same as holotype.

TAXONOMY. - Bouček (1978) reported a single female of this species from India, but he was doubtful about its identity.

HOST. - The type series was reared from eggs of *Physomerus* sp. (Coreidae).

### ***Cryptopristus* Förster (text, p. 165)**

*Cryptopristus* Förster 1856:43. Type-species: *Torymus caliginosus* Walker (monotypic).

*Websterellus* Ashmead 1893a:164. Type-species: *Websterellus tritici* Ashmead (monotypic). [Synonymized by Gahan 1921:237.]

**caliginosus** (Walker). PALEARCTIC: France; Czechoslovakia (Peck *et al.* 1964), Great Britain and Germany (Dalla Torre 1898), CIS (Nikol'skaya and Zerova 1978).

*Torymus caliginosus* Walker 1833:118. 1 ♀, 1 ♂ syntypes, "south of France" (BMNH, examined).

TAXONOMY. - Walker (1871a, 1872a) illustrated the male of this species using illustrations published earlier by Haliday (1841). Distribution. - Although apparently widespread, the species is seldom collected.

**harrisii** (Fitch). NEARCTIC: USA (New York; widespread throughout eastern states: listed by Peck 1963, summarized by Grissell 1979).

*Torymus harrisii* Fitch 1862:838-839. 1 ♀, 1 ♂ syntypes, New York, USA (lost).

*Websterellus tritici* Ashmead 1893a:164 (Figs. II-1, 2; III-3, 4). Lectotype ♀, herein designated, Columbus, Ohio (USNM); 2 ♀, 3 ♂ paralectotypes same data as lectotype. [Synonymized by Gahan 1921:237.]

*Cryptopristus americanus* Girault 1917/316:8. Holotype ♀, Wellington, Kansas, USA (USNM, examined). [Synonymized by Gahan 1921:237.]

**TAXONOMY.** - Although Fitch's description of *harrisii* cited 1 male and 1 female specimen, no types are known to exist according to Gahan (1921), who saw the Fitch collection. The original description of *tritici* stated that Wooster was the type locality, but the specimens are labelled "Columbus."

**HOSTS.** - The types of *tritici* were reared from stems of wheat (*Triticum*) (Poaceae) and that of *americanus* from *Tetramesa* (Eurytomidae). The following eurytomid hosts have also been reported in the literature (see Peck 1963 for specific references): *Tetramesa grandis*, *T. hordei*, *T. tritici*, *T. vagicicola*.

### ***Diomorus* Walker (text, p. 101)**

*Diomorus* Walker 1834:159. Type-species: *Diomorus nobilis* Walker (= *Diomorus armatus* Boheman) (monotypic).

*Dihomerus* Schulz 1906:148. [Invalid emendation.]

***aiolomorphi* Kamijo. PALEARCTIC:** Japan. **ORIENTAL:** Taiwan.

*Diomorus aiolomorphi* Kamijo 1964:16-17 (Figs. 1-3). Holotype ♀, Kyoto, Japan (HU); 5 ♀, 9 ♂ paratypes, same as holotype; 6 ♀, 5 ♂, Kagawa, Shikoku, Japan; 1 ♀, Horisha, Formosa.

**TAXONOMY.** - Graham (1992b:113) stated that this species did not quite fit his definition of the genus. Its placement might also be questioned based upon the host record.

**HOST.** - The holotype was reared from *Aiolomorplus rhopaloides* (Eurytomidae) in *Phyllostachys* (Poaceae).

***ambositrae* Risbec. AFROTROPICAL:** Madagascar.

*Diomorus ambositrae* Risbec 1955:573. [Described in key.]

*Diomorus ambositrensis* Risbec 1956:185-186 (Fig. 7c). Holotype ♀, Ambositra, Madagascar (MNHN).

**TAXONOMY.** - Risbec (1955) published the name *ambositrae* and described it in a key, which apparently was published before the description of *ambositrensis* came out in 1956. There is no doubt that these two names are different spellings for the same species. The date for Risbec (1956) is based upon the date of issue published as February 1956 in the endpapers of volume 124 of the *Annales de Societe Entomologique du France*. *Zoological Records* also cites the date of publication as 1956. The date of issue for the *Bulletin de l'I.F.A.N.* is more problematic. From all indications it was published in 1955. It was listed in the *Zoological Record* for 1955 (although this is not always accurate), and the series appears to have been regularly published in the year it is marked (unlike the *Annales* which varied from year to year).

**armatus** (Boheman). PALEARCTIC: Sweden, England; Austria and Germany (Mayr 1874), Denmark (Hoffmeyer 1930d), European CIS (Nikol'skaya and Zerova 1978), Netherlands (Gijswijt 1974), Japan (Kamijo 1979). AUSTRALIAN: Papua New Guinea (Bouček 1988, ?introduced).

*Torymus armatus* Boheman 1834:336-338. ♀, ♂ syntypes (number unstated), Sweden (depository unknown).

*Diomorus nobilis* Walker 1834:159. ♀ syntype(s) (number unstated), Birchwood, England (BMNH). [Synonymized by ?Mayr 1874:75.]

TAXONOMY. - Mayr (1874:75) transferred *armatus* and apparently was the first to synonymize *nobilis*, although this is not clear from his paper.

HOSTS. - In England, Box (1920) reported the species from cocoons of *Crabro* (now = *Rhopalum clavipes* (Sphecidae). In the Netherlands, Gijswijt (1974) reported the species from *Crabro* ((now = *Crossocerus capitosus* (Sphecidae) in a *Fraxinus* branch (Oleaceae). Kamijo (1979) reported the following hosts in Japan: *Ceratina japonica* (Anthophoridae) in *Rubus* twigs (Rosaceae) and a pupa of Pemphredoninae (possibly *Stigmus*; Sphecidae) in *Sambucus* twigs (Caprifoliaceae).

**calcaratus** (Nees). PALEARCTIC: Italy, France; European CIS, Central Asia, and west Europe (Nikol'skaya and Zerova 1978), Romania (Andriescu 1971).

ORIENTAL: India (Kerala; Narendran 1994)

*Diplolepis calcarata* Spinola 1811:148. [*Nomen nudum*.]

*Torymus calcaratus* Nees 1834:69. ♂ (number unstated), locality unstated (depository unknown).

*Torymus igniventris* Costa 1858:17, 27. ♀ (number unstated), Italy (depository unknown). [Synonymized by Hoffmeyer 1930d:254.]

*Diomorus fertoni* Kieffer 1898:123-124. Holotype ♂, Ajaccio and Toulon, France (MNHN, according to Bouček 1994b). [Synonymized by Masi 1919:131]

*Diomorus violaceus* Kieffer 1898:123. ♀ (number unstated), Sicily, Italy (depository unknown). [Synonymy suggested by Masi 1919:131; synonymized by Hoffmeyer 1930d:254.]

*Diomorus orientalis* of Narendran and Sureshan 1989:51, nec Masi 1926. [Misidentification, see Narendran 1994:25.]

TAXONOMY. - The name *calcarata* was proposed in a list of species by Spinola (1811), but there was no description. Nees (1834) validated the name. Giraud (1866:489) described the female and redescribed the male. Mayr (1874:74) redescribed the species and discussed its hosts. Masi (1919:129-132) discussed its variation. Narendran (1994:25) redescribed the female based upon Indian material. Bouček (1994b:119) discussed *fertoni* and the status of its holotype.

HOSTS. - Giraud (1866:490) listed the host *Stigmus pendulus* (Sphecidae) (in *Rubus* stems, Rosaceae). Mayr (1874:74) reported the species from galls of *Cynips* (now = *Andricus kollari* (Cynipidae) from which also emerged *Omalus auratus* (Chrysididae) and *Cemomus unicolor* (now = *Pemphredon rufiger*; Sphecidae). These aculeate wasps are often found in abandoned galls. Kieffer (1898:123) also reared the type(s) of *violaceus* from cynipid galls (*Cynips argentea*, now = *Adleria quercustozae*) stating that the probable host was a crabronine wasp. The types of *fertoni* were collected in a habitat that also included a crabronid (Sphecidae) and an *Osmia* sp. (Megachilidae). Graham

(1992b) listed the following Sphecidae as hosts: *Stigmus solskyi*, *Ectemnius rubicola*, and *Pemphredon* sp.

**cupreus** (Spinola). PALEARCTIC: Italy, Austria; European CIS, Central Asia, West Europe (all from Nikol'skaya and Zerova 1978). ORIENTAL: Burma (Mani and Kaul 1972).

*Diplolepis cuprea* Spinola 1808:212-213 (Pl. III, Fig. XI). ♀ (number unstated), Italy (depository unknown).

*Diomorus kollari* Förster 1859:102-103. ♀ (number unstated), Austria (depository unknown). [Synonymized by Steffan 1952:293.]

TAXONOMY. - Giraud (1866:488) described the male and redescribed the female of *kollari*. Steffan (1952:293) transferred *cuprea* to *Diomorus*.

HOST. - The original hosts given by Spinola (not listed here) include 7 species of cynipid galls, all of which probably housed aculeate wasps. Giraud (1866) and Enslin (1922) reported as a host *Ectemnius rubicola* (as *Crabro* and *Solenius* respectively; Sphecidae) in stems of *Rubus* (Rosaceae). Mani and Kaul (1972) reported that the species was "widely distributed as parasite of *Osmia* sp. (Megachilidae) and Sphecidae." This species was reared from a *Crabro* sp. in the Commonwealth of Independent States (Nicol'skaya and Zerova 1978).

BIOLOGY. - Enslin (1922) illustrated and discussed the larval and pupal stages of this species (as *Diomorus kollari*).

**indicus** Ahmad. ORIENTAL: India (Bihar).

*Diomorus indicus* Ahmad 1946:6-7 (Fig. 3). Holotype ♀, Chapra, Bihar, India (IARI); ♂ paratype, Pusa, Bihar, India; "several" ♀, ♂ paratypes data unknown.

HOST. - A male specimen (from Pusa) was reared from "larva in *Poinciana pulcherima* stem" (Fabaceae).

**kononovae** Zerova and Seregina. PALEARCTIC: CIS (Kazakhstan).

*Diomorus kononovae* Zerova and Seregina 1991b:3-4 (Pl. 1, Fig. 5-8). Holotype ♀, Kokchetav, Kazakhstan, CIS (IZU).

**magnificus africanus** Risbec. AFROTROPICAL. Republic of South Africa; Zaire (Risbec 1958).

*Diomorus magnificus africanus* Risbec 1955:574. Holotype ♀, Bassouto (= Lesotho), South Africa (MNHN).

TAXONOMY. - Risbec (1958:103) described the male from the Belgian Congo (= Zaire).

**magnificus congoanus** Risbec. AFROTROPICAL: Republic of Congo.

*Diomorus magnificus congoanus* Risbec 1955:574. ♀ (number unstated), San Benito, Congo (MNHN).

**magnificus magnificus** Risbec. AFROTROPICAL: Madagascar.

*Diomorus magnificus* Risbec 1955:574. ♀ (number unstated), Madagascar (MNHN).

*Diomorus magnificus* Risbec 1956:183-185 (Figs. 7 a, b). 3 ♀ syntypes, Bekily, Madagascar (MNHN).



TAXONOMY. - This species was described twice. The 1955 date refers to a key, and 1956 refers to a description. The date of issue of Risbec (1956) is almost certainly correct based upon the date of issue published in the endpapers of volume 124 of *Annales de Societe Entomologique du France*. Zoological Records cites the date of publication as 1956 (see additional discussion under *Diomorus ambositrae*). It is obvious that Risbec expected the description of the species (i.e., 1956:183-185) to be published first, because that is where he described *magnificus* and referred to it as a new species. The "1955" paper is a key with a long, descriptive couplet with the name "*D. magnificus* Risbec type."

***magnificus vassei*** Risbec. AFROTROPICAL: Mozambique.

*Diomorus magnificus vassei* Risbec 1955:574. Holotype ♀, Province du Gorongosa (MNHN).

***mayri*** Cameron. NEOTROPICAL: Guatemala.

*Diomorus mayri* Cameron 1884:106 (Pl. 4, Figs. 17 a-b). ♀, ♂ syntypes (number unstated), San Geronimo, Guatemala (?BMNH).

HOST. - The types were reared from *Cynips guatemalensis* (Cynipidae).

***orientalis*** Masi. ORIENTAL: Taiwan, Philippine Islands; India (Himachal Pradesh, Uttar Pradesh: Mani and Kaul 1972; Kerala: Narendran and Sureshan 1989). AUSTRALIAN: Australia (Queensland: Bouček 1988), Papua New Guinea (Bouček 1988).

*Diomorus orientalis* Masi 1926a:2-4 (Figs. 2 a-d). 9 ♀, 3 ♂ syntypes, Taihorin and Kankau, Formosa (IPAL).

*Macrodomterus silvifilia* Girault 1927/415:555. 2 ♀ syntypes, Cuernos Mountains, Occidental Negros, Negros, Philippine Islands (QM, USNM). [Synonymized by Bouček 1988:147.]

TAXONOMY. - Baltazar (1966:136) transferred *silvifilia*. Bouček (1988:147) confirmed that one female syntype is deposited in QM. The other is in the USNM. A lectotype should be selected. He also confirmed the depository for *orientalis*. Narendran and Sureshan (1989:9-10) redescribed and illustrated (Figs. 19-20) the female of *orientalis*.

HOST. - Mani and Kaul (1972) reported a host "bred as parasite from larva of Sphegidae [sic]." Narendran (1994) gave as host *Hypsipyla robusta* (Pyraliidae).

***rufipes*** Cameron. NEOTROPICAL: Guatemala.

*Diomorus rufipes* Cameron 1884:105-106. ?♂ syntype(s) (number unstated), Cerro Zunil, Guatemala (?BMNH).

***spinosus*** Kamijo. PALEARCTIC: Japan.

*Diomorus spinosus* Kamijo 1979:5-6 (Fig. 5). Holotype ♀, Mitsumine, Honshu, Japan (HU); 2 ♀ paratypes, same as holotype; 1 ♀ paratype, Ohono, Fukui-ken, Japan.

***viridis*** (Provancher). NEARCTIC: Canada (Quebec).

*Haltichella viridis* Provancher 1887:192. Lectotype ♀ [designation by Gahan and Rohwer 1917:427], Hull, Quebec, Canada (LU).

TAXONOMY. - Burks (1963) confirmed the type depository and stated that this may be a synonym of *zabriskiei*.

***zabriskiei*** Cresson. NEARCTIC: USA (New York; widespread as listed by Peck 1963).

*Diomorus zabriskii* Cresson 1878:189. ♀ (number unstated), New Baltimore, New York, USA (?AMNH).

*Diomorus zabriskiei*: Peck 1951:527. [Valid emendation.]

HOSTS. - The type was reared from a nest of *Crabro* (now = *Ectemnius*) *stirpico-la* (Sphecidae). Other records include the sphecids: *Crossocerus fergusonii*, *C. insolens*, *Ectemnius spiniferus*, and *Euplilis arapaho* (now = *Rhopalum pedicellatum*) (all reported by Parker and Bohart 1966); *Ectemnius paucimaculatus* and *Euplilis* (now = *Rhopalum*) *rufigaster* (Krombein 1964); and *Ectemnius lapidarius*, and *Ceratina dupla* (Anthophoridae) (Peck 1951).

BIOLOGY. - Krombein (1964) reported some short biological notes on this species. He suggested that *D. zabriskiei* parasitized several cells in a succession of cells and that oviposition was probably through the wall of the plant stem (*Hibiscus*: Malvaceae) in which *Ectemnius paucimaculatus* nested.

### ***Ditropinotus*** Crawford (text, p. 94)

*Ditropinotus* Crawford 1907b:178. Type-species: *Ditropinotus aureoviridis* Crawford (orig. desig. and monotypic).

***aureoviridis*** Crawford. NEARCTIC: USA (Michigan, Maryland; widespread from coast to coast as listed by Peck 1963). PALEARCTIC: "Central Asia" (Nikol'skaya 1952).

*Ditropinotus aureoviridis* Crawford 1907b:178-179. Lectotype ♀, herein designated, Hudson, Michigan, USA; 7 ♀, 6 ♂ paralectotypes, same as lectotype.

*Ditropinotus flavicoxus* Gahan 1912:5-6. Lectotype ♀, herein designated, Prince Georges County, Maryland, USA (USNM); 5 ♀, 2 ♂ paralectotypes same data as lectotype. [Synonymized by Gahan 1921:236.]

TAXONOMY. - Crawford (1907b) did not list the number of specimens that he saw for *aureoviridis*. Only 14 are extant in the USNM. Gahan (1912) described the species *flavicoxus* from 14 specimens, only 8 of which are now housed in the USNM. Gahan (1934) redescribed the species at length, including illustrations of both female and male, and reviewed all known literature pertaining to the species and discussed its biology. Several dozen papers on all aspects of this species were listed by Peck (1963). Dowell and Gill (1989) consider the species non-native to California, suggesting that it probably occurs in that state as an introduction in 1966 from Oregon.

HOSTS. - The type series of *aureoviridis* was reared from *Tetramesa* (Eurytomidae) in wheat (Poaceae); that of *flavicoxus* was reared in a room with stored cereals. Known hosts include: Cecidomyiidae: *Mayetiola destructor* (though this may only be an "association"); Eurytomidae: *Eurytoma parva*, *Tetramesa linearis*, *T. elymicola*, *T. grandis*, *T. secale*, *T. tritici*, and *T. vaginicola*.

BIOLOGY. - Phillips and Poos (1921) provided an in-depth study including illustrations of adults, larvae, and pupae. It is a primary, solitary ectoparasitoid on *Tetramesa* spp. in grass stems and may also be a facultative secondary parasitoid on insects that attack these hosts. Gahan (1933) reviewed the biology.

**MORPHOLOGY** . - Hill and Pinckney (1940) illustrated the larval and pupal exuvium and described the meconium of this species. They also present a key to parasites of the hessian fly, based upon remains left in the host puparium.

**obscurus** Nikol'skaya. PALEARCTIC: "Central Asia."

*Ditropinotus obscurus* Nikol'skaya 1952:140 (Fig. 176).

**TAXONOMY** . - This species was described in a key, and no information was published with the description.

***Ecdamua* Walker (text, p. 101)**

*Ecdamua* Walker 1862:387-388. Type-species: *Ecdamua macrotelus* Walker (monotypic).

*Monodontomerella* Girault 1925/384:98. Type-species: *Monodontomerella longipilum* Girault (monotypic). [Synonymized by Bouček 1988:147.]

**cadenati** (Risbec). AFROTROPICAL. Senegal; Sierra Leone, Uganda, and Nigeria (Bouček 1976b).

*Pleisostigmus cadenati* Risbec 1951a:321-323 (Fig. 155). 2 ♀ syntypes, Dakar, Senegal (MNHN).

**TAXONOMY** . - Bouček (1976b:347) transferred the species. It is not clear from the discussion if he designated a lectotype. He stated that a paralectotype of *macrotelus* (from Sierra Leone) is actually *cadenati*.

**indica** Walker. ORIENTAL: India (Maharashtra, Bihar, Karnataka; Kerala: Narendran 1984a; Uttar Pradesh: Mani and Kaul 1972); Taiwan (Masi 1926a).

*Ecdamua indica* Walker 1871a:35. ♀ (number unstated), Bombay, India (BMNH).

*Ecdamua mirabilis* Masi 1926a:5-7 (Figs. 2 a-d). ♀ lectotype [designated by Narendran and Sureshan 1988:46], 1 ♂ paralectotype, Polisha, Formosa (IPAL). [Synonymized by Narendran and Sureshan 1988:46.]

*Amonodontomerus indicus* Ahmad 1946:5-6 (Fig. 1). Holotype ♀, Chapra, Bihar, India (IARI). [Synonymized by Farooqi 1985:262.]

*Syntomaspis bangalorensis* Mani and Kurian 1953:1-2 (Figs. 1-4). Holotype ♀, Bangalore, India (SJC). [Synonymized by Narendran 1994:20.]

**TAXONOMY** . - *Ecdamua indica* was redescribed and illustrated by Narendran (1984a:112-114, Pl. II, Figs. 1-2) and again by Mani (1989, as *mirabilis*).

**longipilum** (Girault). AUSTRALIAN: Australia (Queensland).

*Monodontomerella longipilum* Girault 1925/384:98. Lectotype ♀ [designated by Bouček 1988:147], Innisfail, Queensland, Australia (QM); 1 paralectotype ♀, Kuranda, Queensland, Australia.

**TAXONOMY** . - Dahms (1984:772) discussed the type specimens.

**macrotelus** Walker. AFROTROPICAL: Republic of South Africa; Uganda and Kenya to Cape Province: Bouček 1976b).

*Ecdamua macrotelus* Walker 1862:388. Lectotype ♀ [designated by Bouček 1976b:347], Port Natal [= Durban], Republic of South Africa (BMNH); paralectotype ♀ (= *Ecdamua cadenati*), Sierra Leone.

TAXONOMY. - Bouček (1976b) stated that the "paralectotype" from Sierra Leone was *cadenati*. Therefore, *macrotelus* is not known to occur in Sierra Leone even though it was described, in part, from there.

HOSTS. - Bouček (1976b) stated that this was likely to be a parasite of aculeate Hymenoptera nesting in burrows in dead wood.

***nambui* Kamijo. PALEARCTIC: Japan.**

*Ecdamua nambui* Kamijo 1979:1-4 (Figs. 1-4). Holotype ♀, Kodama, Honshu, Japan (HU); 3 ♀ paratypes, same as holotype; 1 ♀ paratype, Urayamaguchi, Honshu, Japan; 1 ♀ paratype, Okaribe, Hokkaido, Japan.

### ***Echthrodape* Burks (text, p. 166)**

*Echthrodape* Burks 1969:73-75. Type-species: *Echthrodape africana* Burks (orig. desig. and monotypic).

***africana* Burks. AFROTROPICAL: Kenya.**

*Echthrodape africana* Burks 1969b:75-76 (Figs. 1-5, 7-8). Holotype ♀, Nairobi, Kenya (USNM); 1 ♀, 4 ♂ paratypes, same data as holotype (USNM, BMNH).

TAXONOMY. - This species was transferred to the family Eucharitidae (Bouček 1988) and placed in its own subfamily. I previously discussed the taxonomy of this species and its placement in Torymidae (see p. 18).

MORPHOLOGY. - Michener (1969) illustrated and described the rather peculiar larva of this species as well as the pupa.

HOST. - This species was reared from nests of *Allodapula* sp. (now = *Braunsapis*) (Anthophoridae) as reported by Burks (1969b) and expounded upon by Michener (1969) who reported the following more detailed host records: *Braunsapis simplicipes*, *B. rolini*, *B. rufipes*.

BIOLOGY. - Larvae of *E. africana* are external feeders on pupae of *Braunsapis*. One parasite was seen per host. The bee is a progressive feeder which uses burrows in the pith of dead stems (but not cells). It moves its progeny about as necessary and does not distinguish between *E. africana* larvae or pupae and its own progeny.

***papuana* Bouček. AUSTRALIAN: Papua New Guinea.**

*Echthrodape papuana* Bouček 1988:517 (Figs. 916-918). Holotype ♀, Port Moresby, Konedobu, Papua New Guinea (BMNH).

### ***Eridontomerus* Crawford (text, p. 96)**

*Eridontomerus* Crawford 1907b:178, 179. Type-species: *Eridontomerus primus* Crawford (= *Eridontomerus isosomatis* Riley) (orig. desig. and monotypic).

*Dibaeomerus* Erdős 1954:150. Type-species: *Cryptopristus laticornis* Förster (orig. desig.). [Subgenus of *Eridontomerus*.]

**algericus** Erdős. PALEARCTIC: Algeria.

*Eridontomerus algericus* Erdős 1964:90-92 (Figs. 2A-B). Holotype ♀, Oran, Algeria ("Granger Collection" = MNHN).

TAXONOMY. - Szelenyi (1981) compared this species to *E. illiesi* Szelenyi.

**arrabonicus** Erdős. PALEARCTIC: Hungary; CIS (Ukraine, Moldavia: Zerova and Seregina 1991a).

*Eridontomerus arrabonicus* Erdős 1954:151, 157-158 (Figs. 1c-g). Lectotype ♀ [designated by Thuroczy 1992:130], Gyorszentivan, Hungary (HNHM, confirmed by Thuroczy 1992:130); 1 ♂ paralectotype same as lectotype.

TAXONOMY. - Erdős (1954) described this species in Hungarian and Latin with some differences in the descriptions (i.e., the Latin in not a direct translation, Steyskal, personal communication). He refers to a holotype but does not state the sex. Szelenyi (1981) compared this species to *illiesi* Szelenyi.

HOST. - The type series was reared from a host in stems of *Stipa ioannis* (Poaceae). Zerova and Seregina (1991a) reported the species from *Tetramesa schepigi* (Eurytomidae) in *Stipa pennata* (Poaceae) and from *Tetramesa* in *Stipa* spp.

**biroi** Ruschka. PALEARCTIC: Hungary.

*Eridontomerus biroi* Ruschka 1923:399. Holotype ♀, Budapest, Hungary (?NMW).

**bouceki** Zerova and Seregina. PALEARCTIC: CIS (Kazakhstan).

*Eridontomerus bouceki* Zerova and Seregina 1991a:142-143 (pl. 1, Figs. 1-4). Holotype ♀, Novo-Kazanka, Uralsk Province, CIS (IZU); 7 ♀, 1 ♂ paratypes same as holotype.

TAXONOMY. - The description was repeated in English by Zerova and Seregina (1992).

HOSTS. - The type series was reared from stems of *Elytrigia repens* and *Agropyron fragile* (Poaceae) containing larvae of *Tetramesa* (Eurytomidae).

**fulviventris** Erdős. PALEARCTIC: Hungary; CIS (Ukraine: Zerova and Seregina 1991a).

*Eridontomerus fulviventris* Erdős 1954:154-155, 160 (Fig. 4). Holotype ♀, Budapest, Hungary (HNHM, confirmed by Thuroczy 1992:131).

*Eridontomerus fulvipes* Erdős 1955:286 (Figs. 2 b-c). [*Lapsus for fulviventris.*]

TAXONOMY. - Erdős (1954) described this species in Hungarian and Latin with some differences in the descriptions (i.e., the Latin in not a direct translation, Steyskal, personal communication). Erdős (1955) described the male of *fulviventris* in a section clearly labeled as this species, but refers to it in the illustration as *fulvipes*. This is obviously a mistake.

HOST. - Zerova and Seregina (1991a) reported this species associated with *Centaurea* sp. (Compositiae).

**illiesi** Szelenyi 1981. PALEARCTIC: Germany.

*Eridontomerus illiesi* Szelenyi 1981:212-214 (Fig. 1c). Holotype ♀, Schlitz, Germany (HNHM, confirmed by Thuroczy 1992:132).

TAXONOMY. - Szelenyi (1981) compared this species to *E. arrabonicus* and *E. algericus*.

***isosomatis*** (Riley). NEARCTIC: USA (Tennessee, Indiana; transcontinental, see state list by Peck 1963). PALEARCTIC: Hungary (Erdős 1954), CIS (Ukraine, Kazakhstan, Tadzhikistan: Zerova and Seregina 1991a), Mongolia (Szelenyi 1973).

*Stictonotus isosomatis* Riley 1882:186. Lectotype ♀, herein designated, Andersonville, Tennessee, USA (USNM, examined); 2 ♂ paralectotypes same as ♀.

*Eridontomerus primus* Crawford 1907b:179. Lectotype ♀, herein designated, Richmond, Indiana, USA (USNM); 3 ♀, 4 ♂ paralectotypes, same as lectotype. [Synonymized by Gahan 1921:236.]

*Eridontomerus pruinosa* of Pettit and McDaniel 1920. [*Lapsus* for *primus*.]

TAXONOMY. - Gahan (1921) discussed the types of *S. isosomatis* but did not designate a lectotype. In early literature there was much confusion between *E. isosomatis* and other chalcidoids reared from grass stems. Erdős (1954) re-described *isosomatis*, based upon the first known Old World specimens from Hungary. He also illustrated the species (Erdős 1954: Figs. 3 a-d).

HOSTS. - Peck (1963) summarized all known Nearctic references pertaining to this species. Previously published Nearctic hosts include: Cecidomyiidae: *Mayetiola destructor*; Eurytomidae: *Tetramesa albomaculata*, *T. linearis*, *T. longula*, *T. festucae*, *T. grandis*, *T. hordei*, *T. maculata*, *T. secale*, *T. tritici*, *T. vaginicola*, and *T. websteri*. Palearctic hosts include: *Tetramesa aciculata* (Nikol'skaya and Zerova 1978), *Tetramesa* (as *Harmolita*) *stipae* in *Stipa capillata* (Graminae; Erdős 1954), and *Tetramesa* species associated with *Cynodon*, *Stipa*, and *Calamagrostis* (Poaceae) in the Commonwealth of Independent States (Zerova and Seregina 1991a).

BIOLOGY. - Phillips and Poos (1927) gave a complete account of this species including illustrations of the egg, 5 larval instars, and adults. The species is primarily ectoparasitic upon *Tetramesa* larvae in grass stems. Up to 5 eggs were observed on a single host, but only one *isosomatis* survived to pupate. Cannibalism was observed. According to Phillips and Poos (1927) the species "undoubtedly becomes secondary when the *Harmolita* [= *Tetramesa*] are heavily parasitized."

***laticornis*** (Förster). PALEARCTIC: Germany; Hungary (Erdős 1954), CIS (Ukraine, Moldavia: Zerova and Seregina 1991a).

*Cryptopristus laticornis* Förster 1859:103. Holotype ♂, Frankfurt, Germany (NMW, see Ruschka 1923).

TAXONOMY. - Ruschka (1923) first suggested that this species might be placed in *Eridontomerus*. Erdős (1954) re-described the male and described the female for the first time based upon specimens from Hungary. He also illustrated the species (1954, Figs. 3 e-j).

HOST. - Zerova and Seregina (1991a) reported this species associated with *Tetramesa* (Eurytomidae) in *Elytrigia* spp. (Poaceae).

***occultus*** Szelenyi. PALEARCTIC: Mongolia.

*Eridontomerus occultus* Szelenyi 1973:189-190. Holotype ♀, nr. Somon Daschineilen, Mongolia (HNHM, confirmed by Thuroczy 1992:132).

***rufipes*** Erdős. PALEARCTIC: Hungary; CIS (Moldavia, Kazakhstan, Tadzhikistan: Zerova and Seregina 1991a).

*Eridontomerus rufipes* Erdős 1954:153, 158-159 (Figs. 2 f-h). Lectotype ♀ [designated by Thuroczy 1992:132], Tomnpa, Hungary (HNHM, confirmed by Thuroczy 1992:132). 7 ♀ paralectotypes, all Hungary: 1, Ujpest; 1, Gyon; 2, Vac; 3, Tompa (HNHM).

HOST. - Zerova and Seregina (1991a) reported this species from *Agropyron* and *Triticum* (Poaceae).

***syrphi*** (Förster). PALEARCTIC: Germany; Hungary (Erdős 1954), CIS (Ukraine: Zerova and Seregina 1991a).

*Cryptopristus syrphi* Förster 1859:105-106. ♀, no other information, (?NMW, see Ruschka 1923).

TAXONOMY. - Ruschka (1923) was apparently the first to place *syrphi* in *Eridontomerus*. Erdős (1954) redescribed and illustrated (Figs. 1 a-b) the species based upon males and females collected in Hungary. No mention is made of Förster's types.

HOST. - Zerova and Seregina (1991a) reported the species reared from *Tetramesa* (Eurytomidae) associated with *Elymus* (Poaceae).

***unidentatus*** Szelenyi. PALEARCTIC: Mongolia.

*Eridontomerus unidentatus* Szelenyi 1973:188-189. Holotype ♀, 10 km n Ulan-Baator, Mongolia (HNHM, confirmed by Thuroczy 1992:133).

### ***Erimerus* Crawford (text, p. 92)**

*Erimerus* Crawford 1914:123. Type-species: *Torymus wickhami* Ashmead (orig. desig. and monotypic).

***wickhami*** (Ashmead). NEARCTIC: USA (Utah).

*Torymus wickhami* Ashmead 1904c:302. Lectotype ♀, herein designated, Milford, Utah, USA (USNM, examined); 1 paralectotype ♀ same as lectotype.

TAXONOMY. - Crawford (1914) described a new genus and subfamily for this species.

HOST. - The species was reared from galls on *Hilaria* (Poaceae). In all likelihood the host is *Tetramesa* (Eurytomidae), a common gall-former in grass stems.

### ***Exopristus* Ruschka (text, p. 167)**

*Exopristus* Ruschka 1923:400. Type-species: *Cryptopristus trigonomerus* Masi (monotypic).

*Exopristoides* Bouček 1982:184-186. Type-species: *Exopristoides dentatus* Bouček (orig. desig. and monotypic). [Synonymized earlier in the present work.]

***dentatus*** (Bouček). PALEARCTIC: Turkey, Tunisia. **New combination.**

*Exopristoides dentatus* Bouček 1982:186 (Figs. 3-6). Holotype ♀, Ankara, Turkey (BMNH, examined); 1 ♀ paratype same as holotype; 1 ♂ paratype, Gafsa, Tunisia.

***trigonomerus*** (Masi). PALEARCTIC: Italy; Romania (Andriescu 1971); Hungary (Erdős 1960), Mongolia (Szelenyi 1973), northern Africa (Bouček 1978).

*Cryptopristus trigonomerus* Masi 1916:74-75 (Figs. 1, 2). Lectotype ♀, herein designated, Is. Giglio, Italy (MCSN, examined); 5 ♀ paralectotypes, 2 ♂ paralectotypes same data as lectotype (MCSN, USNM, examined).

TAXONOMY. - Ruschka (1923) transferred the species from *Cryptopristus*.

HOSTS. - Associated with gall formers on *Papaver* sp. (Papaveraceae), *Verbascum* sp. (Scrophulariaceae), and *Centaurea* (Asteraceae) (Erdös 1960, Andriescu 1971). Sellenschlo (1984b) reported this species on flowers of *Cirsium vulgare* (Asteraceae) that were infested with tephritid and weevil larvae; however, no eggs of the parasite were found.

### *Glyphomerus* Förster (text, p. 169)

*Glyphomerus* Förster 1856:43-44. Type-species: *Ichneumon stigma* Fabricius (orig. desig.).

*Oligosthenus* Förster 1856:145. Unnecessary new name for *Glyphomerus* Förster, thought to be pre-occupied by *Glyptomerus* Müller (1856)(see Dalla Torre 1897:87).

***carinatus*** Nikol'skaya. PALEARCTIC: CIS ("Central Asia;" Tadzhikistan, Tashkentistan: Bouček 1970), Mongolia (Szelenyi 1973).

*Glyphomerus carinatus* Nikol'skaya 1952:142. [Only data given for type is "Central Asia." Type presumably in ZIAN, see Kamijo 1963.]

TAXONOMY. - Kamijo (1963) borrowed a paratype female of *carinatus* from Nikol'skaya and compared it (in a key) to *stigma*. Bouček (1970) also saw a paratype and stated that *signifer* Steffan is probably a synonym of this species.

HOST. - Bouček (1970) reported the species from *Diplolepis mayri* (Cynipidae).

***europaeus*** (Erdös). PALEARCTIC: Hungary (Erdös 1957, 1960), Yugoslavia, Czechoslovakia (Bouček 1970).

*Ditropinotus europaeus* Erdös 1957:348-349 (Fig. 2). Holotype ♂, Szod, Hungary (HNHM, confirmed by Thurocz 1992:131); 2 ♂ paratypes, Nagykovacsi, Hungary.

TAXONOMY. - Bouček (1970) discovered the female of this species, figured it, and transferred the species to *Glyphomerus*.

***signifer*** Steffan. PALEARCTIC: Austria.

*Glyphomerus signifer* Steffan 1962a:184-186 (Figs. 6-7). Holotype ♀, Austria (MNH); 3 ♀ paratypes, same as holotype.

TAXONOMY. - Bouček (1970) suggested that this name was a synonym of *carinatus* Nikol'skaya and that it was probably introduced into Austria from the Commonwealth of Independent States. He did not formally synonymize the two names.

HOST. - The type series was reared from *Diplolepis spinosissimae* (Cynipidae).

***stigma*** (Fabricius). NEARCTIC: Canada (Ontario); USA (transcontinental, see state list by Peck 1963). PALEARCTIC: Widespread in CIS (see Zerova and D'Yakonchuk 1976) and Western Europe; Japan (Kamijo 1963), Turkey (Doganlar 1984).

*Ichneumon stigma* Fabricius 1793:188. [Type data not given; 2 badly broken syntypes, ZMC, examined; other specimens in ?Bosc collection, Paris (Petersen, personal communication).]



*Oligosthenus bimaculatus* Provancher 1887:196. Lectotype ♀ [designated by Gahan and Rohwer 1918:104], Ottawa, Ontario (CNC, examined). [Synonymized by Peck 1951:530.]

TAXONOMY. - Förster (1856) transferred this species to his new genus *Glyphomerus*. Ashmead (1887) was the first to report *stigma* in the Nearctic, and he proposed *Monodontomerus viridaeneus* Provancher as a synonym, but *M. viridaeneus* is a synonym of *Monodontomerus dentipes* (see p. 211). Burks (1963) verified the synonymy of *bimaculatus*. Bouček (1970) gave characters to distinguish this species from *tibialis*, with which he stated it was often confused.

HOSTS. - All hosts are in the family Cynipidae. The types of *stigma* were reared from *Diplolepis rosae*. Kamijo (1963) reported the species from *Diplolepis fukudae* in Japan. Peck (1963) summarized the known Nearctic host information, which included *Diplolepis polita* and *D. rosae*. In addition to these hosts, Constantineau *et al.* (1956a) reported *Diplolepis centrifoliae*, *D. eglanteriae*, and *Xestophanes potentillae* in Romania. Zerova and D'Yakonchuk (1976) reported the species from *Diplolepis mayri* in the Commonwealth of Independent States and Nieves Aldrey (1983) reported the same host from Spain. A Nearctic record for Apidae (Patton 1897) most likely pertains to a species of *Monodontomerus* and should be dismissed.

MORPHOLOGY. - Tachikawa (1971) photo-illustrated the wing of this species. Sellenschlo (1984b, c) discussed and illustrated larval morphology and later (1989) discussed the cephalic gland structure of the larva.

***tibialis*** (Förster). PALEARCTIC: Germany; "widely distributed in central and southern Europe" (Bouček 1970) including, England, Yugoslavia, Czechoslovakia, CIS, Mongolia (Szelenyi 1973), Finland (Vikberg 1982), Spain (Nieves Aldrey and Chicote 1986).

*Oligosthenus tibialis* Förster 1859:107. Holotype ♂, nr. Aachen, Germany (?NMW).

TAXONOMY. - Hoffmeyer (1930d) transferred the species to *Glyphomerus*. Bouček (1970) discussed variation in the species.

HOSTS. - Bouček (1970) reported the species from *Tetramesa brevicornis* or *T. brevicollis* (Eurytomidae) in *Festuca ovina* (Poaceae). Vikberg (1982) reported it from galls of *Diastrophus mayri* (Cynipidae) on *Potentilla argentea* (Rosaceae) in Finland. Nieves Aldrey and Chicote (1986) reported the species from *Aulacidea subterminalis* (Cynipidae) on *Hieracium pilosella* (Asteraceae) in Spain.

### ***Gummilumpus*** Grissell (text, p. 135)

*Gummilumpus* Grissell 1995:135-137. Type-species: *Neopalachia bouceki* Grissell (orig. desig. and monotypic).

***bouceki*** (Grissell). NEOTROPICAL: Dominican Republic (amber). **New combination.**

*Neopalachia bouceki* Grissell 1980:255-257 (Figs. 8-11). Holotype ♀, northwest of Santiago, Dominican Republic (FSCA, examined).

TAXONOMY. - Earlier in this paper (p. 135) I described the new genus *Gummilumpus* and transferred *bouceki* to it.

***Idarnotorymus* Masi (text, p. 93)**

*Idarnotorymus* Masi 1916:59-60. Type-species: *Idarnotorymus pulcher* Masi (monotypic).

*Slanecia* Bouček 1955:307-309. Type-species: *Slanecia elongata* Bouček (orig. des). [Synonymized by Erdős 1963:283.]

***pulcher* Masi. PALEARCTIC:** Italy, Czechoslovakia; Hungary (Erdős 1960), Bulgaria (Pelov 1975), CIS (Uzbekistan: Bouček 1965).

*Idarnotorymus pulcher* Masi 1916:60-63 (Figs. 2, 3). Holotype ♀, Is. Giglio, Italy (MCSN, examined).

*Slanecia elongata* Bouček 1955:309-310 (Fig. 1). Holotype ♀ (No. 3046) and 1 ♂ allotype (No. 3047), Slanec, Eastern Slovakia (NMP). [Synonymized by Erdős 1963:283-285.]

TAXONOMY. - Pelov (1975:64-68) redescribed and illustrated (Figs. 1-9) this species.

HOST. - Reared from *Tetramesa* sp. (Eurytomidae) on *Bromus* sp. (Poaceae) in Bulgaria (Pelov 1975:63).

***Idiomacromerus* Crawford (text, p. 85)**

*Lochites* Förster 1856:43-44. Type-species: *Lochites papaveris* Förster (monotypic). [Preocc. by *Lochites* Gistel 1848 (Protozoa).]

*Idiomacromerus* Crawford 1914:124-125 [26 September 1914]. Type-species: *Idiomacromerus bimaculipennis* Crawford (orig. desig. and monotypic).

*Liodontomerus* Gahan 1914:159 [16 December 1914]. Type-species: *Liodontomerus perplexus* Gahan (orig. desig. and monotypic). [Synonymized with *Lochites* by Peck 1951:528; synonymized with *Idiomacromerus* earlier in the present work.]

*Lochitisa* Ghesquière 1946:368. [Objective replacement name for *Lochites* Förster nec Gistel.] [Synonymized with *Liodontomerus* by Peck 1951:528.]

*Lochimerus* Szelenyi 1957b:382-383. Type-species: *Liodontomerus balasi* Szelenyi (orig. desig. and monotypic). [Synonymized as subgenus of *Liodontomerus* by Bouček 1982:191.]

*Liotorymus* Steffan 1962b:31. Type-species: *Liotorymus regillus* Steffan (monotypic). [Synonymized as subgenus of *Liodontomerus* by Bouček 1982:191.]

*Liodontomerus* subgenus *Conolochites* Bouček 1982:189-190. Type-species: *Liodontomerus (Conolochites) nitens* Bouček (orig. desig. and monotypic).

Records of *Idiomacromerus* (as *Liodontomerus*) reared in association with bark beetles (e.g., *Ips*, *Dendroctonus*, *Polygraphus*) as reviewed by Bushing (1965) are certainly incorrect and are omitted here. These records most likely pertain to *Roptrocerus*, a pteromalid with an exerted ovipositor.

***africanus* (Erdős). PALEARCTIC:** Algeria. **New combination.**

*Liodontomerus africanus* Erdős 1964:92-93 (Figs. 2 D-E). Holotype ♀, Oran, Algeria (Granger Collection in MNHN).

***arcus* (Bouček). PALEARCTIC:** Bulgaria. **New combination.**

*Liodontomerus arcus* Bouček 1970a:36-37 (Fig. II-3). Holotype ♀, Sandanski, Bulgaria (NMP); 43 ♀, 8 ♂ paratypes same as holotype.

**augustini** (Erdős). PALEARCTIC: Algeria. **New combination.**

*Liodontomerus augustini* Erdős 1964:92 (Fig. 2C). 2 ♀ syntypes, Oran, Algeria ("Granger Collection" in MNHN and "Erdős Collection").

TAXONOMY. - Thuroczy (1992:130) could not find the types in HNHM (Erdős Collection).

**balasi** (Szelenyi). PALEARCTIC: Hungary. **New combination.**

*Liodontomerus balasi* Szelenyi 1957a:118-119 (1 Fig., unnumbered). Holotype ♀, Budapest, Hungary (HNHM, examined); 2 ♀ paratypes same as holotype.

TAXONOMY. - In the original description Szelenyi (1957a) stated that males were unknown, but that the "holotype and allotype" were placed in the Hungarian National Museum. The reference to an allotype was obviously a mistake.

HOSTS. - The type series was reared from galls of *Clinorrhyncha* (now = *Ozirhincus*) *anthemidis* (Cecidomyiidae). [Bouček (1977) listed *Clinorrhyncha artemidis* on *Artemisia* as a host; this apparently is an error for *anthemidis*, a species that does not occur on *Artemisia*; R. Gagne, person. comm.]

**bimaculipennis** Crawford. NEARCTIC: USA (Utah; Kansas: Bugbee 1941).

*Idiomacromerus bimaculipennis* Crawford 1914:124-125. Holotype ♀, American Fork Canyon, Utah, USA (USNM, examined).

HOST. - This species has been reared from *Eurytoma seminis* (Eurytomidae) from the seeds of *Rhus trilobata* (Anacardiaceae) (Bugbee 1941).

**budensis** (Erdős). PALEARCTIC: Hungary. **New combination.**

*Liodontomerus budensis* Erdős 1955:289 (Fig. 3). 1 ♀, 1 ♂ syntype, Budensibus, Hungary; 1 ♀ syntype, Sashegy, Hungary (Erdős Collection).

**carayoni** (Steffan). PALEARCTIC: France. **New combination.**

*Liodontomerus carayoni* Steffan 1986:274-276 (Figs. 1-6). Holotype ♀, Marseille, France (MNHN); 3 ♀, 2 ♂ paratypes same as holotype.

HOST. - Some members of the type series were collected at the seed heads of *Centaurea aspera* (Asteraceae), but no specific relationship was given.

**centaureae** (Askew and Nieves). PALEARCTIC: Spain. **New combination.**

*Liodontomerus centaureae* Askew and Nieves 1988:358-359 (Figs. 5-7). Holotype ♀, Guadalajara, Pozo de Guadalajara, Spain (MND); 3 ♀ paratypes, same as for holotype (BMNH).

HOST. - Type series reared from *Phanacis centaureae* (Cynipidae) from stems of *Centaurea scabiosa* (Asteraceae).

**curticaudatus** (Szelenyi). PALEARCTIC: Hungary. **New combination.**

*Liodontomerus curticaudatus* Szelenyi 1981:211-212 (Fig. 1b). Holotype ♀, Naszaly, Hungary (HNHM, confirmed by Thuroczy 1992:131).

**gallicola** (Risbec). AFROTROPICAL: Madagascar. **New combination.**

*Epicopterus gallicola* Risbec 1952:313-315. 2 ♂ syntypes, Route de Tamatave, Madagascar (MNHN).

TAXONOMY. - Although described as a pteromalid by Risbec (1952), Risbec (1956)

later transferred this species to the genus *Lochistica*, which was subsequently synonymized with *Liodontomerus*.

HOST. - The syntypes were reared from galls on racemes of Orchidaceae.

**gregarius** (Silvestri). PALEARCTIC: Italy. **New combination.**

*Lochites gregarius* Silvestri 1943:224-227 (Figs. XXII-XXIII). ♀, ♂ syntypes (number unstat- ed), Italy (depository unknown).

HOST. - The type series was reared from the stylopid *Mengenilla quaesita* (Menge- nillidae).

BIOLOGY. - Silvestri (1943) described and illustrated the egg and larval stages of this species and discussed the method of oviposition into the host. This species is a gregarious, internal parasite.

**insuetus** (Gahan). NEARCTIC: USA (Arizona; central states west, see list by Peck 1963). NEOTROPICAL: Mexico (De Santis 1979). PALEARCTIC: CIS (Uzbekistan: Nikol'skaya 1934), Romania (Perju 1961). **New combina- tion.**

*Liodontomerus insuetus* Gahan 1917:208-209. Lectotype ♀, herein designated, Tempe, Arizona, USA (USNM); 5 ♀ paralectotypes same as lectotype.

TAXONOMY. - Butler and Hansen (1958) discussed this species and its relationship to other *Liodontomerus*.

HOST. - The syntype series was reared from "*Bruchophagus funebris*" (Eurytomi- dae) in alfalfa seeds, but this record should actually be *B. roddi*. *Bruchopha- gus funebris* was the name used at that time for *Bruchophagus* associated with alfalfa seeds. Since that time it has been shown that only *B. roddi* is reared from alfalfa. Perju (1961) gave the host record of *B. gibbus* on *Trifolium* spp. The lepidopteran *Bucculatrix thurberiella* (Lyonetiidae) was reported by De Santis (1979), but this is certainly a misidentification.

**kaszabi** (Szelenyi). PALEARCTIC: Mongolia. **New combination.**

*Liodontomerus kaszabi* Szelenyi 1973:194-195 (Figs. 3b, 4b). Holotype ♀, 44 km. ssw Baru- un, Mongolia (HNHM, confirmed by Thuroczy 1992:132); 3 ♀ paratypes, same as holo- type.

**longfellowi** (Girault). NEARCTIC: USA (Minnesota, Idaho; transcontinental, see state list by Peck 1963). PALEARCTIC: CIS (Uzbekistan: Nikol'skaya 1934), Romania (Perju 1961). AUSTRALIAN: New Zealand (Dumbleton 1964).

*Idiomacromerus longfellowi* Girault 1917/317 (May 3):8. Lectotype ♀, herein designated, St. Paul, Minnesota, USA (USNM, examined); 1 paralectotype ♂ same as lectotype.

*Liodontomerus secundus* Gahan 1917 (May 26):208. Lectotype ♀, herein designated, Caldwell, Idaho, USA (USNM); 8 ♀, 1 ♂ syntypes, same data as lectotype. [Synonymized by Peck 1951:528.]

TAXONOMY. - Peck (1951) transferred *longfellowi* to *Liodontomerus*. Butler and Hansen (1958) discussed this species.

HOSTS. - Girault (1917/317) described *longfellowi* from syntypes reared from "clover seeds" infested with *Bruchophagus funebris* (now = *gibbus*) (Euryto- midae). Gahan (1917) described *Liodontomerus secundus* also reared from the same host (although the type of seed was not stated in the paper, see Urbahns

1919 who supplied the specimens to Gahan).

**BIOLOGY.** - Urbahns (1919) discussed the biology of this species and illustrated the larva and pupa. It is a parasite of the larvae of *Bruchophagus*.

*lysander* (Szelenyi). PALEARCTIC: Hungary. **New combination.**

*Liodontomerus lysander* Szelenyi 1959:143-145 (Figs. 1B, 1b). Holotype ♀, Agasegyhaza, Hungary (HNHM, confirmed by Thuroczy 1992:132); 3 ♀, 4 ♂ paratypes same as holotype.

**HOSTS.** - The type series was reared from seeds of *Medicago minima* infested by *Bruchophagus* sp. Additional rearings were reported from *Bruchophagus roddi* in *Medicago sativa* (Aeschlimann and Vitou 1989).

*mayri* (Wachtl). PALEARCTIC: Austria; Hungary (Szelenyi 1973). **New combination.**

*Lochites mayri* Wachtl 1883:9-10. ♀, ♂ syntypes (number unstated), Austria (depository unknown).

*Callimome scorzonerae* Giraud, in Giraud and Laboulbene 1877:425. [*Nomen nudum*.] ["Synonymized" by Hoffmeyer 1938a:28.]

**TAXONOMY.** - Hoffmeyer (1930a:28) examined 3 female specimens in the Giraud collection (now MNHN) that Giraud referred to as *scorzonerae* without publishing a description. Based upon this examination, he transferred *scorzonerae* to *Lochites* and synonymized it with *mayri* even though *nomen nuda* have no official standing. It is possible that Hoffmeyer's few descriptive words constitute a description and that he, not Giraud, should be credited with the name *scorzonerae*.

**HOSTS.** - Syntype specimens were reared from galls of *Aulax* (now = *Aulacidea*) *scorzonerae* (Cynipidae). Szelenyi (1973) reported the species from *Aulacidea* sp. on *Tragopogon orientalis* (Asteraceae) in Hungary.

*nitens* (Bouček). PALEARCTIC: Italy, Spain, Algeria, Jordan. **New combination.**

*Liodontomerus (Conolochites) nitens* Bouček 1982:190 (Figs. 10-12). Holotype ♀, Villasimius, Sardinia, Italy (BMNH); 1 ♀, 1 ♂ paratype same as holotype (examined); 1 ♂ paratype, nr. Madrid, Spain; 2 ♀ paratypes, Oran, Algeria (examined); 1 ♀ paratype nr. Romana, Jordan.

*obscuripennis* (Szelenyi). PALEARCTIC: Mongolia. **New combination.**

*Liodontomerus obscuripennis* Szelenyi 1973:195-196 (Figs. 3c, 4c). Holotype ♀, 20 km s Somon Delgerzagt, Mongolia (HNHM, confirmed by Thuroczy 1992:132); 1 ♂ paratype, 10 km s Somon Chongor, Mongolia; 1 ♂ paratype, 40 km from Somon Tamzagbulag, Mongolia.

*pannonicus* (Ruschka). PALEARCTIC: Hungary; Italy (Ferrière 1952), ?Turkey (Doganlar 1984, see host record, below). **New combination.**

*Lochites pannonicus* Ruschka 1923:406-407. 6 ♀ syntypes, Budapest, Hungary (NMW).

**TAXONOMY.** - Erdős (1956:187) described the first males, redescribed and illustrated the female (his Fig. 5), listed other distribution records in Hungary, and transferred the species to *Liodontomerus*. This species is "probably identical

with *L. perplexus*" according to Aeschlimann and Vitou (1989), but it was not clear if they meant that *pannonicus* was misidentified in their studies or that *pannonicus* was a synonym of *perplexus*.

HOST. - Aeschlimann and Vitou (1989) reported this species from *Bruchophagus roddi* in seeds of *Medicago sativa*. Doganlar (1984) stated that this species was reared from Tephritidae in the flowerheads of *Carduus* spp. and that this record was also reported by Nikol'skaya (1952). Nikol'skaya, however, reported no host for this species, and it is likely that some misidentification of the Turkish species has occurred.

*papaveris* (Förster). PALEARCTIC: Germany; Hungary (Szelenyi 1957a), Italy (Masi 1916), Spain (Nieves Aldrey and Chicote 1986), France (Askew and Nieves 1988). **New combination.**

*Lochites papaveris* Förster 1856:44, 120. ♀, ♂ syntypes (number unstated), Germany (?NMW, USNM, examined).

TAXONOMY. - Hoffmeyer (1930a:28) incorrectly stated that Giraud and Laboulbene (1877) were the authors of *papaveris*. This was a mistake, because they cited the species to Förster. Peck (1951) transferred the species to *Liodontomerus*. Szelenyi (1981) figured the wing (his Fig. 1a) of this species, based upon "an original specimen" that Förster identified as *papaveris*.

HOSTS. - The syntypes were reared from *Aulax rhoeadis* (now = *Aylax papaveris*) (Cynipidae) in seedpods of *Papaver rhoeas* (Papaveraceae). Hosts, all Cynipidae, were reported by Szelenyi (1957a) as *Xestophanes szepligetii* on *Potentilla* (Rosaceae) (in Hungary) and by Nieves Aldrey and Chicote (1986) and Askew and Nieves (1988) as *Aylax minor* galls in *Papaver* seed capsule (in France, Spain) and *Aylax oraniensis* (in Spain).

*perplexus* (Gahan). NEARCTIC: USA (Arizona; midwest to California, see list by Peck 1963); Canada (Alberta: Richards and Hanna 1982). NEOTROPICAL: Uruguay (De Santis 1979). PALEARCTIC: CIS (Uzbekistan: Nikol'skaya 1934; se Russia: Artokhin 1983); Yugoslavia (Spasic *et al.* 1988). **New combination.**

*Liodontomerus perplexus* Gahan 1914:159-160. Lectotype ♀, herein designated, Yuma, Arizona, USA (USNM, examined); 39 ♀, ♂ paralectotypes, same as lectotype.

TAXONOMY. - Burks (1958a) keyed and figured (Fig. 5) this species.

HOSTS. - The type series was reared from "alfalfa seed pods" infested with "*Bruchophagus funebris*" (Eurytomidae). We now know that only *B. roddi* attacks alfalfa seed, and this should be the correct host. The record given by Peck (1951, 1963) as *B. gibbus* is in error; he merely cited Gahan's record of *funebris*, which became a synonym of *gibbus*. Batiste (1967) reported *B. kolobovae* (now = *platypterus*) as a host. Richards and Hanna (1982) reported *Eurytoma onobrychidis* (Eurytomidae) in seed of *Onobrychis viciaefolia* (Fabaceae).

BIOLOGY. - Urbahns (1919) discussed the biology of this species and illustrated the larva and pupa. The material studied by him was used for the species description of Gahan (1914). The species is an external, solitary, primary or secondary parasitoid of its host larva or pupa in leguminous seeds. It is probable that Urbahns report on this biology is a composition of both *perplexus* and

*longfellowi* because he noted that *perplexus* adults varied and showed a “stigmatal cloud in the wing.” *Idiomacromerus perplexus* does not have a cloud, but *longfellowi* does. Thoenes and Moffett (1987) reported emergence from two year old seed that amounted to 7% of the first year emergence, and they also showed (Thoenes and Moffett 1990) that females outnumbered males by about 4 to 1. Artokhin (1983) reported two generations per year and 18% parasitism rate on *B. roddi*.

***regillus* (Steffan). PALEARCTIC: Italy. New combination.**

*Liotorymus regillus* Steffan 1962:31-33 (Figs. 4-9). Holotype ♀, Taormina, Sicily, Italy (IZ, examined).

TAXONOMY. - Viggiani (1966) redescribed the female and described the male for the first time.

HOST. - This species was reared from the gallery of *Tetramesa russoi* and *Tetramesa* sp. (Eurytomidae), both in the stems of *Ampelodesmus* (= *Ampelodesmos*) *tenax* (Poaceae) Viggiani (1966).

MORPHOLOGY. - Viggiani (1966) illustrated the female and male antenna and female forewing.

***splendidus* (Szelenyi). PALEARCTIC: Hungary. New combination.**

*Liodontomerus splendidus* Szelenyi 1957a:116-118 (1 Fig., unnumbered). Holotype ♀, Nagykovacs, Hungary (HNHM, confirmed by Thuroczky 1992:133); 6 paratypes same as holotype.

*Liodontomerus splendens*: Bouček 1982:191. [*Lapsus*.]

HOSTS. - Unknown, but associated with “*Caricetum humilis*” and “*Festucetum sulcatae*.” Neither of these hosts can be confirmed in any of the standard botanical listings (Wasshausen, pers. comm.), but it is possible that the former is *Carex humilis* and the later *Festuca rupicola rupicola* (of which *F. sulcata* is a synonym) (both Poaceae) (Kirkbride, pers. comm.).

***terebrator* (Masi). PALEARCTIC: Italy. New combination.**

*Lochites terebrator* Masi 1916:66. 2 ♀ syntypes, Isola del Giglio, Italy (?MCSN).

TAXONOMY. - Ruschka (1923) translated the original description into German.

***trachypogonis* (Risbec). AFROTROPICAL: Madagascar. New combination.**

*Lochistica trachypogonis* Risbec 1956:156-158 (Fig. 3). 2 ♀ syntypes, Tananarive, Madagascar (MNHN).

HOST. - The syntypes were reared from stem galls on *Trachypogon polymorphum* (Asteraceae).

***variegatus* (Szelenyi). PALEARCTIC: Hungary. New combination.**

*Liodontomerus variegatus* Szelenyi 1959:145-146 (Figs. 1A, 1a). Holotype ♀, Vac, Naszaly, (n of Budapest), Hungary (HNHM, confirmed by Thuroczky 1992:133).

HOSTS. - Unknown, but associated with “*Festucetum sulcatae*.” This host cannot be confirmed in any of the standard botanical listings (Wasshausen, pers. comm.), but it is possible that this name refers to *Festuca rupicola rupicola* (Poaceae) (of which *F. sulcata* is a synonym) (Kirkbride, pers. comm.).

***Lissotorymus* Kamijo (text, p. 101)**

*Lissotorymus* Kamijo 1961:66. Type-species: *Lissotorymus laevigatus* Kamijo (orig. desig. and monotypic).

***laevigatus* Kamijo. PALEARCTIC: Japan.**

*Lissotorymus laevigatus* Kamijo 1961:66-68 (Figs. 1-3). Holotype ♀, Aizankei, Hokkaido, Japan (HU); 2 ♀ paratypes, Sapporo, Japan; 1 ♀ paratype, Esashi; 1 ♂ paratype, Tomakomai, Japan; 1 ♀ paratype Hikosan, Japan.

HOST. - Kamijo (1979) reported the species from galls of *Neuroterus* sp. (Cynipidae) on *Quercus serrata* (Fagaceae).

***Mantiphaga* Ferrière (text, p. 150)**

*Mantiphaga* Ferrière 1955:212-213. Type-species: *Podagrion pseudocreobotrae* Risbec (orig. desig. and monotypic).

***apperti* (Risbec). AFROTROPICAL: Senegal.**

*Podagrion apperti* Risbec 1954b:1085-1086. 1 ♀, 1 ? syntypes, Bambey, Senegal (MNHN).

TAXONOMY. - The species was transferred by Ferrière (1955:213).

HOST. - The type series was reared from a mantid egg case.

***bekiliensis* (Risbec). AFROTROPICAL: Madagascar.**

*Podagrion bekiliensis* Risbec 1956:171-173 (Figs. 5b, e). 10 ♀ syntypes, Bekily, Madagascar (MNHN).

TAXONOMY. - Although Risbec described the male, he did not list it with any of the specimens examined. The species was transferred by Ferrière (1955:213).

***capensis* Ferrière. AFROTROPICAL: South Africa.**

*Mantiphaga capensis* Ferrière 1958:287-289 (Fig. IV). 6 ♀, 1 ♂ syntypes, Port Saint-John, Pondoland, South Africa (BMNH).

TAXONOMY. - It is not clear from the description whether a type is designated.

***gongylusae* (Risbec). AFROTROPICAL: Senegal.**

*Podagrion gongylusae* Risbec 1951a:311. 26 ♀, 18 ♂ syntypes, Bambey, Senegal; 7 ♀, Sangalkam, Senegal (all MNHN).

TAXONOMY. - The species was transferred by Ferrière (1955:213).

HOSTS. - The syntype series was reared from mantid egg cases of *Blepharodes* (now = *Phlaebarodes*) *sudanensis*, *Pseudocreobotra ocellata*, and *Gongylus* (now = *Empusa*) *guttula*.

***hoplocoryphae* (Risbec). AFROTROPICAL: Senegal.**

*Podagrion hoplocoryphae* Risbec 1951a:311-312. 4 ♂ syntypes, Bambey, Senegal (MNHN).

TAXONOMY. - The species was transferred by Ferrière (1955:213).

***pseudocreobotrae* (Risbec). AFROTROPICAL: Senegal.**

*Podagrion pseudocreobotrae* Risbec 1951a:309-311 (Figs. 151 a-d). 13 ♀, 2 ♂ syntypes, Bambey, Senegal (MNHN, examined).



**TAXONOMY.** - Although described from 15 specimens, as stated in the description, I examined a slide-cell mount of Risbec identified as the syntype series of this species. All of the label data was the same as presented in the original description. There are 2 males and 38 female specimens present. This problem will have to be resolved when someone revises the group. The species was transferred by Ferrière (1955:213) as the type species of his new genus *Mantiphaga*.  
**HOST.** - The type series was reared from an egg case of *Pseudocreobotra* (Mantidae).

***Mesodimorus* Strand (text, p. 102)**

*Mesodimorus* Strand 1911b:93-94. Type-species: *Mesodimorus compressus* Strand (orig. desig. and monotypic).

***compressus* Strand. ORIENTAL: Taiwan.**

*Mesodimorus compressus* Strand 1911b:94. Holotype ♂, Formosa (ZMB).

***Microdontomerus* Crawford (text, p. 78)**

*Microdontomerus* Crawford 1907b:179. Type-species: *Torymus anthonomi* Crawford (orig. desig. and monotypic).

*Antistrophoplex* Crawford 1914:125. Type-species: *Antistrophoplex bicoloripes* Crawford (orig. desig. and monotypic). [Synonymized by Grissell in Bouček 1982:189.]

*Paraholaspis* Masi 1921a:168-169. Type-species: *Paraholaspis cothurnata* Masi (monotypic) [= *annulata* Spinola]. [Synonymized with *Antistrophoplex* by Bouček 1976b:347.]

*Plastotrymus* Masi 1921b:235-236. [Unnecessary n. name for *Paraholaspis* Masi 1921a, believed preoccupied by *Paraholaspis* Berlese 1918:174 (Arachnida).]

Several species, as noted below, were transferred from *Microdontomerus* to other genera earlier in the revisionary part of this paper. Fritz *et al.* (1986) reported a species of *Microdontomerus* that was parasitic or hyperparasitic in the eggs of *Hemileuca oliviae* (Saturniidae) in Mexico and also was reared from pentatomid eggs. This is an undescribed species, based upon specimens sent to me by Fritz and now in the USNM. In *Microdontomerus* egg parasitism is known for *M. ovivorus* and possibly *M. senegalensis*.

***africanus* Crosby.** See *Pseudotorymus africanus* (Crosby).

***albipes* (Giraud).** PALEARCTIC: Algeria.

*Callimome albipes* Giraud 1869:482. ♀, ♂ syntypes (number unstated), Algeria, (depository unspecified, but NMW, in part, according to Ruschka 1923).

**TAXONOMY.** - Ruschka (1923) transferred this species to *Plastotorymus*. Dalla Torre (1898) assumed that the type locality of this species was in France, but Ruschka (1923:401) demonstrated that the region of Biskra, Algeria, was the correct location. Records of this species occurring in Hungary (Dalla Torre 1898) and Greece (Mayr 1874) are most likely the result of incorrect identifications according to Ruschka (1923:401).

HOST. - The type material was reared from *Oecocecis guyonella* (Gelechiidae) on *Limoniastrum guyoniamum* (Plumbaginaceae).

*amygdali* Bouček. See *Adontomerus amygdali* (Bouček).

***annulata*** (Spinola). PALEARCTIC: Libya, Italy (also Steffan 1962b); Turkey (Doganlar 1984).

*Diplolepis annulata* Spinola 1808:215. Neotype ♀, designated by Graham 1994b:99, Lago di Bolsena, Italy (BMNH).

*Paraholaspis cothurnata* Masi 1921a:169-171 (Figs. 1a-d). Lectotype ♀, herein designated, Bengasi, Libya (MCSN, examined); 1 ♂ paralectotype same as lectotype; 2 ♀ paralectotypes Pantano. [Synonymized by Graham 1994b:99.]

TAXONOMY. - The generic placement of this species was discussed at some length in the generic section (p. 80). Graham (1994b) discussed the taxonomy of *annulata* and its synonym.

HOST. - Steffan (1962b) recorded this species from *Olethreutes sororiana* (Tortricidae) in stems of *Phlomis fruticosa* (Lamiaceae).

***anthidii*** (Ashmead). NEARCTIC: USA (California).

*Torymus anthidii* Ashmead in Davidson 1896:26. Lectotype ♀, herein designated, Los Angeles County, California, USA (USNM, examined); ♀, ♂ paralectotypes same data as lectotype.

TAXONOMY. - Huber (1927) transferred *anthidii* from *Torymus*.

HOST. - The type series was reared from *Dianthidium pudicum consimile* (as *Anthidium consimile*) (Megachilidae).

***anthonomi*** (Crawford). NEARCTIC: USA (Texas; transcontinental: see state list in Peck 1963 and Grissell 1979).

*Torymus anthonomi* Crawford 1907a:133. Lectotype ♀, herein designated, Waco, Texas, USA (USNM); 1 ♂ paralectotype same as lectotype, 2 ♀ paralectotypes, Hallettsville, Texas.

TAXONOMY. - Crawford (1907b) transferred *anthonomi* to *Microdontomerus*.

HOSTS. - The original hosts were reported as *Brachytarsus* (now = *Trigonorhinus*) (Anthribidae) in heads of *Sideranthus rubiginosus* (= *Machaeranthera phyllocephalus*) (Asteraceae). This record, however, is undoubtedly wrong. The type material all bear labels reading "*Anthonomus grandis*" (Curculionidae) (see discussion in Turner *et al.* 1990). Peck (1963) gave a list of papers relating to hosts of this species. Hetz and Johnson (1988) added many new hosts, especially related to leguminous seedpods. Turner *et al.* (1990) summarized the known hosts and biology and added several new host records. The known host range includes Bruchidae: *Acanthscelides aureolus*, *A. compressicornis*, *A. desmanthi*, *A. derifieldi*, *A. horni*, *A. mixtus*, *A. pullus*, *Bruchus brachialis*, *B. pisorum*, *Sennius morosus*, *Stator limbatus*, *S. pruininu*; Curculionidae: *Anthonomus grandis*; Coleophoridae: *Coleophora malivorella*; Tortricidae: *Ancylys comptana*; Braconidae: *Bracon mellitor*. In addition, *M. anthonomi* has been reared from insects introduced into the Nearctic as biological control agents of various weeds, including the weevils *Rhinocyllus conicus* on thistle (*Carduus* spp.: Wilson and Andres 1986, Littlefield 1991), *Bangasternus orientalis* on yellow starthistle (*Centaurea solstitialis*), and *Microlarinus lareynii*

on puncturevine (*Tribulus terrestris*) and also the tephritid *Urophora affinis* on spotted knapweed (*Centaurea maculosa*) (see Turner *et al.* 1990; and Goeden and Ricker (1970), where the species was referred to as *Microdontomerus* sp.).

**BIOLOGY.** - Early work on the biology of this species was done by Pierce (1908a, 1908b, 1910) and Pierce *et al.* (1912, including figures of egg, pupa, and adult). These papers were reviewed by Turner *et al.* (1990). The species is a solitary ectoparasitoid and also functions as a facultative hyperparasitoid. It is considered to be a host-species generalist, but a microenvironment specialist on hosts enclosed in plant tissue. It is not too surprising, then, that it has adapted to hosts introduced from Europe into the United States for biological control.

***bicoloripes*** (Crawford). NEARCTIC: USA (Kansas; Iowa: Brandhorst 1964).

*Antistrophoplex bicoloripes* Crawford 1914:125. Lectotype female, herein designated, Garden City, Kansas, USA (USNM); 5 female paralectotypes same as lectotype.

**HOST.** - The type series was reared from *Antistrophus* galls (Cynipidae). Brandhorst (1964) reared the species from fusiform galls of *Antistrophus pisum* (= *lygodesmiaepisum*) (Cynipidae) on *Lygodesmia juncea* (Asteraceae) in Iowa.

*crassipes* Bouček. See *Adontomerus crassipes* (Bouček).

***fumipennis*** Crawford. NEARCTIC: USA (New Mexico; western states, see Grisell 1979).

*Microdontomerus fumipennis* Crawford 1916:141-142. Lectotype ♀, herein designated, Maxwell, New Mexico (USNM, examined); 7 ♀, 3 ♂ paralectotypes same as lectotype.

**HOSTS.** - The type series was reared from *Malacosoma fragile* (now = *californicum fragile*: Lasiocampidae). Knowlton and Allen (1937) reported it from *Choristoneura rosaceana* (Tortricidae). Niwa (1988) reared it from *Rhyacionia zozana* (Tortricidae). Peigler (1985) reported it from an Ophioninae cocoon (Ichneumonidae) within the cocoon of *Agapema galbina anona* (Saturniidae). Witter and Kulman (1972) summarized earlier literature resources for this species.

**BIOLOGY.** - Witter and Kulman (1972) treated *M. fumipennis* as an egg parasite based upon Langston (1957), but Langston does not mention anything about life stages attacked so the notion is invalid. Peigler (1985) demonstrated that this species is a hyperparasite, possibly in a facultative manner. Niwa (1988) reported *fumipennis* as an extremely rare parasite (ca. 4 specimens from 4500 host pupae) which attacked host pupae in the fall and emerged in the spring.

*impolitus* Askew and Nieves. See *Adontomerus impolitus* (Askew and Nieves).

*mesembryanthemumi* Cameron. See *Pseudotorymus mesembryanthemumi* (Cameron).

***ovivorus*** (Steffan). PALEARCTIC: Algeria.

*Paraholaspis ovivorus* Steffan 1967:150-152 (Figs. 1-3). Holotype ♀, nr. Beni-Abbes, Algeria (MHNG); 4 ♀ paratypes same as holotype.

**TAXONOMY.** - Besuchet (pers. comm.) confirms that the holotype is in MHNG.

Bouček (1982) transferred the species to *Microdontomerus*. I have examined specimens determined by Bouček as this species, and I agree with the generic placement.

HOST. - The type series was reared from eggs of *Sterspispis speciosa* (Buprestidae).

*robustus* Bouček. See *Adontomerus robustus* (Bouček).

*senegalensis* (Risbec). AFROTROPICAL: Senegal.

*Lioterphus senegalensis* Risbec 1951a:323-325 (Figs. 154c-f). 17 ♀, 10 ♂ syntypes, Bambey, Senegal (MNHN, examined).

TAXONOMY. - Bouček (1976b) transferred this species to *Antistrophoplex* (now = *Microdontomerus*) with the note that it was "relatively more different from the other species of that genus." I examined the syntype series, and the species is *Microdontomerus* as defined by wing venation, antenna, hind femur, propodeum, and lack of occipital carina. In overall coloration it appears much like *Torymus* or *Torymoides*, being metallic green with yellow legs (including coxae) and abdomen. It also bears an overall similarity to *Ditropinotus* because of an elongated body shape and abdomen, but this is superficial. Males have the forefemur enlarged, a character I have not noted in other torymids.

HOST. - The type series was reared from unknown mantid eggs. Later, Risbec (1954b:1084) reported this species from eggs of *Tarachodes saussurei* (Mantidae). Under the cover slip of one of the type slides of this species is a specimen of *Podagrion*, a known mantid egg parasite. It is possible that *M. senegalensis* is a parasite of this genus, rather than of the mantid eggs themselves.

### *Micropodagrion* Ferrière (text, p. 157)

*Micropodagrion* Ferrière 1955:210-211. Type-species: *Micropodagrion pauliani* Ferrière (orig. design. and monotypic).

*pauliani* Ferrière. AFROTROPICAL: Ivory Coast.

*Micropodagrion pauliani* Ferrière 1955:211-212 (Fig. 3). Holotype ♀, Reserve de Banco, Ivory Coast (MNHN, examined); 2 ♀, 1 ♂ paratypes same as holotype; 1 ♀ paratype, Danani, Ivory Coast.

TAXONOMY. - The specimen called "type" in Ferrière's paper is marked "lectotype" on the specimen. I do not know who designated this. Ferrière was relatively clear in referring to a "Type" in his paper.

HOSTS. - The type series was reared from egg cases of *Sphodromantis* sp. (at de Banco) and *Polyspilota aeruginosa* (at Danani) (Mantidae).

### *Monodontomerus* Westwood (text, p. 125)

*Monodontomerus* Westwood 1833:443. Type-species: *Monodontomerus obscurus* Westwood (monotypic).

*Paroligostenus* Cameron 1913a:94-95. Type-species: *Paroligostenus trichioptthalmus* Cameron (= *Monodontomerus obscurus* Westwood) (monotypic). [Synonymized by Waterston 1922:2.]

Some of the host records listed below for this genus are suspect and in need of confirmation. It is difficult to identify species of *Monodontomerus*, and some common species are apparently facultatively hyperparasitic. As a result, exact host relationships are not always known. Not listed below is a host record for the social wasp *Mischocyttarus flavitarsis* (Vespididae) in Arizona (Litte 1979), reported for an unknown species of *Monodontomerus*. The only torymid known from nests of a social vespid is *Monodontomerus aeneus* (given as *obsoletus* in Bouček 1977), reared from *Polistes* in Europe. There is a record for an unknown species of *Monodontomerus* reared from *Eutachyptera psidii* (Lasiocampidae) in Honduras (Passoa 1982).

***aeneus*** (Fonscolombe). NEARCTIC: This species was introduced into the Nearctic and first discovered in the 1930's (Johansen and Eves 1966), but it was misidentified as *M. obscurus*. Its correct identity as *M. obsoletus* was reported in 1989 (in Tepedino 1989; based upon my identification). The name has since been changed to *aeneus* by Graham (1992a). During revisionary work on *Monodontomerus*, I discovered that almost all previously published records for *M. obscurus* were wrong and that most should now refer to *M. aeneus*; both *aeneus* and *obscurus* are widespread, but all records need to be confirmed by reexamination of available specimens. PALEARCTIC: Reportedly widespread in western Europe (Nikol'skaya and Zerova 1978) and perhaps often confused with *M. obscurus*, which has the same distribution and general host range.

*Ichneumon obsoletus* Fabricius 1798:230. ?Holotype ♀, Italy (MNHN, Bosc Collection, examined), preocc. by *Ichneumon obsoletus* Gmelin in Linnaeus 1790:2687.

*Cinips aenea* Fonscolombe 1832:286. Neotype ♀ [data unstated] [designated by Graham 1992a:143], (OUM).

*Monodontomerus nitidus* Newport 1849a:25-26. [Description based upon immatures, depository unknown, specimens not located (see Graham 1992a:145)]. [Indirect indication of synonymy by Steffan 1952:291; synonymized by Graham 1992a:145.]

*Monodontomerus retusa*: Dalla Torre 1898:288. [*Nomen nudum*.]

*Monodontomerus vacillans* Förster 1860:106-107. 2 ♀ syntypes, Aachen, Germany (?NMW). [Apparently synonymized with *nitidus* by Dalla Torre 1898:288.]

*Monodontomerus punctatus* Thomson 1876:69. ♀ lectotype [designated by Graham 1992a:145], France (MZL). [Synonymized by Graham 1992a:143.]

TAXONOMY. - Graham 1992a:143 explained the homonymy problem for *obsoletus* and designated a neotype for *Cinips aenea*. Newport, in a series of papers read to the Linnean Society and Royal Entomological Society between 1849 and 1853, described *nitidus* first, based upon larvae (1849a:25-26; 1849b:35-37) and then adults (1852). His own view of the name for this species was confused: he first called it *nitidus* (1849a:25), then *obsoletus* (1849b:35), then *nitidus* again (1850b:42, 1852:67). Dalla Torre (1898) cited the name "*retusa* Newport, Proc. Linn. Soc. London II. 1850:70-71" as being without description. I have seen Newport's 1850 paper (see 1850a), and he did not call the species by any name at all. Therefore, Dalla Torre (1898) created a *nomen nudum* by assigning the name *retusa* to Newport's species. The synonymies of both *aeneus* and *obscurus* are complex and may possibly never be corrected,

especially because the species are difficult to distinguish from each other and are reared from the same sorts of hosts. Hansson (1991) reported a syntype of *M. punctatus* Thomson in the Museum of Zoology, Department of Entomology, Lund and stated that Graham (*in litt.* to Hansson) considered the Thomson name to be a homonym, preoccupied by *Cynips punctatus* Geoffroy 1785. Graham (1992a) altered this opinion and placed *punctata* Thomson as a synonym of *aeneus*. I place *punctatus* Geoffroy as an unplaced species at the end of *Monodontomerus*. Hohmann (1978) illustrated the adult of this species (as *obsoletus*), and Zerova and Romasenko (1986) key and figure this species (as *obsoletus*) in a paper on the parasites of megachilid bees in the Commonwealth of Independent States.

**HOSTS.** - There are a great number of hosts listed for this species (as *obsoletus*) in the Old World. Many of these records are Lepidoptera and sawflies, but I am convinced these are based upon misidentifications. For example, Liao *et al.* (1987) listed the species from the People's Republic of China with Tortricidae as the host, Mamedov (1988) listed it from the Commonwealth of Independent States as a parasite of brown-tail and gypsy moths, and Kolomiets *et al.* (1972) listed it for pine sawfly. I question the authenticity of all these records, the first of which is the only record of the species from PRC. This species is reliably parasitic upon aculeate Hymenoptera, and I present here only records that reflect this. The types of *nitidus* were reared from *Anthophora retusa* (Anthophoridae). In the Old World Dalla Torre (1898) listed *Ceratina callosa* (Anthophoridae) and *Osmia* (now = *Hoplitis*) *adunca* as hosts (Megachilidae). Steffan (1952) listed the following hosts: Vespidae: *Polistes gallicus* (now = *diminulus*), *Eumenes pomiformis*, *Odynerus* (now = *Ancistrocerus*) *parietum*; Megachilidae: *Chalicodoma muraria* (and *Stelis nasuta* a parasite of this host), *Osmia emarginata*, and *O. cornuta*. Hohmann (1978) listed *Chalicodoma sicula* (Megachilidae) as a host in Germany, and Bonelli and Campadelli (1990) listed *Chalcidodoma parietina* as a host in Sardinia. In Spain Vicens *et al.* (1993) reported *aeneus* (as *obsoletus*) from the following species of *Osmia* (Megachilidae): as common parasites of *rufa*, *cornigera*, and *fulviventris* and as occasional parasites of *coerulescens*, *latreillei*, *submicans*, and *tricornis*. Bosch *et al.* (1993) reported *aeneus* (as *obsoletus*) from the megachilids: *Anthidium florentinum*, *Hoplitis adunca*, *Megachile apicalis*, and *Metallinella brevicornis*. In the New World, verifiable records for this species include only *Megachile rotundata* (Megachilidae). Some specimens reported by Peck (1969; in CNC) as *M. obscurus* from this host are, in fact, specimens I have subsequently identified as *M. aeneus*.

**BIOLOGY.** - Newport (1849a, 1852, 1853) provided information and illustrations of the larvae, their digestive tract, and feeding habits. Johansen and Eves (1966) and Eves (1970) (and possibly Hobbs and Kronic 1971) published biological information on this species (as *obscurus*, reidentified by me, based upon Eves' specimens at WSU) as a parasite of *Megachile rotundata*. Females oviposited through the leaf-lined cell and/or cocoon of the host. Between 3 and 51 eggs were laid externally on the host. An average of 10 survived in one study (Johansen and Eves 1966), but Bonelli and Campadelli (1990) gave an average of 24 (range = 10 to 51 adults for 15 bee cells). All immature stages

of the host are vulnerable to attack but parasitization of early instars is rarely successful. Larvae are non-cannibalistic. The life cycle can be completed in about 20 days. Goodpasture (1975) detailed the mating behavior of *aeneus* (reported as *obscurus*, vouchers in UCD subsequently confirmed by me as *aeneus*). Tepedino (1988a) demonstrated that 7-12% of females mated before emergence from the host cocoon. He also showed (Tepedino 1988b) that females had an initial obligatory requirement for host cocoon and prepupal authenticity, but after 24 hours this would break down and females would oviposit into gelatin capsules holding bee prepupae or even agar replicates of bees. Females oviposited into fresh host prepupae or prepupae that were up to 16 days old. Tepedino (1988c) showed that superparasitism occurs but that rates go down as resident parasites become older. In Spain, rates of parasitism for *aeneus* (reported as *obsoletus*) on *Osmia cornuta* (Megachilidae) varied from 0.5% (Bosch 1994b) to 73% (Bosch 1994a). According to Bosch (1993) 53-76% of managed bee cocoons were parasitized when paper straws containing bee cells were extracted from their nesting blocks, but cells left in grooved boards were left untouched. In the Nearctic this parasite (as *obscurus*) reportedly replaced the native species *M. montivagus* in the mid-1960's as the most important parasite of the alfalfa leafcutting bee in North America, but then was itself replaced by a pteromalid in the mid 1970's (Eves 1982). A paper on control of an unknown species of *Monodontomerus* in Utah by Brindley (1976) undoubtedly refers to this species.

**MORPHOLOGY.** - Goodpasture illustrated the karyotype of *aeneus* (1975, reported as *obscurus* but confirmed as *aeneus* by me by subsequent examination of vouchers from which chromosome material was chosen). The chromosomes number 4 in males, 8 in females. Goodpasture (1975) illustrated male scapes, and Walther (1983) illustrated antennal sensillae of this species.

***aereus* Walker.** NEARCTIC: USA (introduced from Europe, now widespread in New England states). PALEARCTIC: Widespread in region (Bouček 1970b), Turkey (Doganlar 1982). ORIENTAL: India (Himachal Pradesh, Jammu-Kashmir; Dharmadhikari *et al.* 1985, Narendran 1994).

*Monodontomerus aereus* Walker 1834:158-159. ♀, number unknown (more than one measurement given), "near Paris", France (BMNH).

*Torymus anephelus* Ratzeburg 1844:177-178. ♀ (number unknown), "Reissig", Germany (type material presumed destroyed). [Synonymized by Mayr 1874:70.]

*Monodontomerus aereus viridanae* Mayr 1874:71. ♀, ♂ syntypes (number unstated) "Leopoldsbearge bei Wien", Austria (2 ♀, 2 ♂, ?syntypes, NMW, examined).

*Monodontomerus kashmiricus* Narendran 1994:37-38 (Figs. 32-34). ♀ holotype, Kashmir, Srinagar, India (UCK); 7 ♀, 1 ♂ paratypes same as holotype (dates variable). **New synonymy.**

**TAXONOMY.** - I do not know who proposed the synonymy of *M. a. viridanae*, but I agree with it. I have seen 2 females and 2 males of *M. a. viridanae* from NMW which agree with the type data but are not marked as types in the usual manner of Mayr specimens. They are identified as *viridanae* by Mayr and if not types at least they represent Mayr's concept of the species. These are extremely small specimens of *aereus* (females 1.8 mm plus ovipositor = 2.3 mm,

males 1.6 mm). I have seen topotypic specimens (3 females, 1 male, USNM) of *kashmiricus* with the same date and host data as given for 4 female and 1 male paratypes in the original description. There is no doubt that this is a synonym of the widespread species *aereus*.

**HOSTS.** - The syntype(s) of *anephelus* was reared from *Liparis chrysorrhoea* (now = *Euproctis chrysorrhoea*) (Lymantriidae), and those of *M. a. viridanae* from *Tortrix viridana* (Tortricidae). The Nearctic published records (from Peck 1963, Grissell 1979 except as noted) include as primary lepidopterous hosts: Tortricidae: *Archips argyrospila*, *Choristoneura rosaceana* (Brown *et al.* 1988); Lymantriidae: *Orgyia leucostigma*, *Lymantria* (as *Porthetria*) *dispar*, *Euproctis chrysorrhoea* (as *Nygmia phaeorrhoea*); Lasiocampidae: *Malacosoma americanum*. Secondary hosts through Lepidoptera include: Tachinidae: *Blepharipa scutellata* (now = *pratensis*), *Carcelia laxifrons*, *Compsilura concinnata*, *Exorista larvarum*, *Townsendiellomyia nidicola*; Braconidae: *Apanteles* (now = *Dolichogenidea*) *lacteicolor*, *A.* (now = *Cotesia*) *melanoscelus*, *Meteorus versicolor*; Ichneumonidae: *Iseropus coelebs*, *Phobocampe uncinata*. Old World hosts (summarized from the literature by Bouček and Sedivy (1954) and Bouček (1977) except as noted) include the primary lepidopterous hosts: Arctiidae: *Hyantria cunea*; Lasiocampidae: *Dendrolimus pini*, *Malacosoma franconica* (Doganlar 1984), *Malacosoma neustria*; Lymantriidae: *Leucoma salicis* (Doganlar 1984), *Lymantria dispar* (also as hyperparasite), *Lymantria monacha*, *Lymantria obfuscata* (Dharmadhikari *et al.* 1985), *Euproctis chrysorrhoea* (as *Nygmia phaeorrhoea*); Pieridae: *Aporia crataegi*, *Pieris rapae* (Constantineanu *et al.* 1956b); Yponomeutidae: *Yponomeuta malinella*, *Yponomeuta rorella* (as *Hyponomeuta rorellus*, Malyavin and Iskhakova 1971). Secondary hosts are: Chalcididae: *Brachymeria intermedia*; Ichneumonidae: *Coccygomimus* spp. (as *Pimpla*) (Dharmadhikari *et al.* 1985); Tachinidae (all from Doganlar 1982): *Alsomyia nidicola* (now = *Townsendiellomyia nidicola*), *Exorista segregata*, *Sturmia scutellata* (now = *Blepharipa pratensis*). The Symphyta *Trichiocampus ulmi* (Tenthredinidae; Haeselbarth 1983) and *Diprion pini* (Diprionidae; in Bouček 1977) are also listed as hosts for this species but might be questioned based upon the majority of host records. Constantineanu *et al.* (1956b) listed *Megachile muraria* (Megachilidae), but this is almost certainly an error based upon all other host records.

**BIOLOGY AND INTRODUCTION.** - This species was introduced into Massachusetts in 1906 (Muesebeck 1931) and is now widespread in the New England states. Howard and Fiske (1911) gave a detailed account of the introduction of this wasp to control gypsy moth and browntail moth. They illustrated the egg, larval, pupal, and adult stages. The parasite has one generation per year and is a primary parasite of the pupal stage of moths, but may also act as a secondary parasite of tachinids, sarcophagids, braconids, ichneumonids, and chalcidids in the primary host. Muesebeck (1931) summarized the known information up to the 30's; Clausen (1978) summarized additional information about the species.

***anthidiorum*** (Lucas). PALEARCTIC: Algeria.

*Diplolepis anthidiorum* Lucas 1849:319-320 (pl. 18, Fig. 6). "Paralectotype" ♀, Oran, Algeria (MNHH, examined, collected by H. Lucas, Algeria, marked "*Diplolepis anthidiorum* Lucas").



**TAXONOMY.** - Based upon the single measurement, it would appear that only one specimen was described. Steffan (1952:292) transferred the species to *Monodontomerus*. I do not know the reason for the "paralectotype" designation, or, in fact, if this is a type at all. There is no question that it represents Lucas' concept of the species he described.

**HOST.** - The original type(s) was reared from larva of *Anthidium* (now = *Rhodanthidium*) *sticticum* (Megachilidae).

**argentinus** Brèthes. NEOTROPICAL: Argentina; Colombia (Sakagami and Sturm 1965).

*Monodontomerus argentinus* Brèthes 1913:106-107. ♀ syntype(s), (number unknown), Rosario, Prov. Santa Fe, Argentina (MBR, examined in part).

**TAXONOMY.** - No specimens marked as "type" are located in Museo Bernardino Rivadavia, but one slide is deposited there labeled "*Monodontomerus argentinus* Brèthes" apparently in Brèthes' handwriting. Additional label data read "Rosario - Hübrich", which corresponds with the type locality and collector. This is obviously part of the syntype series. De Santis (1960) saw a female in MBR and stated it represented a valid species.

**HOSTS.** - Sakagami and Sturm (1965) reported this species attacking pupae in cells of *Euplusia longipennis* (now = *Eufriesea nigrescens*) (Apidae).

**bakeri** Gahan. NEARCTIC: USA (Colorado; new records: Utah, Idaho); Canada (Alberta, new record).

*Monodontomerus bakeri* Gahan 1941:475-476. Holotype ♀, "Amile Hill," Colorado, USA (USNM, examined).

*Monodontomerus emarginatus* Gahan 1941:476-477. Holotype ♀, Radium, Colorado, USA (USNM, examined). **New synonymy.**

**TAXONOMY.** - The original descriptions of *M. bakeri* and *M. emarginatus* were based upon one female for each species. They were distinguished from each other on the basis of color, ratio of malar distance to eye height, ratio of lateral ocellus to ocellular distance, and the condition of tergum 3. I have seen several hundred specimens of *M. bakeri*, and *M. emarginatus* falls well within the range of variation for color and ratios of malar and ocellular distances. The condition of tergum 3 in *M. emarginatus* I believe to be an aberration. Of the thousands of *Monodontomerus* specimens I have seen, none has shown any inclination towards emargination in tergum 3. The fact that *M. emarginatus* is otherwise identical to *M. bakeri*, itself a fairly unique species, and comes from the same state as *M. bakeri*, leads me to conclude that the type (and only) specimen of *M. emarginatus* is an aberrant specimen.

**HOSTS.** - The type of *emarginatus* was reared from a "leaf-cutter bee (?*Megachile*)" (Megachilidae) in an aspen log. Based upon my examination of specimens, the following are new host records (all from the cells of megachilid bees): *Megachile pugnata*, *M. relativa*, *Osmia coloradensis*, and *O. texana*.

**bensoni** E. Blanchard. *Nomen nudum*.

*Monodontomerus bensoni* E. Blanchard 1941a:16. Argentina.

**TAXONOMY.**-- This species was listed as a parasite of an unknown Lepidoptera on *Verbena* (Verbenaceae).

***canariensis*** Hedqvist. PALEARCTIC: Canary Islands.

*Monodontomerus canariensis* Hedqvist 1979:78 (Fig. 1). Holotype ♀, Tenerife, Canary Islands (University of La Laguna); 15 ♀, 13 ♂ paratypes same as holotype.

TAXONOMY. - The species is compared in detail to *M. strobili* by Hedqvist (1979).

HOST. - The type series was reared from *Dasychira fortunata* (Lymantriidae).

***clementi*** Grissell. NEARCTIC: USA (Wyoming).

*Monodontomerus clementi* Grissell 1973:235-236 (Figs. 1, 7, 11). Holotype ♀, Yellowstone National Park, Wyoming, USA (USNM, examined); 8 ♀, 3 ♂ paratypes same as holotype; 16 ♀, 7 ♂ paratypes same but laboratory cultured.

HOSTS. - The type series was reared from *Dianthidium heterulkei* (Megachilidae) in Wyoming and from *Megachile rotundata* (Megachilidae) in the laboratory.

BIOLOGY. - Clement (1976) found this species feeding on prepupae in cocoons of *D. heterulkei*. Goodpasture (1975) described the mating behavior, which is identical to that of *Monodontomerus montivagus*.

***cubensis*** Gahan. NEOTROPICAL: Cuba.

*Monodontomerus cubensis* Gahan 1941:466-467. Holotype ♀, Santiago de las Vegas, Cuba (USNM, examined); 6 ♀ paratypes same as holotype.

HOST. - The type series was reared from *Euproctis* (now = *Leucophobetron*) *argentiflua* (Limacodidae).

***dentipes*** (Dalman). NEARCTIC: USA (introduced from Europe, widespread in southeastern Canada and northeastern USA). PALEARCTIC: People's Republic of China (Liao *et al.* 1987), western Europe (Nikol'skaya and Zerova 1978).

*Torymus dentipes* Dalman 1820:173, 178 (Pl. 7, Figs. 23-25). ♀ syntype(s), Sweden (depository unknown, not in SMNH).

*Torymus dentipes* Boheman 1834:335-336. 2 ♀ syntypes, "Westgothiae and Oelandiae" (SMNH, examined).

*Monodontomerus viridaeneus* Provancher 1881:290-291. Lectotype ♀ [designated by Burks 1963:1259], Canada (LU). [Synonymized by Burks 1963:1259.]

TAXONOMY. - *Torymus dentipes* Dalman was described in a key and illustrated. *Torymus dentipes* Boheman was described by Boheman apparently based upon his belief that Dalman did not validly publish the name in 1820. In Boheman's introduction to his paper he stated that "I have decided to continue the description of those genera ... that were left unfinished by Dalman, maintaining the names that were chosen by him" (I thank Dr. Torbjorn Kronesdtedt, SMNH, for this translation). There are 2 syntypes of *dentipes* Boheman in SMNH, and these lend substance to the fact that Boheman considered his description as valid and not just a redescription of Dalman's species. Dalla Torre (1898) recognized this and cited the synonymy as given above. The report by Paik (1978) of *dentipes* in Korea almost certainly refers to *minor* based upon the host.

HOSTS. - Gahan (1941) suggested that many Old World host records for this species were in error, citing the fact that *dentipes* identified by Mayr (1874) actually was *virens* Thomson (now = *minor* Ratzeburg), a species with numerous

host records in several orders. Hoffmeyer (1930d), Steffan (1952), and Kamiyo (1963) also held this view. Zerova and Nikol'skaya (1978) rejected all host records for this species except for sawflies. European sawfly records include: Morawski (1934) who listed *Diprion similis* (Diprionidae), *Nematus* sp. (Tenthredinidae), and *Cimbex variabilis* (Cimbricidae) (he also included several Lepidoptera and the Braconidae that parasitized them, but I suggest that these pertain to *minor* or *aereus*); Györfi (1941) reported *Lophyrus* (now = *Gilpinia*) *abieticolor* (= *abieticola*) or *polytomus* (= *polytoma*) (Diprionidae) as hosts but did not know from which the parasite emerged. Peck (1963) listed numerous Nearctic host citations (subsequently dropped by Grissell 1979) for this species that include Lepidoptera, Diptera, and sawflies, but he questioned all except the sawflies. He suggested that at least several records referred to misidentifications of *Monodontomerus aereus*. In the Nearctic I can confirm no other records except sawflies based upon several hundred reared specimens in the USNM collection. Below I list only the known sawfly records. Recorded Nearctic hosts summarized by Grissell (1979) include Diprionidae: *Diprion similis*, *Neodiprion lecontei*, *N. excitans*, and *Gilpinia hercyniae*. Other reported Nearctic hosts missed by Grissell (1979) include *Gilpinia frutetorum* and *Neodiprion pinetum* (Raizenne 1957), *N. abietis* (as reported by Peck 1963), *N. sertifer* (Finlayson 1960), and *N. swaini* (Becker and Benjamin 1964). Raizenne (1957) and Finlayson (1963) gave comprehensive summaries of reared sawflies and their parasites in Canada.

**BIOLOGY.** - Morris *et al.* (1937) provided some information on biology and also cite a number of other papers. *Monodontomerus dentipes* is a gregarious, external parasitoid of the prepupal stage. Though they suggest that the species might also be a secondary parasitoid, they give no support for the statement. There appear to be 2 generations per year. Five or 6 eggs are laid per host. Adults emerge over an extended period, even from the same host pupa (in some cases adults emerge in the fall while sister larvae overwinter and emerge in the spring). Larvae take from 3 to 4 weeks to pupate and then take up to another 3 weeks to eclose. Drooz and Fedde (1972) demonstrated some degree of host specificity because *dentipes* would not attack cocoons of *Pristiphora erichsonii* (Tenthredinidae) but would attack *Neodiprion lecontei* and *N. excitans* (Diprionidae). Drooz *et al.* (1985) transferred the species from Wisconsin to North Carolina, where it effected a high level of control (up to 45%) on *Diprion similis*.

**MORPHOLOGY.** - Bucher (1948) provided an exhaustive study of the adult morphology of this species. Morris *et al.* (1937) illustrated the egg, mature larva, and pupa. Finlayson (1960) illustrated and described the spiracle and cephalic structures of final-instar larvae.

**INTRODUCTION.** - Although Burgess (1915) was the first to report this species in the New World, it is likely he actually reared *Monodontomerus aereus* instead, based upon the lepidopterous host records he cites. Weiss (1917) was the first to report this species in the New World (at least based upon the correct host association).

***dianthidii*** Gahan. NEARCTIC: USA (California; new record: Indiana).

*Monodontomerus dianthidii* Gahan 1941:464-465. Holotype ♀, Boulevard, California, USA (USNM, examined); 2 ♀, 10 ♂ paratypes same as holotype.

HOSTS. - The type series was reared from a resin nest of *Dianthidium* sp. (Megachilidae). A new record is a cell of *Parancistrocerus vagus* (Vespidae).

***indiscretus*** Gahan. NEARCTIC: USA (Maine; new records: Ohio, Missouri).

*Monodontomerus indiscretus* Gahan 1941:469-470. Holotype ♀, Bar Harbor, Maine, USA (USNM, examined); 3 ♀ paratypes same as holotype.

HOSTS. - The type series was reared from *Phyllotoma* (= *Heterarthrus*) *nemoratus* (Diprionidae), a European birch leaf-mining sawfly introduced into the United States.

***japonicus*** Ashmead. PALEARCTIC: Japan; "China" (Gahan 1941).

*Monodontomerus japonicus* Ashmead 1904b:83. 2 ♀, 1 ♂ syntypes, Nikko, Japan (USNM, examined).

TAXONOMY. - Ashmead (1904b) did not state the number of specimens in the type series. He described both females and males, and there are 2 females and 1 male in the USNM. I consider this to be the syntype series. Gahan (1941) re-described this species.

HOSTS. - Gahan (1941) reported *Diprion nipponicum* (Diprionidae) as a host for this species. *Monodontomerus japonicus* was released into Canada to control *Diprion* [= *Gilpinia*] *hercyniae* (Diprionidae), but it was never recovered (McGugan and Coppel 1962, Clausen *et al.* 1978). Iida (1932) reported the host *Osmia taurus* (Megachilidae) but this is undoubtedly an error for *Monodontomerus osmiae*.

***laricis*** Mayr. PALEARCTIC: Germany, Japan. **New status.**

*Monodontomerus dentipes laricis* Mayr 1874:72. ♀, ♂ syntypes (number unstated, but multiple specimens based upon description), Germany, (NMW, examined, in part).

*Monodontomerus virens laricis* Mayr: Dalla Torre 1898:290. [New combination.]

*Monodontomerus calcaratus* Kamijo 1963:95-96 (Fig. 8). Holotype ♀, Misawa, Japan (HU); 5 ♀, 4 ♂ paratypes, Bibai, Japan; 4 ♀, 1 ♂ paratypes, Nopporo, Japan; 1 ♀ paratype, Sapporo, Japan; 3 ♀ paratypes Ina, Japan; 1 ♀, 1 ♂ paratype Komaba, Japan; 1 ♀ paratype same as holotype. **New Synonymy.**

TAXONOMY. - Mayr (1874:72) proposed the new variety *laricis* for *dentipes*. Thomson (1876:100) stated that his name *virens* was the same as *dentipes* of Mayr (1874) *nec* Dalman (1820). Dalla Torre (1898:290) placed *laricis* as a variety of *virens* Thomson. Steffan (1952) synonymized *dentipes* of Mayr (*nec* Dalman) with *minor*, and also indirectly *virens* Thomson (1876:68). I have seen 4 females of *M. dentipes* "variety" *laricis* determined by Mayr from the NMW. Although none of these is labeled as type, one specimen has a small pink tag and Dr. Max Fischer implies that at least this one specimen can be called type. These specimens are neither *dentipes* nor *minor* but are a valid species, having Mt2 sculptured in the apical half and the hind-femoral tooth dull as for *dentipes* but removed from the apex as in *minor*. The tooth is not remarkably sharp as in *minor*. The species has the inner hind-tibial spur two-

thirds the length of the basitarsus, which is the same as found for *calcaratus* (in *minor* and *dentipes* the spur is one-half or less). Both *laricis* and *calcaratus* are the same in hind-femoral structure and the sculptured posterior half of Mt2. The rearing of *calcaratus* from *Ptycholomoides* also links the two, as this host is from the same tribe of larch-feeding tortricids that *laricis* parasitizes (see hosts, next).

**HOSTS.** - The original descriptor of *laricis* reported the series reared from *Tortrix* (Tortricidae) on larch (*Larix*: Pinaceae). According to Ron Hodges (pers. comm.) this record might apply to any of 9 genera of Archipini in the Tortricinae. The holotype of *calcaratus* was reared from *Dendrolimus spectabilis* (Lasiocampidae). Paratypes were reared from cocoon of Ichneumonidae, *Ptycholomoides aeriferana* (Tortricidae), *Ariola pulchra* (Noctuidae), and *Neodiprion sertifer* (Diprionidae).

***laticornis*** Grissell and Zerova. PALEARCTIC: CIS (Russia, Kazakhstan, Ukraine, Moldavia).

*Monodontomerus laticornis* Grissell and Zerova (in Zerova and Grissell) 1985:203-206 (Figs. 1-10). Holotype ♀, Mt. Yershov, Saratovskaya Prov., Russia, CIS (IZU, examined); 7 ♀, 1 ♂ paratypes Dubossary, Moldavia, CIS; 14 ♀, 3 ♂ paratypes, vic. Krasnodar, Russia, CIS; 7 ♀, 3 ♂ paratypes, Omsk Province, Russia, CIS; 11 ♀ paratypes, vic. Alma-Ata, Kazakhstan, CIS (IZU, USNM).

**TAXONOMY.** - Zerova and Romasenko (1986) key and figure this species in a paper on the parasites of megachilid bees in the Commonwealth of Independent States.

**HOSTS.** - The type series was reared from *Megachile rotundata* (Megachilidae). Zerova and Romasenko (1986) also reported this species from the megachilids *Megachile centuncularis* and *Anthidium florentinum*.

**BIOLOGY.** - This is a gregarious parasite within cocoons of the host.

***lymantriae*** Narendran. ORIENTAL: India (Assam).

*Monodontomerus lymantriae* Narendran 1994:39-40 (Figs. 35-37). Holotype ♀, Umaling, Assam, India (UCK); 5 ♀ paratypes same as holotype.

**HOSTS.** - The types were reared from *Lymantria* sp. and *Lymantria concolor* (Lymantriidae).

***mandibularis*** Gahan. NEARCTIC: USA (Missouri; widespread throughout eastern USA, see Peck 1963, Grissell 1979).

*Monodontomerus mandibularis* Gahan 1941:474-475. Holotype ♀, St. Louis, Missouri, USA (USNM, examined); 76 ♀, 19 ♂ paratypes from numerous localities.

**HOSTS.** - Most of the type series (as well as the holotype) was reared from *Anthophora abrupta* (Anthophoridae) from many localities (Illinois, Ohio, Washington, D.C., Maryland). Gahan (1941:474) also reported it from the anthophorids *Melitoma taurea* (Washington, D.C.) and *Anthophora bomboides bomboides* (New York). Rau (1947) listed *Osmia cordata* (Megachilidae).

**BIOLOGY.** - Rau (1947) published some preliminary information on the life history of this species, which he concluded had one or two generations per year. He believed the wasp to be a primary, gregarious parasitoid of its host.

**mexicanus** Gahan. NEOTROPICAL: Mexico (Hidalgo). NEARCTIC: (Records for California and Indiana (Grissell 1979) are in need of confirmation).

*Monodontomerus mexicanus* Gahan 1941:468-469. Holotype ♀, Jacala, Hidalgo, Mexico (USNM, examined); 19 ♀, 7 ♂ paratypes same as holotype.

HOSTS. - The type series was reared from cocoons of *Trypoxylon mexicanum* (Sphecidae). Rau (1947) listed *Passaloeucus* (= *Polemistus pusillus* (Sphecidae) and *Megachile peruviana* (Megachilidae) as hosts of this species (Mexico). Torchio (1974) listed *Ancyloscelis armata* (now = *apiformis*) (Anthophoridae) as a host (Mexico). A new host record is *Trypoxylon monteverde* (Sphecidae).

**minor** (Ratzeburg). NEARCTIC: USA (northern USA, coast to coast, see Grissell 1979). PALEARCTIC: Widespread in western Europe and CIS (Nikol'skaya and Zerova 1978), Japan (Kamijo 1963), Korea (Paik 1978), People's Republic of China (Liao *et al.* 1987). ORIENTAL: Pakistan (Narendran 1994).

*Torymus minor* Ratzeburg 1848:178. ♀, ♂ syntypes (number unstated), Germany (depository unknown, types probably destroyed).

*Monodontomerus interruptus* Förster 1860:133-135. ♀, ♂ syntypes (number unstated), Aachen, Germany (?NMW). [Synonymized by Steffan 1952:293.]

*Monodontomerus dentipes*: Mayr 1874:71-72 (nec Dalman, 1820). Misidentification.

*Monodontomerus virens* Thomson 1876:68. ♀ lectotype [validated by Hansson 1991:10], Germany (MZL). [Synonymized by Bouček 1954b:68.]

*Monodontomerus spectabilis* Matsumura 1926:33-34. "Numerous" ♀, ♂ syntypes, Chosen, Japan (?HU). [Synonymized by Kamijo 1963:96.]

*Monodontomerus dilinae* Palmen 1940:32-34 (Figs. 1-3). Holotype ♀, Porvoo [= Borga], Finland (University of Helsinki); 5 ♀, 1 ♂ paratypes same as holotype. [Synonymized by Steffan 1952:293.]

*Monodontomerus subobsoletus* Gahan 1941:480-482. Holotype ♀, Newark, Delaware (USNM, examined); 3 ♀ paratypes same as holotype; 10 ♀, 4 ♂ paratypes Brooklyn, New York; 2 ♀, 1 ♂ paratype Moorestown, New Jersey. [Synonymized by Steffan 1952:293.]

TAXONOMY. - Steffan (1952:293) transferred *minor* Ratzeburg to *Monodontomerus*. Thomson (1876:100) synonymized his name *virens* with *dentipes* Mayr (nec Dalman), but Bouček (1954b:68) synonymized *virens* with *minor*. Dalla Torre (1898:290) placed *M. dentipes laricis* Mayr (1874:72) as a variety of *virens* (and thus eventually *minor*), but I disagree with this placement for reasons stated under *M. laricis* (p. 213). Hansson confirmed the presence of the lectotype of *virens* in MZL. Ishii (1938) apparently incorrectly synonymized *M. spectabilis* under his concept of *dentipes*. This is not clearly stated in his paper. Kamijo (1963:96) placed *spectabilis* Matsumura and *dentipes* of Ishii (1938) (nec Dalman 1820) as a synonym of *minor*, and this is likely to be correct based upon the host records. The record of *dentipes* in Korea (Paik 1978), reared from the same host as *spectabilis*, most likely pertains to *minor*, and I include it here.

HOSTS. - The hosts of the type series of *subobsoletus* were *Malacosoma americanum* (Lasiocampidae), *Spilocryptus* (now = *Gambrus*) *extrematis* (Ichneumonidae) in cocoons of *Samia* (now = *Hyalophora*) *cecropia* (Saturniidae) and *Grapholita molesta* (Tortricidae). The host of the type series of *dilinae* was *Rogas* (now = *Aleiodes*) sp. (Braconidae) in *Dilina* (now = *Mimas*) *tiliae*

(Sphingidae). The types of *spectabilis* were reared from *Dendrolimus spectabilis* (Lasiocampidae). Nearctic records other than those listed for the type material above are (from Peck 1963 and Grissell 1979 unless otherwise noted): *Phryganidia californica* Diptidae, *Thyridopteryx ephemeraeformis* (Psychidae) and its parasite *Itopectis conquistator* (Ichneumonidae) (Kulman 1965b), the tortricids: *Archips argyrospila* (Legner 1962), *Rhyacionia buoliana* (Harman and Kulman 1962), and *Choristoneura fumiferana*, and as hyperparasites of Tachinidae in *Hyalophora cecropia* (Peigler 1985). The following host list is compiled from the Old World literature. These represent original reports for the host and subsequent records are not cited. The records are listed by country and author to make it easier for those who wish to check the original literature: FRANCE - Steffan 1952: *Diprion pini* (Diprionidae), *Apanteles* (now = *Cotesia*) *glomerata* (Braconidae) in *Pieris brassicae* (Pieridae), *Pimpla varicornis* (now = *Ephialtes compunctor*) Ichneumonidae in *Porthesia* (now = *Euproctis*) *chrysorrhea* (Lymantriidae), a tachinid in *Thaumetopoea processionea* (Thaumetopoeidae), *Spilocryptus* (now = *Agrotherutes*) *migrator* (Ichneumonidae) in *Trichiosoma tibialae* (Cimbicidae). CZECHOSLOVAKIA - Bouček 1954b: *Orgyia antiqua* (Lymantriidae), *Trichiosoma* sp. (Cimbicidae), *Hyphantria cunea* (Arctiidae); Capek 1963: *Chloephora bicolorana* (now = *prasinana*) (Noctuidae). NETHERLANDS - Gijswijt 1974: *Cryptus subquadratus* (Ichneumonidae) probably from *Trichiosoma lucorum* (Cimbicidae). JAPAN - Kamijo 1963: *Malacosoma neustria* (Lasiocampidae), *Dendrolimus spectabilis* (Lasiocampidae), *Lymantria dispar* (Lymantriidae), *Cryptothelea formosicola* (Psychidae), *Pieris rapae* (Pieridae), *Rhythmnotus* (now = *Hyposoter*) *takagii* (Ichneumonidae), and *Apanteles* (now = *Glyptapanteles*) *liparidis*; Nishida 1983: hyperparasite of *Eumeta japonica* and *Eumeta minuscula* (Psychidae); Iwata and Tachikawa 1966: *Coelichneumon* (now = *Ichneumon*) *garugawensis* (Ichneumonidae) and *Theronia atalantae gestator* (Ichneumonidae) in pupa of *Euproctis similis* (Lymantriidae). KOREA - Paik 1982: *Dendrolimus superans* (Lasiocampidae). PEOPLE'S REPUBLIC OF CHINA - Liao *et al.* 1987: parasite of sawflies. CIS - Nikol'skaya and Zerova 1978: parasite of sawflies; Kolomiets 1962: from *Zenillia libatrix* (Tachinidae) in pupa of *Euproctis similis* (Lymantriidae), *Masicera zimini* (now = *sphingivora*) (Tachinidae); Kulenova 1965: *Hyponomeuta* (now = *Yponomeuta*) *evonymella* (Yponomeutidae). PAKISTAN - Narendran 1994: in pupa of *Archips* sp. (Tortricidae) and *Gilpinia* sp. (Diprionidae).

BIOLOGY. - Based upon host records, *M. minor* appears to be a secondary parasite of Hymenoptera and Diptera through Lepidoptera and Symphyta. Iwata and Tachikawa (1966) and Kulman (1965b) present evidence of this from dissected material. Steffan (1952) stated that the species might also be a primary (as well as secondary) parasite. The number of *M. minor* feeding within a single lepidopterous pupa varies from 1 to 10 (Iwata and Tachikawa 1966, Kulman 1965a) with females predominating.

**montivagus** Ashmead. NEARCTIC/NEOTROPICAL: Widespread throughout southern Canada and USA, with a single record from southern Mexico (Guerrero) (based upon research in preparation).

*Monodontomerus montivagus* Ashmead 1890:25. Holotype ♀, West Cliff, Colorado, USA (USNM, examined).

*Monodontomerus americanus* Girault 1917/316:11. Holotype ♀, Los Angeles Co., California, USA (USNM, examined). [Synonymized by Gahan 1941:472.]

TAXONOMY. - Cockerell (1896) described the male of what he considered to be *montivagus*, but this is, in fact, the male of an undescribed species.

HOSTS. - This species is parasitic on a large number of solitary bee species. Based upon personal examination I can confirm the following hosts as valid (an \* indicates a new host record): Anthophoridae: *Xylocopa tabaniformis orpifex*; Megachilidae: *Anthidium* nest, \**Ashmediella californica*, \**Hoplitis anthocopoides* nest, *Megachile centuncularis*, \**M. relativa*, *M. rotundata*, *Osmia* sp. cocoon (in *Trypoxylon politum* nest), \**O. kincaidii*, \**O. lignaria*, \**O. ribifloris*, \**O. sarrafaelae*. Sphecidae: \**Sceliphron caementarium* nest, \**Trypargilum tridentatum*. Vespidae: \**Euodynerus* sp., \**Microdynerus bakerianus*. There are numerous literature records that I have not been able to confirm based upon examination of specimens. Because it is fairly difficult to identify *Monodontomerus*, these past records are in need of confirmation. All records except one are from aculeate Hymenoptera and these are likely to be correct. Hosts from the literature are: Anthophoridae: *Anthophora bombooides neomexicana*, *A. linsleyi*, ?*A. occidentalis*, ?*A. vallorum*, ?*Melissoides* sp.; Apidae: *Bombus morrisoni*; Megachilidae: *Anthidium emarginatum*, *Dianthidium pudicum pudicum*, *D. p. consimile*, *D. curvatum sayi*, *Osmia cordata*, *O. texana*; Mutillidae: *Sphaerophthalma unicolor*; Sphecidae: *Oryttus mirandus*, *Trypoxylon* sp. near *palliditarsus* (= *albitarse*); Vespidae: *Ancistrocerus tuberculocephalus*. An odd record for *Choristonerua fumiferana* (Tortricidae) seems highly unlikely and should be discarded until proven correct. Peck (1963) lists the references to all of these hosts, and his paper should be consulted for further information. No additional hosts were added in the 1979 Hymenoptera Catalog (Grissell 1979).

BIOLOGY. - This is a gregarious, external parasitoid of aculeate Hymenoptera. Although there are numerous references to this species in the literature (see Peck 1963), most of these are simply host records without biological data. A few papers cited by Peck are of interest and are cited below. Davidson (1893:153) stated that females of *M. montivagus* deposited 10 to 20 eggs in each cell of *Xylocopa tabaniformis orpifex* and that some broods were all males while others were all females. Hicks (1926:224) stated that *montivagus* was parasitic both on *Anthophora occidentalis* and its parasite *Oryttus mirandus* thus acting as a primary and secondary parasite. Mickel (1928:72-73) reared 415 specimens, of which 94% were females, from 21 cells of *Anthophora occidentalis*. He found no hyperparasitic relationship on the same bee host as reported by Hicks (1926). Linsley and MacSwain (1942:409-411) also reported *montivagus* as both a primary and a hyperparasite on *Anthophora linsleyi* and its mutillid parasite *Photopsis auraria* (now = *Sphaerophthalma unicolor*). These authors discussed the courtship behavior of *montivagus* and stated that its larvae fed on the prepupal stage of the bee. They stated that only one cell (of 9) had mixed sexes of this parasite, the others being either female (average 26 per cell) or male (average 40 per cell). In later rearings, however, MacSwain (1958:395)



found mixes of males and females in each of four cells of *A. occidentalis*. The sex ratio (males:females) varied from 1 to 12 to 1 to 30. Rau (1922) found a ratio of 1 to 6. Goodpasture (1975) described and illustrated the courtship behavior of *montivagus*. It is apparent from the literature and from reared specimens that *M. montivagus* is parasitic on bees, wasps, and their nest associates. New and old nests of aculeate Hymenoptera are complex sites of diverse taxa, behavioral types, and successional faunas. Therefore, our biological knowledge of *M. montivagus* is almost wholly inadequate.

**MORPHOLOGY.** - Goodpasture (1975) described and illustrated the male scapes and the haploid karyotype. This species has 6 chromosomes in males, 12 in females.

***noyesi*** Narendran. **ORIENTAL:** Pakistan.

*Monodontomerus noyesi* Narendran 1994:40-41 (Figs. 41-43). Holotype ♀, Swat, Gabral, Pakistan (BMNH, examined).

**TAXONOMY.** - Based upon a preponderance of characters, this species is nearly identical to *minor*. It differs slightly in sculpture of the frenal area and is reared from a different host. Additional specimens are needed to assess the stability of the character used to separate this species.

**HOSTS.** - The type specimen was reportedly reared from *Gilpinia hercyniae* (Diprionidae) (incorrectly cited as "*Gilponia hercymiae*"), but according to Dave Smith (pers. comm.), *hercyniae* has not been reported from Pakistan (or India) and is often misidentified for *G. polytoma* which is known from Pakistan. Therefore this latter name should be treated as the correct host.

***obscurus*** Westwood. **NEARCTIC:** During my revisionary work on *Monodontomerus* I discovered that almost all previous Nearctic records for this species are in error and refer to *M. aeneus*; *obscurus* is, in fact, widespread, but all records need to be confirmed by reexamination of available specimens; this species was undoubtedly introduced into the Nearctic along with its host the alfalfa leafcutting bee. **PALEARCTIC:** Reportedly widespread in western Europe (Nikol'skaya and Zerova 1978) and probably often confused with *M. aeneus* which appears to be sympatric. **ORIENTAL:** India (based upon *trichiophthalmus*).

*Callimome pubescens* Walker 1833 [January]:138-139. Lectotype ♀ [designated by Graham 1992a:145], (syntypes unknown) "nr London and south of France" (Holiday Collection, National Museum of Ireland, according to Graham 1992a:145).

*Monodontomerus obscurus* Westwood 1833 [June]:443 (Fig. 1). Lectotype ♀ [designated by Kerrich and Graham in Eady 1959: 270.], Warwick, England (OUM, examined); 5 ♀ paralecotypes (4 with no data, 1 not ledgible).

*Torymus dresdensis* Ratzeburg 1844a:177. ♀ (number unstated), Dresdan, Germany (type presumed destroyed). [Apparently synonymized by Dalla Torre 1898:289.]

*Torymus metallicus* Ratzeburg 1844a:177. ♀ (number unstated), Dresdan, Germany (type presumed destroyed) [Apparently synonymized by Dalla Torre 1898:289.]

*Monodontomerus anthophorae* Walker 1852 [January]:43. ♀, ♂ syntypes (number unstated), England (no longer extant). [Synonymized by Steffan 1952:290.]

*Monodontomerus intermedius* Förster 1860:106-107. ♀ syntypes, (number unstated), Frankfurt, Germany (?NMW). [Apparently synonymized by Dalla Torre 1898:289.]

*Paroligosthenus trichiophthalmus* Cameron 1913:95. Lectotype ♀ [publication of this lectotype designation cannot be confirmed], Dehra Dun, India (BMNH, examined). [Synonymized by Mani and Kaul 1972:316-317.]

*Monodontomerus masii* Hoffmeyer 1929:332-333 (Fig. 14). Holotype ♀, Skovfrokontoret, Denmark (Hoffmeyer Collection). [Synonymized by Hoffmeyer 1930d:258.]

*Monodontomerus obscurus steffani* Bouček 1954b:64-66 (Figs. 2-4). Holotype ♀, Velký Vřestov (Bohemia), Czechoslovakia (NMP); 2 ♀ paratypes, Libochovice, Czech.; 2 ♀ paratypes, Praha-Sarka, Czech.; 1 ♀ paratype, Střechov (Bohemia), Czech.; 1 ♀ paratype, Syrovín (Moravia), Czech.; 1 ♀ paratype, Bratislava, Czech.; 2 ♀ paratypes, Sturovo, Czech.; 3 ♀ paratypes, "Podolia Rossia," Czech. [Synonymized by Bouček 1965:544.]

I have cited Palearctic information below as correct, because I have not been able to check it. Most likely there may be some confusion with *aeneus*. Nearctic information is given with reservations as noted.

TAXONOMY. - Graham (1992a) noted that Walker (1834) synonymized his species *obscurus* with *pubescens* and stated that no one had taken note of it, i.e., the name *obscurus* was still being used. Dalla Torre (1898) and Eady (1959) both list the synonymy, but neither bothered to determine which name had priority. Graham (1992a:145) stated that *pubescens* Walker (1833) was published in January but did not give a month for *obscurus* Westwood (1833). In a letter to me in 1993, Graham explained that Westwood 1833 dates to June of that year, based upon publication dates given in part 12 of the London and Edinburgh Philosophical Magazine and Journal. Thus *pubescens* has priority. I agree with Graham (1992a), who follows the ICZN ruling (1985: Art. 23(b), 79(c)) that "existing usage be maintained until the case can be decided by the [International] Commission." Although Mani and Kaul (1972) synonymized *trichiophthalmus*, Farooqi (1986) and Narendran (1994) considered *obscurus* and *trichiophthalmus* distinct species. Narendran (1994), however, did not see the type of *obscurus*. I have seen the types of both species and consider them conspecific. The synonymy of *M. anthophorae* is open to some speculation, because according to Newport (1852:69, May or June) his new species *nitidus* (which he was describing as new, but for which he had already described the larvae and given a name in 1849a) was the same as that described by Walker (1852:43, January) and attributed to Newport as "*Monodontomerus Anthophorae*, Newp." However, Smith (1849) gave Walker some material reared from the same host, and it was not Newport's material that Walker examined. Because both *aeneus* (*obsoletus* in the sense of this discussion) and *obscurus* can be reared from the same host, the automatic synonymy of *anthophorae* with *nitidus* (= *aeneus*) proposed by Newport (1852) does not necessarily follow. I defer to Graham (1992a), who has studied this problem extensively and who agrees with Steffan's (1952) placement of *anthophorae* as a synonym of *obscurus* while placing *nitidus* as a synonym of *aeneus*. Because original specimens of neither *anthophorae* nor *nitidus* now appear to exist (Graham 1992a), the point is perhaps beyond additional concern. Zerova and Romasenko (1986) key and figure this species in a paper on the parasites of megachilid bees in the Commonwealth of Independent States.

HOSTS. - The host of *trichiophthalmus* was purported to be a "cocoon," possibly of a moth (this seems unlikely, however, based upon a preponderance of evidence

from other hosts). Old World host records include: France: Steffan (1952) - *Osmia rufa* and *O.* (now = *Hoplitis*) *adunca* (Megachilidae); Italy: Bouček (1970b) - *Eumenes pomiformis* (Vespidae), in nest of *Chalicodoma* sp. (Megachilidae), and in nest of *Sceliphron destillatorium* (Sphecidae); Denmark: Holm and Skou (1972) - *Megachile willughbiella* (Megachilidae); India: Sihag (1992) - *Xylocopa fenestrata* (Anthophoridae). Nearctic hosts confirmed by my study include: *Osmia cordata*, *O. lignaria*, and *Megachile rotundata* (all Megachilidae). It is likely that both *obscurus* and *aeneus* overlap in distribution and host range, but their misidentifications have been more common than not in the Nearctic. *Monodontomerus aeneus* is much more common than *M. obscurus*. I confirmed the correct identifications for *obscurus* from voucher specimens for the following literature citations: Rau 1937 (reported as *M. montivagus*); Krombein 1967; Peck 1969 (in part); Baker *et al.* 1985. Some other host records exist for this species (e.g., mantid egg cases and syrphid pupae as cited by Steffan 1952), but these seem rather unlikely (see also Bouček 1970b).

**BIOLOGY.** - As explained above, some published biological reports for this species in the Nearctic pertain to *Monodontomerus aeneus*. In Spain, *obscurus* is considered to be extremely destructive to the alfalfa leafcutting bee industry and chemical methods of control have been devised (Asensio 1982). Kronic and Radovic (1973) reported that *obscurus* can go through a number of generations without diapause and that diapause could be interrupted by keeping them for a time at 5°C. Prepupae of *obscurus* were killed at temperatures below 32°C and pupae below 25°C.

**MORPHOLOGY.** - Radu and Botoc (1968) illustrated female genitalia in detail. MacDonald and Kronic (1971) illustrated the somatic chromosomes for *obscurus*, which number 6 in males and 12 in females. (This differs from *aeneus* and thus strengthens the case for potential reproductive isolation between these two nearly identical species.) Baker *et al.* (1985) described and illustrated the last instar larva and pupa of this species (adult identity confirmed by examination of voucher specimens in North Carolina State University Insect Collection).

***osmiae* Kamiyo.** PALEARCTIC: Japan. CIS: (Russian Far East: Zerova and Romasenko 1986).

*Monodontomerus obscurus japonicus* Masi 1937:101-102. 2 syntype ♀, Kashii, Kyushu, Japan (Kyushu University).

*Monodontomerus osmiae* Kamiyo 1963:93-94 (Figs. 5-7). [New status and new name for *M. o. japonicus* Masi 1937, nec *M. japonicus* Ashmead 1904b.]

**TAXONOMY.** - Masi (1937) described the variety *M. o. japonicus*, based upon the two specimens cited. Kamiyo (1963) considered this subspecies to be a valid but undescribed species and described both females and males. Because Masi provided a description for the species, Kamiyo's description cannot be considered the original one. Kamiyo simply recognized the status of *o. japonicus* as a valid species and elevated it to species status, creating the homonymy with *M. japonicus* Ashmead. Therefore, Kamiyo's name is simply a new name not a valid species description. It is a much better description than Masi's. Zerova and Romasenko (1986) key and figure this species in a paper on the parasites of megachilid bees in the Commonwealth of Independent States.

HOSTS. - Kamijo reported the species from *Osmia taurus* and *O. excavata* in 1963 and *O. cornifrons* in 1965 (Megachilidae).

BIOLOGY. - Iwata and Tachikawa (1966) reported a preponderance of females for rearings of this species from *Osmia taurus*. From 61 cocoons emerged 87 males and 726 females. The number of parasites per host (counted for 4 cocoons only) varied from 14 to 26.

***primaveus*** Brues. PALEARCTIC: Baltic amber.

*Monodontomerus primaveus* Brues 1923:345-346. Holotype ♀, "baltic amber" (University Museum, Königsberg).

***rasputin*** Fernando. ORIENTAL: Sri Lanka.

*Monodontomerus rasputin* Fernando 1958:91 (Fig. 29). 1 ♀, 1 ♂ syntypes, Marawila, Sri Lanka (University of Ceylon).

***rugulosus*** Thomson. PALEARCTIC: Sweden, France; Austria (Bouček 1965), England (Bouček and Graham 1978a), CIS: (southern CIS and Caucasus: Zerova and Romasenko 1986).

*Monodontomerus rugulosus* Thomson 1876:68. Lectotype ♀ [designated by Bouček 1965:544], Sweden (MZL).

*Monodontomerus gladius* Steffan 1962a:181-183 (Figs. 1-4). Holotype ♀, Montpellier, France (MNHN); 3 ♀, 1 ♂ paratypes same as holotype. [Synonymized by Bouček 1965:543.]

TAXONOMY. - Hansson (1991:10) confirmed the presence of *rugulosus* in MZL. Zerova and Romasenko (1986) key and figure this species in a paper on the parasites of megachilid bees in the Commonwealth of Independent States.

HOST. - Zerova and Romasenko (1986) report this species from *Megachile rotundata* (Megachilidae).

***schrottkyi*** Brèthes. NEOTROPICAL: Colombia.

*Monodontomerus schrottkyi* Brèthes 1916a:414. Lectotype ♀, herein designated, Colombia (MBR, examined); 5 ♀, 1 ♂ paralectotypes same as lectotype.

TAXONOMY. - MBR contains 6 females, 1 male (on 4 cards) labelled as *schrottkyi*, "Typus," "Col. J. Brèthes." I have selected a female as lectotype, indicated by a black arrow on the card upon which it is mounted.

HOST. - The type series was reared from *Eumenes* sp. (Vespidae).

***strobili*** Mayr. PALEARCTIC: Austria; Italy (Masi 1933), Yugoslavia (Vasic and Sisojevic 1955).

*Monodontomerus strobili* Mayr 1874:67. 19 ♀ syntypes, Austria (NMV, examined, in part).

TAXONOMY. - Steffan (1955) redescribed the female of this species and described the male for the first time.

HOSTS. - Mayr described this species reared from cones of *Abies excelsa* and *Pinus sylvestris*. *Monodontomerus strobili* was believed to be phytophagous (Steffan (1952), until Vasic and Sisojevic (1955) demonstrated that it was parasitic within cocoons of *Diprion pini* (Diprionidae).

***usticensis*** Riggio and Destefani. PALEARCTIC: Italy.

*Monodontomerus usticensis* Riggio and de Stefani-Perez 1888:148-149 (pl. 1, Fig. 4). Syntype ♀, Isola di Ustica, Italy (depository unknown).

TAXONOMY. - This species appears to have been described from two females, based upon the two measurements given.

***vicicellae*** (Walker). PALEARCTIC: Austria, Italy; widely distributed in Europe (Bouček 1970b), Mongolia (Szelenyi 1973).

*Torymus Vicicellae*, Kollar: Walker 1847:227. Lectotype ♂ [designated by Bouček 1970b:39], Austria (OUM); 3 ♀ paralectotypes same as lectotype.

*Monodontomerus robustus* Giraud 1877 (in Giraud and Laboulbene 1877):423. [*Nomen nudum.*] [Synonymized by Steffan 1952:293.]

*Monodontomerus* [sic] *nubecula* Rondani 1877:188 (Pl 4, Fig. 151). Lectotype ♀ [designated by Bouček 1974:261], Italy (FM). [Synonymized by Bouček 1974:261.]

*Monodontomerus viciellae*: Mayr 1874:73. [Misspelling.]

*Monodontomerus viciellae* Förster: Steffan 1952:293. [Misspelling and incorrect author.]

TAXONOMY. - Walker (1847) attributed this species to Kollar who merely named it in a collection. Walker's description validates the name and places him as the author of the species. Bouček (1970b:38-39) discussed the nomenclatural problems involved with *vicicellae* and later (1974) did the same for the species *nubecula*. Steffan (1952) synonymized *robustus* presumably based upon the host of this *nomen nudum* which was given as *Zygaena onobrychis* (Zygaenidae), the genus from which many host records of *vicicellae* have been reported.

HOSTS. - The type series of *nubecula* was reared from cocoons of *Cryptus xylocopae* (Ichneumonidae) in the nest of *Megachile "ramulorum* Rond." apparently a *nomen nudum*. The following hosts were listed by Steffan (1952): Psychidae: *Psyche* (now = *Megalophanes*) *viciella* and *constancella*, *Acanthopsyche atra*, *Pachytelia villosella*; Zygaenidae: *Zygaena filipendulae*, *Z. transalpina*, *Z. carniolica*, *Z. occitanica*, and *Z. sarpedon*. Additional hosts are: Cimbicidae: *Trichiosoma betuleti* (now = *lucorum*; Mayr (1874) given as host for *obsoletus* but this was a misidentification of *vicicellae*, see Vikberg and Viitasaari 1991); *Trichiosoma nanae* (Vikberg and Viitasaari 1991). Lymantriidae: *Orgyia antiquoides* (Vikberg and Viitasaari 1991). Ichneumonidae: *Spilocryptus* (now = *Agrotheruetes*) *adustus* in cocoon of *Diprion pini* (Diprionidae) (Bouček 1970b). Also reported as a hyperparasite through *Rhyacionia buoliana* (Tortricidae; Bouček 1977).

***viridiscapus*** Gahan. NEARCTIC/NEOTROPICAL: Southern British Columbia to southern Mexico (based upon my unpublished revisionary work).

*Monodontomerus viridiscapus* Gahan 1941:467-468. Holotype ♀, Orizaba, Mexico (USNM, examined); 3 ♀, 1 ♂ paratypes same as holotype.

*Monodontomerus saltuosus* Grissell 1973:232-234 (Figs. 3, 8, 14). Holotype ♀, east of Placerville, California, USA (USNM, examined); 53 ♀, 18 ♂ paratypes essentially same data as holotype. **New synonymy.**

TAXONOMY. - Nothing was known of *M. viridiscapus* since its original description from southern Mexico in 1941. In 1973 I described *M. saltuosus*, based upon

reared specimens from California and New Mexico. After examining the types of *viridiscapus*, it is now apparent that the only difference between the two species is that the hind tibia of the Mexican population is weakly infused with metallic green, whereas populations from New Mexico northward are entirely yellow. This difference alone does not seem to be of specific value, and because the females and males cannot otherwise be distinguished, I place the name *saltuosus* as a junior subjective synonym of *viridiscapus*.

HOSTS. - The type series of *viridiscapus* was not reared; that of *saltuosus* was reared from *Hemerocampa* (now = *Orgyia*) *pseudotsugata* (Lymantriidae). Other hosts (from my unpublished manuscript) include *Malacosoma disstria* (Lasiocampidae), *Eucheira socialis* (Pieridae), a saturniid cocoon, and the ichneumonids *Gambrus canadensis*, *Phytodietus fumiferanae*, and *Scambus hispae*.

BIOLOGY. - Dahlsten *et al.* (1977) considered this species a secondary parasite on ichneumonids through Lepidoptera. Goodpasture (1975) described and photo-illustrated the mating behavior (as *saltuosus*).

MORPHOLOGY. - Goodpasture (1975) illustrated the haploid karyotype (as *saltuosus*). The number of chromosomes in males is 5, that of females is 10.

#### Unplaced species of *Monodontomerus*

***punctatus*** (Geoffroy). PALEARCTIC: France.

*Cynips punctatus* Geoffroy (in Fourcroy) 1785:381.

TAXONOMY.-- It is no longer possible to know to which species the name *punctatus* Geoffroy refers. The types are not extant and the later redescriptions by Olivier (1790:742) and Fonscolombe (1832:286) tell us little. Steffan (1952:291) examined specimens in the Fonscolombe collection identified as "*punctatus*" and stated that they represented both *M. obscurus* and *M. obsoletus* (now = *aeneus*). Because these latter two species are difficult to tell apart and have been so confused it is quite possible that "*punctatus*" is an older name for either one of them but we shall most likely never know. Graham (1992c) stated that Fonscolombe had 3 species under the name "*punctata*" in various collections (Museum National d'Histoire Naturelle, Paris; Naturhistorisches Museum, Vienna), and concluded that *punctatus* was a *species dubia*.

***rodophthalmus*** (Rossi). PALEARCTIC: Italy.

*Ichneumon rodophthalmus* Rossi 1792:125-126.

TAXONOMY.-- This name (incorrectly spelled *rodophthalmus*) was listed as a questionable synonym of *Monodontomerus virens* Thomson by Dalla Torre (1898:289). Rossi described the overall color as reddish brown and golden-green and then went on to compare it to *Ichneumon* (= *Torymus*) *bedeguaris* (L.), a well-known parasite of rose galls in Europe. The coloring of *rodophthalmus* is more like that of species of *Torymus* (which are often bright metallic green, blue, or coppery red with golden reflections) than of *Monodontomerus* (which are always dull, blackish green or blue). It is possible that this species belongs in *Torymus*. Whatever the case, the description does not allow for positive identification at the genus level, let alone that of species.

***Neopalachia* Bouček (text, p. 139)**

*Neopalachia* Bouček 1978:104. Type-species: *Neopalachia noyesi* Bouček (orig. desig. and monotypic).

***noyesi* Bouček. NEOTROPICAL: Tobago Island.**

*Neopalachia noyesi* Bouček 1978:104-105 (Figs. 20-23). Holotype ♀, Tobago Island, West Indies (BMNH, examined).

***Odopoa* Walker (text, p. 102)**

*Odopoa* Walker 1871a:36. Type-species: *Odopoa ara* Walker (monotypic).

*Odopoea*: Dalla Torre 1898:315. [Misspelling.]

*Australtorymus* Girault 1925/384:97. Type-species: *Australtorymus dentatinotus* Girault (monotypic). [Synonymized by Bouček 1988:148.]

*Ua* Girault 1929/430:2. Type-species: *Ua maria* Girault (monotypic) [Synonymized by Bouček 1988:148.]

*Pauliana* Risbec 1952:375. Type-species: *Pauliana philippiae* Risbec, (monotypic). [Synonymized by Bouček 1978:130.]

***ara* Walker. ORIENTAL: Sri Lanka.**

*Odopoa ara* Walker 1871a:36. ♀ lectotype [designated by Bouček 1978:130], (original number unstated), Ceylon (BMNH).

TAXONOMY. - The lectotype of this species was redescribed by Narendran (1994).

***dentatinota* (Girault). AUSTRALIAN: Australia (Queensland).**

*Australtorymus dentatinota* Girault 1925/384:97-98. Lectotype ♀ [designated by Bouček 1988:148], Cedar Creek, Queensland, Australia (QM).

*Ua maria* Girault 1929/430:2 (pages unnumbered). Lectotype ♀ [designated by Bouček 1988:148], Gold Creek, Queensland, Australia (QM). [Synonymized by Bouček 1988:148.]

TAXONOMY. The type depository for *dentatinota* and *maria* was confirmed by Dahms (1983:218; 1984:795), and according to him the single specimen of each represents the holotype. The species *dentatinota* was transferred [and synonymized] by Bouček (1988:148) who illustrated the forewing (his Fig. 217).

***josephinae* Bouček. AUSTRALIAN. Australia (Northern Territory, Western Australia, New South Wales).**

*Odopoa josephinae* Bouček 1988:148, 155 (Fig. 218). Holotype ♀, "30 km [sic] of Alice Spring," Northern Territory, Australia (ANIC); 2 ♀, 3 ♂ paratypes, same as holotype; 3 ♂ paratypes, 29 km SSE of Coolgardie, Western Australia, Australia; [number, sex unstated], 32 km SE Bourke, New South Wales.

***philippiae* Risbec. AFROTROPICAL: Madagascar.**

*Odopoa philippiae* Risbec 1952:375-378 (Fig. 58). Holotype ♂, Ambatoloana, Madagascar (MNHN).

TAXONOMY. - Bouček (1978:130) transferred the species.

***Oopristus* Steffan (text, p. 129)**

*Oopristus* Steffan 1968:212. Type-species: *Oopristus safavii* Steffan (orig. desig. and monotypic).

***turkestanica*** (Skriptshinsky). PALEARCTIC: CIS (Uzbekistan), Iran; Iraq (Bouček 1978). ORIENTAL: Pakistan (Bouček 1978).

*Chalcis turkestanica* Skriptshinsky 1929:322. Lectotype ♀ [designated by Bouček 1978:105], Taschkent, Taschkentistan (ZIAN); 2 ♀ paralectotypes same data.

*Oopristus safavii* Steffan 1968:212-215 (Figs. 3-6). Holotype ♀, Tehran, Iran (MHNG); 5 ♀ paratypes same data (MHNG, MNHN; 1 ♂ MNHN, examined). [Synonymized by Bouček 1978:105.]

TAXONOMY. - Bouček (1978) moved *turkestanica* from *Chalcis* to *Oopristus*.

HOSTS. - The type series of *safavii* was reared from eggs of *Apodiphus amygdalis* (Pentatomidae). Bouček (1978) reported the species from the eggs of *Sarju eremica* (Pentatomidae) in Pakistan and from unspecified pentatomid eggs in Iraq and Pakistan.

***Ophiopinotus* Husain and Kudesia (text, p. 97)**

*Ophiopinotus* Husain and Kudesia 1987:175. Type-species: *Ophiopinotus pinotus* Husain and Kudesia (orig. desig. and monotypic).

***pinotus*** Husain and Kudesia. ?ORIENTAL: ?India.

*Ophiopinotus pinotus* Husain and Kudesia 1987:175 (Figs. 1-7). ♀. [No data was published with the description.]

TAXONOMY. - Requests to borrow the material in question have gone unanswered. The original data does not even include the country from which the specimen was collected. It is presumed to be India, based upon the location of the describers.

***Ovidia* Girault (text, p. 102)**

*Ovidia* Girault 1924/378:172. Type-species: *Ovidia conicicollis* Girault (monotypic).

***conicicollis*** Girault. AUSTRALIAN: Australia (Queensland).

*Ovidia conicicollis* Girault 1924/378:172. [3 ♀ syntypes], Nelson [= Gordonvale], Queensland, Australia (QM).

TAXONOMY. - Dahms (1983:194) discussed the types of this species. Girault did not state the number of specimens in his paper.

***Palachia* Bouček (text, p. 137)**

*Palachia* Bouček 1970a:39-40. Type-species: *Palachia pulchra* Bouček (orig. desig. and monotypic).

***caudata*** Bouček. AFROTROPICAL: Zimbabwe.

*Palachia caudata* Bouček 1978:99-101 (Figs. 10, 11). Holotype ♀, Salisbury-Chishawasha, Zababwae (BMNH, examined); 4 ♀ paratypes same as holotype; 2 ♀, 2 ♂ paratypes Salisbury, Zimbabwe; 1 ♂ paratype, Cross Koppie, Zimbabwe.



**hayati** Narendran and Sureshan. ORIENTAL: India (Uttar Pradesh).

*Palachia hayati* Narendran and Sureshan 1989:3-5 (Figs. 1-6). Holotype ♀, Aligarh, India (UCK); 1 ♀ paratype, Kerala, India.

TAXONOMY. - The female was redescribed by Narendran (1994).

**indica** Farooqi, Husain, and Ghai. ORIENTAL: India (Delhi).

*Palachia indica* Farooqi, Husain, and Ghai 1990:48. Holotype ♂, New Delhi, India (IARI); 6 ♂ paratypes same as holotype.

**mangalae** Narendran. ORIENTAL: India (Kerala).

*Palachia mangalae* Narendran 1984a:110-112 (Figs. 1-4). Holotype ♀, Kerala, India (IEA); 13 ♀, 2 ♂ paratypes same as holotype (except BMNH, USNM, ZMC, UCK, and Zoological Survey of India, Calcutta).

TAXONOMY. - The female was redescribed by Narendran (1994).

HOST. - The type series was reared from a mantid egg case.

**medleri** Bouček. AFROTROPICAL: Nigeria.

*Palachia medleri* Bouček 1978:94-95 (Figs. 1, 2, 13). Holotype ♀, Idanre, Nigeria (BMNH, examined).

**mira** Bouček. AFROTROPICAL: Zimbabwe, Malawi.

*Palachia mira* Bouček 1978:98-99 (Figs. 5, 7). Holotype ♀, Salisbury, Zimbabwe (BMNH, examined); 1 ♀, 6 ♂ paratypes same as holotype; 1 ♀ paratype, Lingadzi, Malawi.

**oculata** Bouček. AFROTROPICAL: Nigeria.

*Palachia oculata* Bouček 1978:95-97 (Figs. 4, 8). Holotype ♀, Ile-Ife, Nigeria (BMNH, examined).

**pulchra** Bouček. PALEARCTIC: Yugoslavia.

*Palachia pulchra* Bouček 1970a:40-42 (Figs. IV 1-3). Holotype ♂, Srebreno nr. Dubrovnik, Yugoslavia (Bouček collection).

**punctifronta** Narendran and Sureshan. ORIENTAL: India (Kerala).

*Palachia punctifronta* Narendran and Sureshan 1989:7-8 (Figs. 13-18). Holotype ♀, Chindaki, India (UCK); 1 ♀ paratype Agali, India.

TAXONOMY. - The female was redescribed by Narendran (1994).

**punctigastra** Narendran and Sureshan. ORIENTAL: India (Kerala).

*Palachia punctigastra* Narendran and Sureshan 1989:5-7 (Figs. 7-12). Holotype ♀, Calicut University [Kerala], India (UCK).

TAXONOMY. - Although the male was described, it was not listed as a paratype. The female was redescribed by Narendran (1994).

**turneri** Bouček. AFROTROPICAL: South Africa. ORIENTAL: India (Delhi: Farooqi *et al.* 1990).

*Palachia turneri* Bouček 1978:97-98 (Fig. 9). Holotype ♀, Port St. Johns, South Africa (BMNH, examined); 4 ♂ paratypes same as holotype.

TAXONOMY. - The male was illustrated by Farooqi *et al.* (1990: Figs. 5-9, mislabelled *turnneri*) based upon specimens from India.

***Palmon* Dalman (text, p. 158)**

*Palmon* Dalman 1825:388-390. Type-species: *Palmon bellator* Dalman (desig. by Gahan and Fagan 1923:103).

*Pachytomoides* Girault 1913/140:143. Type-species: *Pachytomoides mirus* Girault (orig. desig.). [Synonymized earlier in the present work.]

***ashmeadi* (Crawford). ORIENTAL: Philippine Islands. New combination.**

*Podagrion ashmeadi* Crawford 1910a:128. Holotype ♀, Manila, Philippine Islands (USNM, examined).

TAXONOMY. - Habu (1962:193) transferred this species to *Pachytomoides*. Earlier I synonymized *Pachytomoides* with *Palmon*.

***bellator* Dalman. Gum copal, origin unknown.**

*Palmon bellator* Dalman 1825:390 (Pl. V Figs. 21-23). Holotype ♀, Copal inclusion, locality unspecified (SMNH, examined).

TAXONOMY. - According to George Steyskal, who translated the Dalman paper for me, Dalman was hoping to determine the origin of the copal from the identity of the specimens in it. Apparently Dalman believed the copal came from either "Amerika" or "Afrika." According to Dalla Torre (1898:369) the locality for this species was France, but this is not apparent from the original description. The type specimen is wrapped in paper with some abbreviations on it, but I cannot make them out, much less make sense of them.

***bicinctus* (Girault). AUSTRALIAN: Australia (Tasmania). New combination.**

*Pachytomoides bicinctus* Girault 1929/431:342. Holotype ♀, Launceston, Tasmania (SAM).

TAXONOMY. - Dahms (1983) discussed the type and confirmed its depository.

***frater* (Girault). AUSTRALIAN: Australia (New South Wales). New combination.**

*Pachytomoides frater* Girault 1915/243:94. Holotype ♀, Chindera, New South Wales (QM).

TAXONOMY. - Dahms (1984) discussed the type and confirmed its depository.

***ghesquierei* (Ferrière). AFROTROPICAL: Republic of the Congo. New combination.**

*Pachytomoides ghesquierei* Ferrière 1958:278-281 (Figs. I- 1,2; II-1; III-1). 20 ♀, 20 ♂ syntypes, Eala, Belgian Congo (MRCB).

***greeni* (Crawford). ORIENTAL: Sri Lanka, Taiwan. New combination.**

*Podagrion greeni* Crawford 1912a:3-4 (Fig. 1). 5 ♀, 1 ♂ syntypes, Punduloya, Ceylon (USNM).

*Pachytomoides hornianus* Masi 1926a:176-178 (Figs. 15a-f). Holotype ♀, Kosempo, Formosa (IPAL or MCSN). [Synonymized by Narendran 1994:84.]

*Podagrion ixion* Fernando 1959:96 (Pl. 8 Figs. 34-38). 2 ♀ syntypes, Vavuniya, Ceylon (UC).  
[Synonymized by Narendran 1994:84.]

TAXONOMY. - Girault (1913/140:143) transferred *greeni* to *Pachytomoides*.

***insolens* (De Santis). NEOTROPICAL: Argentina. New combination.**

*Podagrion insolens* De Santis 1975:186-187 (Figs. 1, 2). Holotype ♀, Rio Ceballos, Argentina (FCNM); 6 ♀ paratypes same as holotype (FCNM, examined in part).

TAXONOMY. - Grissell and Goodpasture (1981:233) transferred this species to *Pachytomoides*.

***kivuensis* (Ferrière). AFROTROPICAL: Republic of the Congo. New combination.**

*Pachytomoides kivuensis* Ferrière 1958:285 (Fig. II-4). 2 ♀ syntypes, Rwankwi, Belgian Congo (MRCB).

***megarhopalus* (Masi). ORIENTAL: Taiwan. New combination.**

*Pachytomoides megarhopalus* Masi 1926a:266-268 (Figs. 17a-c, 18). Holotype ♀, Taihorin, Formosa (IPAL or MCSN).

***megistus* (De Santis). NEOTROPICAL: Argentina. New combination.**

*Podagrion megistus* De Santis 1968:4-6 (Figs. 1, 2). Holotype ♀, Isla Martin Garcia, Argentina (FCNM); 1 ♀ paratype same as holotype (examined).

TAXONOMY. - Grissell and Goodpasture (1981:233) transferred this species to *Pachytomoides* and illustrated the propodeum (Fig. 16).

***mirus* (Girault). AUSTRALIAN: Australia (Queensland). New combination.**

*Pachytomoides mirus* Girault 1913/140:143-144. Holotype ♀, Brisbane, Queensland, Australia (QM, examined).

TAXONOMY. - Girault (1915/243:293) redescribed the female. Dahms (1984) discussed the type and its depository. The body is missing, but parts still remain on a slide.

***orchesticus* (Masi). ORIENTAL: Taiwan, Sri Lanka; India (Uttar Pradesh: Mani and Kaul 1972; Kerala, Andhra Pradesh: Narendran 1994). New combination.**

*Pachytomoides orchesticus* Masi 1926a:264-266 (Figs. 16a-f). 2 ♀, 1 ♂ syntypes, Anping, Formosa (IPAL and/or MCSN).

*Podagrion iago* Fernando 1957b:16-17 (Figs. 38-40). 2 ♀ syntypes, Habarana, Ceylon (UC).  
[Synonymized by Narendran 1994:85.]

TAXONOMY. - Mani (1989) redescribed the female of *orchesticus* and Narendran (1994) the female and male.

HOST. - The types of *orchesticus* were reared from a mantis "cocoon."

***polyspilota* (Ferrière). AFROTROPICAL: Republic of the Congo. New combination.**

*Pachytomoides polyspilota* Ferrière 1958:283-284 (Figs. II-3; III-2). 31 ♀, 2 ♂ syntypes, Bikoro, Belgian Congo (MRCB).

HOST. - The type series was reared from an egg case of *Polyspilota variegata* (now = *aeruginosa*) (Mantidae).

***queenslandica*** (Girault). AUSTRALIAN: Australia (Queensland). **New combination.**

*Pachytomoides queenslandica* Girault 1913:159:96. Holotype ♀, Nelson (= Gordonvale), Queensland, Australia (QM).

TAXONOMY. - Dahms (1986) discussed the type and confirmed the depository. Girault (1915/243) redescribed the female.

***seyrigi*** (Ferrière). AFROTROPICAL: Madagascar. **New combination.**

*Pachytomoides seyrigi* Ferrière 1958:281-283 (Figs. I-3; II-2). Holotype ♀, Ivondro, Madagascar (MRCB).

***sphodromantidis madagascariensis*** (Risbec). AFROTROPICAL: Madagascar. **New combination.**

*Podagrion sphodromantidis madagascariensis* Risbec 1956:175-176. 1 ♀ syntype Tananarive, Madagascar; 2 ♀ syntypes, Bekily, Madagascar (MNHN).

TAXONOMY. The placement of this subspecies is tentative. Ferrière (1955) transferred the nominate subspecies from *Podagrion* to *Pachytomoides*. He apparently did not know of Risbec's subspecies, as it was described the same year. I transfer it here on the basis of the subspecific association. An examination of the type material might show that it is a valid species or that it is a true *Podagrion*.

***sphodromantidis sphodromantidis*** (Risbec). AFROTROPICAL: Senegal, Ivory Coast. **New combination.**

*Podagrion sphodromantidis* Risbec 1951a:304-306 (Fig. 151e). 2 ♀, 1 ♂ syntypes, Bambey, Senegal; 42 ♀, 9 ♂ syntypes, Abengourou, Ivory Coast (all MNHN).

TAXONOMY. - Ferrière (1955:210) transferred this species to *Pachytomoides* and later (1958) illustrated the antenna (Fig. I-5) and hind femur of females (Fig. II-5) and males (Fig. III-3) of this species.

HOST. - The series from Senegal was reared from an egg case of *Sphodromantis* sp. (Mantidae).

***turneri*** (Ferrière). AFROTROPICAL: South Africa. **New combination.**

*Pachytomoides turneri* Ferrière 1958:285-286 (Figs. I-4; III-4). 7 ♀, 2 ♂, Port Saint-John, Pondoland, South Africa (BMNH).

***zygas*** (Grissell and Goodpasture). NEARCTIC: USA (Florida). **New combination.**

*Pachytomoides zygas* Grissell and Goodpasture 1981:232 (Figs. 6, 7, 15). Holotype ♀, Gainesville, Florida, USA (USNM); 2 ♀ paratypes same as holotype.

***Perissocentrus* Crawford (text, p. 126)**

*Perissocentrus* Crawford 1910c:235. Type-species: *Perissocentrus chilensis* Crawford (orig. desig.)

***argentinae* Crawford.** NEOTROPICAL: Argentina; Paraguay, Brazil, Uruguay, Chile (Grissell 1992b).

*Perissocentrus argentinae* Crawford 1910c:236. Lectotype ♀ [designated by Grissell 1992b:95], Ceres, Argentina (USNM, examined); 2 ♀, 1 ♂ paralectotypes same as lectotype.

*Perissocentrus argentinae* Brad.; Brèthes 1917b:374 (Fig. II), 377. [Erroneously attributed to "Bradford."]

HOSTS. - The syntype series was not reared. Hosts reported in the literature are the psychids *Oiketeticus platensis* (Brèthes 1917a, 1917b, 1920b) and *Oiketeticus ?geyeri*, an arctiid chrysalid (Parker *et al.* 1953), and the papilionid *Battus polydamas* (Grissell 1992b).

***caridei* Brèthes.** NEOTROPICAL: Argentina; Brazil, Uruguay (Grissell 1992b).

*Perissocentrus caridei* Brèthes 1917a:340. [*Nomen nudum*]

*Perissocentrus argentinae* var. *caridei* Brèthes 1917b:377-378. Neotype ♀ [designated by Grissell 1992b:96], Pelotas, Argentina (MBR, examined); 1 ♀, 1 ♂ syntypes, Argentina (destroyed).

*Perissocentrus caridei* Brèthes; De Santis 1967:185. [Revised status.]

HOSTS. - The syntype series was reared from *Oiketeticus platensis* (Psychidae), although this is not stated explicitly. De Santis (1967) also reported *Oiketeticus geyeri* and *Battus polydamas* (Papilionidae).

ILLUSTRATION. - Havrylenko and Winterhalter (1949) provided a habitus drawing of this species, but it is so generalized that it could be almost any species of tolymid.

***chilensis* Crawford.** NEOTROPICAL: Chile.

*Perissocentrus chilensis* Crawford 1910c:235-236. Lectotype ♀ [designated by Grissell 1992b:97], Santiago, Chile (USNM, examined); 6 ♀, 5 ♂ paralectotypes same data as lectotype.

HOSTS. - The type series was reared from *Ormiscodes crinita* (now = *cinnamomea*) (Saturniidae). De Santis (1979) also reported as hosts *Cercophora* (= *Cercophana*) *frauenfeldii* (Saturniidae) and *Thanatopsyche chilensis* (Psychidae).

***phormio* (Walker).** NEOTROPICAL: Chile; Bolivia to Argentina (Grissell 1992b).

*Torymus phormio* Walker 1843b:113. Lectotype ♀ [designated by Bouček, in Grissell 1992b:98], Valparaiso, Chile (BMNH, examined).

*Megastigmus porteri* Brèthes 1916b:9. 1 ♀, 1 ♂ syntypes, Santiago, Chile (?MBR, presumably lost). [Synonymized by Grissell 1992b:98.]

*Monodontomerus vianai* E. Blanchard 1936:7-9 (Figs. 1a-d). Number of syntypes unknown, "provincia Salta." [Types reported in the author's collection and the entomology laboratory of the "Division de Zoología Agrícola del Ministerio de Agricultura de la Nación".] [Synonymized by Grissell 1992b:98.]

TAXONOMY. - *Torymus phormio* was transferred first to *Monodontomerus* by Künckel (1905:227-228) then to *Perissocentrus* by Bouček (in De Santis 1983:2). *Megastigmus porteri* was transferred to *Perissocentrus* by Brèthes (1920a:15).

**HOSTS.** - Only the type series of *vianai* was reared. It was reported by E. Blanchard (1936) from *Parapechthis bazani* (Ichneumonidae) and *Alabama argillacea* (Noctuidae). Other known hosts include *Oiketicus antiqua* (Psychidae) (Brèthes 1920a, 1920b, Pairoa 1944, Etcheverry and Ramirez 1964). Grissell (1992b) also reported the following as hosts: *Leucania* sp. (Noctuidae), *Melipotis* sp. (Noctuidae), *Ormiscodes* sp. (Saturniidae), *Orygia* sp. (Lymantriidae). *Psyche* (now = *Lumacra*) *kunckeli* (Psychidae) was listed by Künckel (1905) and Künckel and Heylaerts (1908) as a host. Crawford (1910c:236) stated that Ashmead made this identification, but Ashmead most likely had never seen Walker's species. I doubt the validity of this host record as it stands.

**BIOLOGY.** - The species is a gregarious parasite of Lepidoptera, as well as a secondary parasite attacking ichneumonids.

***striatulus*** Grissell. NEOTROPICAL: Colombia, Ecuador.

*Perissocentrus striatulus* Grissell 1992b:99 (Figs. 6, 7, 9, 26). Holotype ♀, Cundinamarca, Zipaquira, Colombia (USNM); 27 ♀, 23 ♂ paratypes same as holotype (USNM, CNC, BMNH); 15 ♀, 20 ♂, Boyaca, Tunja, Colombia (USNM); 1 ♂, Narino, Pasto, Colombia (USNM); 1 ♀, Pichincha, Ecuador (USNM); 3 ♀, 1 ♂, Salcedo, Ecuador (USNM).

**HOSTS.**-- The holotype (and paratypes) was reared as a secondary parasite of Geometridae. The paratypes from Narino and Salcedo were reared from pupa of *Cyanotricha necyria* (Dioptidae). The paratype from Pichincha was reared as a secondary from *Casinaria cavigena* (Ichneumonidae) on *Leuculopsis pulverulenta* (Geometridae).

***tumidulus*** Grissell. NEOTROPICAL: Chile.

*Perissocentrus tumidulus* Grissell 1992b:100-101 (Figs. 2, 12, 18, 22, 23). Holotype ♀, Cautin, Temuco, Chile (USNM); 7 ♀, 2 ♂ paratypes same as holotype (USNM); 9 ♀, 5 ♂ paratypes, LaCruz Chile (USNM, CNC); 4 ♀, 2 ♂ paratypes, Santiago, Chile (USNM).

**HOSTS.**-- The holotype and paratypes from Temuco were reared from a "butterfly." The paratypes from LaCruz and Santiago were reared from *Thanatopsyche chilensis* (Psychidae) and some additional paratypes from LaCruz were reared from *Cercophana* sp. (Saturniidae).

### ***Physothorax*** Mayr (text, p. 102)

*Physothorax* Mayr 1885:159, 196. Type-species: *Physothorax disciger* Mayr (desig. by Gahan and Fagan 1923).

?*Plesio stigma* Mayr 1885:158, 226-227. Type-species: *Plesio stigma bicolor* Mayr (monotypic). [Questionable synonymy by Müller 1886:xi; followed by Bouček 1993:206.]

***annuliger*** Mayr. NEOTROPICAL: Brazil (Santa Catarina).

*Physothorax annuliger* Mayr 1885:198. ♂ (s) (number unstated), St. Catharina, Brazil (?NMW).

**HOST.** - The type(s) was reared from fruits of *Ficus gomelleira* (as *Ficus* No. 5 = *Ficus doliaria* see Mayr 1906) (Moraceae) (see also Bouček 1993).

**bicolor** (Mayr). NEOTROPICAL: Brazil.

*Plesio stigma bicolor* Mayr 1885:227-228 (Figs. 39, 40). ♂ syntypes, Brazil (?NMW).

TAXONOMY. - This species was discussed in the phylogenetic section under its generic heading (p. 103). Bouček (1993) placed it provisionally in this genus, but the types could not be located.

HOST. - The types were reared from fruits of *Ficus gomelleira* (as *Ficus* No. 5 = *Ficus doliaria* see Mayr 1906) (Moraceae).

**bidentulus** Burks. NEARCTIC: USA (Florida).

*Physothorax bidentulus* Burks 1969a:118. Holotype ♀, Miami, Florida, USA (USNM); 13 ♀, 13 ♂ paratypes as holotype; 2 ♀, 2 ♂ paratypes, Richmond, Florida, USA; 3 ♀ paratypes, Key Largo, Florida, USA; 1 ♀ paratype, Plantation Key, Florida, USA.

HOSTS. - The holotype was reared from fruits of *Ficus laevigata* (now = *citrifolia*) (Moraceae). Other paratypes were reared from fruits of *Ficus altissima*, *Ficus aurea*, and "a wild fig." To the contrary, however, Roskam and Nadel (1990) stated that they never reared *bidentulus* from *Ficus aurea*, but only from *Ficus citrifolia*, and then as a parasite of the cecidomyiid *Ficomyia perarticulata* (rearing reported again by Nadel *et al.* 1992).

**disciger** (Mayr). NEOTROPICAL: Brazil (Santa Catarina); St. Vincent (Ashmead 1900b).

*Physothorax disciger* Mayr 1885:197-198. ♂ (s) (number unstated), St. Catharina, Brazil (NMW, lost).

*Diomorus variabilis* Mayr 1885:228-229. ♀, ♂ syntypes (number unstated), Brazil (?NMW). [Synonymized by Müller 1886:xi; Mayr 1906:186.]

*Physothorax dorsiger* Mayr: Ashmead 1904a:400. [Misspelling.]

TAXONOMY. - The species *variabilis* and *disciger* were described by Mayr in the same paper (1885). According to Bouček (1993), *disciger* Mayr represents brachypterous males of *variabilis* Mayr, which has winged males and females. Ashmead (1904a:400) placed the name "*dorsiger*," an apparent misspelling of *disciger*, as a junior synonym of *variabilis*. However, Mayr (1906:186) placed the name *variabilis* as a junior synonym of the correctly spelled *disciger*. Bouček (1993) considered Mayr (1906) as the "first revisor", based upon the fact that Ashmead (1904a) placed an invalid name into synonymy. There is a cotype of *variabilis* Mayr in the USNM, obtained in exchange by Gahan.

HOSTS. - Types of both the above names were reared from fruits of *Ficus gomelleira* (Moraceae), according to Bouček (1993).

**mayri** Ashmead. NEOTROPICAL: Brazil.

*Physothorax mayri* Ashmead 1904a:400. Holotype ♀, Brazil (USNM).

TAXONOMY. - No specific locality was given for the type.

**pallidus** Ashmead. NEARCTIC: USA (Florida). NEOTROPICAL: St. Vincent; Puerto Rico (De Santis 1979).

*Physothorax pallidus* Ashmead 1900b:254-255. Lectotype ♀ [designated by Burks 1969a:117], Coconut Grove, Florida, USA (USNM, examined); 7 ♀, 3 ♂ paralectotypes same data as lectotype; 1 ♀ (not found), St. Vincent, West Indies.

TAXONOMY. - Ashmead (1900b) listed one female specimen from St. Vincent, but I cannot find that specimen in the USNM. It may be at BMNH.

HOST. - The type series from Florida was reared from *Ficus pedunculata* (now = *citrifolia*) (Moraceae). Additional records are *Ficus aurea* (Burks 1969a, Roskam and Nadel 1990). Nadel *et al.* (1992) also reported *F. citrifolia*.

***percaudatus*** Bouček. NEOTROPICAL: Colombia.

*Physothorax percaudatus* Bouček 1993:208. Holotype ♀, Fugasagusa, Colombia (BMNH), 1 ♂ paratype, same data.

HOST. - Reared from fruits of *Ficus lapaithifolia* (Moraceae).

***russelli*** Crawford. NEARCTIC: Florida.

*Physothorax russelli* Crawford 1910b:204. Lectotype ♀ [designated by Burks 1969b:117], Cutler, Florida, USA (USNM, examined); 1 paralectotype ♀ same as lectotype.

HOSTS. - The types of this species were reared from fruits of *Ficus aurea* (Moraceae). Roskam and Nadel (1990) dissected specimens of *russelli* from enlarged ovaries of the same fig (host fig reported again by Nadel *et al.* 1992).

BIOLOGY. - Butcher (1964) observed females of this species inserting their ovipositors into the sides of *Ficus* receptacles.

***serratus*** Mayr. NEOTROPICAL: Brazil; Colombia (Bouček 1993).

*Physothorax serratus* Mayr 1906:185-186. Lectotype ♀ [designation by Bouček 1993:208], Brazil (NMW).

TAXONOMY. - There is an undesigned paralectotype of *serratus* in the USNM, obtained in exchange by Gahan.

HOST. - The types were reared from fruits of *Ficus gomelleira* (as *Ficus* No. 5: *Ficus doliaria* see Mayr 1906) (Moraceae). Bouček (1993) added the host *Ficus lapaithifolia*.

### ***Platykula*** Huber (text, p. 114)

*Platykula* Huber 1927:106. Type-species: *Syntomaspis albihirta* Ashmead (orig. desig. and monotypic).

***albihirta*** (Ashmead). NEARCTIC: USA (Florida; widespread in eastern states based upon specimens in USNM).

*Syntomaspis albihirta* Ashmead 1887:187. Holotype ♀, Jacksonville, Florida (USNM, examined).

*Lochites punctata* Ashmead 1887:185. Holotype ♂, Jacksonville, Florida (USNM, examined). [Synonymized by Grissell 1992a:275.]

TAXONOMY. - Both *albihirta* and *punctata* were described in the same paper from the same locality and are opposite sexes of the same species.

### ***Plesiostigmodes*** Ashmead (text, p. 103)

*Plesiostigmodes* Ashmead 1904a:243, 400. Type-species: *Plesiostigmodes brasiliensis* Ashmead (orig. desig. and monotypic).



***brasiliensis*** Ashmead. NEOTROPICAL: Brazil (Mato Grosso).

*Plesiostigmodes brasiliensis* Ashmead 1904a:243, 400. Holotype ♂, Corumba, Brazil (USNM, examined).

TAXONOMY. - The holotype is a male and not a female, as stated by Ashmead (1904a; see also Gahan 1948), and is the only specimen known.

***Podagrion*** Spinola (text, p. 161)

*Podagrion* Spinola 1811:147. Type-species: *Podagrion splendens* Spinola (monotypic).

*Priomerus* Walker 1833:116, 118. Type-species: *Priomerus pachymerus* Walker (monotypic). [Synonymized by Walker 1871:28.]

*Pachytomus* Westwood 1847:260. Type-species: *Palmon (Pachytomus) klugianus* Westwood (monotypic). [Synonymized by Mayr 1974:63.]

*Bactyrischion* Costa 1856:18-19 (repeated 1857:223-225). Type-species: *Bactyrischion bicoloratum* Costa (= *Podagrion splendens* Spinola) (monotypic). [Synonymized by Walker 1871:28.]

*Blephonira* Holmgren 1869:438. Type-species: *Blephonira fulvipes* Holmgren (monotypic). [Synonymized as *Blaphonira* by Ashmead 1904a:368.]

*Cleptimorpha* Walker 1872b:85. Type-species: *Cleptimorpha binotata* Walker (monotypic). [Synonymized by Graham 1981:5-6.]

*Cyanostola* Saussure 1890:Pl. 15, Fig. 30. Type-species: *Cyanostola coerulea* Saussure (monotypic, illustration only). [Synonymized by Ferrière 1955:207.]

*Coquerelia* Saussure 1890:Pl. 20, Fig. 7. Type-species: *Coquerelia insidiosa* Saussure (monotypic). [Synonymized by Masi 1940:251, footnote.]

*Podagrion* Schulz 1906:150. [Invalid emendation.]

*Pachytomoidella* Girault 1913/172:40. Type-species: *Pachytomoidella magniclavus* Girault (orig. desig. and monotypic). [Synonymized by Baltazar 1966:137.]

*Propodagrion* Girault 1915/243:287. Type-species: *Podagrion worcesteri* Girault (orig. desig. and monotypic). [Synonymized by Baltazar 1966:137.]

*Coquereliana* Gahan and Fagan 1923:39. [Objective replacement name for *Coquerelia* Saussure nec Kraatz.]

***abbreviatum*** Cockerell. AUSTRALIAN: New Caledonia.

*Podagrion abbreviatum* Cockerell 1930:3-4 (Figs. 6-10). Holotype ♀, Noumea, New Caledonia (AMNH); "many ♀ and two ♂" same data as holotype.

HOST. - The type series was reared from mantid "egg-cases."

***ahlonei*** Mani and Kaul. ORIENTAL: Burma.

*Podagrion ahlonei* Mani and Kaul 1972:320-321 (Figs. 4a-h). Holotype ♀, Ahlone area, Rangoon, Burma (SJC); ♀ paratypes (number unstated) same as holotype.

TAXONOMY. - Mani (1989) redescribed and figured the female.

HOST. - The type series was reared from ootheca of a mantid.

***aligarhensis*** Narendran. ORIENTAL: India (Uttar Pradesh).

*Podagrion aligarhensis* Narendran 1994:74 (Figs. 104-106). Holotype ♀, Aligarh, Uttar Pradesh, India (UCK).

***ambatobeensis*** Risbec. AFROTROPICAL: Madagascar.

*Podagrion ambatobeensis* Risbec 1956:167-170 (Figs. 4a-h). 2 ♀, 27 ♂ syntypes, Ambatobe, Tananarive, Madagascar; 10 ♀, 9 ♂ syntypes, Parc de Tsimbazana, Tananarive; 19 ♀, 4 ♂ syntypes, Ambohidrapeto, Tananarive (all MNHN).

***armigerum*** Masi. AFROTROPICAL: Somalia. PALEARCTIC: Cape Verde Islands (Ferrière 1960).

*Podagrion armigerum* Masi 1940:254-257 (Figs. IIa-c). 3 ♀, 4 ♂ syntypes, Villaggio Duca [Jawhar], Somalia (?MCSN).

***bambeyi*** Risbec. AFROTROPICAL: Senegal.

*Podagrion bambeyi* Risbec 1951a:308-309 (Fig. 152d). Holotype ♀, Bambey, Senegal (MHNH).

***batesi*** Girault. AUSTRALIAN: Australia (Queensland).

*Podagrion batesi* Girault 1915/243:292. Holotype ♀, Cloncurry, Queensland, Australia (QM).

TAXONOMY. - Dahms (1983:117) discussed the type of this species.

HOST. - The type was reared from a "mantid eggcase."

***beharaensis*** Risbec. AFROTROPICAL: Madagascar.

*Podagrion beharaensis* Risbec 1956:174-175 (Fig. 5a). Holotype ♂, Behara, Madagascar (MHNH).

***beneficium*** Girault. AUSTRALIAN: Australia (Queensland).

*Podagrion beneficium* Girault 1914/198:138. [*Nomen nudum*.]

*Podagrion beneficium* Girault 1914/219:113-114. Numerous ♀, ♂ syntypes, "Nelson near Cairns," Queensland, Australia (QM, USNM).

TAXONOMY. - Girault described the species again in 1915 (1915/243:289-290) with a different number of type specimens. The type situation is confused for this species, and Dahms (1983:122) discussed the situation but did not resolve the problem of the primary type.

HOST. - The syntypes were reared from "mantid eggs".

***binotata*** (Walker). PALEARCTIC: Madeira.

*Cleptimorpha binotata* Walker 1872b:85. ♂ (number unstated), Madeira (type lost).

TAXONOMY. - Graham (1981) discussed the identity and type situation with this species.

***brasiliense*** Howard. NEOTROPICAL: St. Vincent; Grenada, Mexico (Morelos). NEARCTIC: USA (Idaho, California, Nevada, Utah, Colorado, New Mexico, Arizona, Florida) (records from Grissell and Goodpasture (1981) except type locality).

*Podagrion brasiliensis* Howard 1894:83. Lectotype ♀ [designated by Grissell and Goodpasture 1981:233], St Vincent, West Indies (BHMN, examined); paralectotype ♀ same as lectotype (USNM, examined).

*Podagrion brasiliense*: Burks 1967:253. Valid emendation.

TAXONOMY. - Grissell and Goodpasture (1981) redescribed and discussed this species.

HOST. - The only reared specimens are from mantid eggs on *Baccharis* from Florida (Grissell and Goodpasture 1981).

***caloepulum*** Mani and Kaul. ORIENTAL: India (Uttar Pradesh).

*Podagrion caloepulum* Mani and Kaul 1972:317-320 (Figs. 3a-h). Holotype ♀, Sukna, Kurseong, India (SJC); ♀ paratypes (number unstated) same as holotype.

TAXONOMY. - Mani (1989) redescribed and figured the female.

***capitellatum*** Dalman. Gum copal, origin unknown.

*Palmon capitellatum* Dalman 1825:391-392. ?Holotype ♀, Copal inclusion, locality unspecified (SMNH).

DISTRIBUTION. - Dalman believed the copal came either from "Amerika" or "Afrika." No locality is specified in the original description (see also discussion for *P. bellator*).

***charybdis*** Fernando. ORIENTAL: Sri Lanka.

*Podagrion charybdis* Fernando 1957a:217-218 (Pl. XLIV, Fig. 4; Pl. XLV, Figs. 3, 6). 14 ♀, 6 ♂ syntypes, Gammaduwa, Ceylon (UC).

***chatterjeei*** Mani and Kaul. ORIENTAL: India (Uttar Pradesh).

*Podagrion chatterjeei* Mani and Kaul 1972:325-328 (Figs. 8 a-h). Holotype ♀, Dehra Dun, India (SJC).

TAXONOMY. - Mani (1989) redescribed and figured the female.

***chichawatnensis*** Mani and Kaul. ORIENTAL: India (Punjab).

*Podagrion chichawatnensis* Mani and Kaul 1972:322-323 (Figs. 5 a-h). Holotype ♂, Chichawatni, Punjab, India (SJC); 1 ♂ paratype same as holotype.

TAXONOMY. - Mani (1989) redescribed and figured the male.

***clavellatum*** (Dalman). Gum copal, origin unknown.

*Palmon clavellatus* Dalman 1825:391-392. ?Holotype ♀, Copal inclusion, locality unspecified (SMNH, examined).

DISTRIBUTION. - Dalman believed the copal came either from "Amerika" or "Afrika." No locality is specified in the original description (see also discussion for *P. bellator*).

***coerulea*** (Saussure). AFROTROPICAL: Madagascar.

*Cyanostola coerulea* Saussure 1890:Pl. 15, Fig. 30. ♂ (no specimens), Madagascar.

TAXONOMY. - The validity and identity of this species is based solely upon an illustration. I checked MHNG and MNHN for types associated with this name and found none.

***coeruleoviride*** Strand. NEOTROPICAL: Surinam; Trinidad (Callan 1978).

*Podagrion coeruleo-viride* Strand 1911c:154-155. 29 ♀, 2 ♂ syntypes, Paramaribo, Surinam (ZMB, examined).

HOST. - The syntype series was reared from mantid eggs. A series from Trinidad was also reared from mantid oothecae (Callan 1978). In BMNH I examined a series of 7 females, 1 male reared from a "hesperiid pupa" collected in Colombia. There is no doubt that the specimens emerged from the pupa because the pupal case is with the specimens and there is still one female parasite inside it. There are 2 complete emergence holes visible in the venter of the pupa and 1 complete hole dorsally. Within the case and surrounding each hole appears to be a brown septa which partitions the case into cells.

***crassiclava*** Gahan. NEARCTIC: USA (Texas; Arizona). Mexico (Morelos, Yucatan) (records from Grissell and Goodpasture (1981) except type locality).

*Podagrion crassiclava* Gahan 1922a:6-7. Holotype ♀, Brownsville, Texas, USA (USNM, examined); 8 ♀, 3 ♂ paratypes same as holotype.

TAXONOMY. - Grissell and Goodpasture (1981) redescribed the species.

HOST. - The type series was reared from mantid "eggs". Additional material was reported by Roberts (1937) from *Stagmomantis limbata* (Mantidae) in Arizona.

***cyaneus*** Ashmead. NEOTROPICAL: Brazil.

*Podagrion cyaneus* Ashmead 1904a:402. Holotype ♀, Santarem, Brazil (USNM, examined).

***dalbergium*** Mani and Kaul. ORIENTAL: India (Uttar Pradesh, Punjab).

*Podagrion dalbergium* Mani and Kaul 1972:323-325 (Figs. 6 a-h, 7 a-d). Holotype ♀, New Forest, Dehra Dun, India (SJC); ♀, ♂ paratypes (number unstated) same as holotype.

TAXONOMY. - Mani (1989) redescribed and figured females and males.

***dentatum*** Strand. NEOTROPICAL: Paraguay.

*Podagrion dentatum* Strand 1911c:155-156. Holotype ♀, San Bernardino, Paraguay (ZMB, examined).

***descampsi*** Risbec. AFROTROPICAL: Cameroons.

*Podagrion descampsi* Risbec 1954a:889-894 (Figs. 1a-e, 2a-e). 24 ♀, 18 ♂ syntypes, Garoua, Cameroons (MNHN).

***dineni*** Narendran. ORIENTAL: India (Kerala).

*Podagrion dineni* Narendran 1994:71-72 (Figs. 89-91). Holotype ♀, Palghat Dist. Anakatty, Kerala, India (UCK).

***diospiri*** Risbec. AFROTROPICAL: Senegal.

*Podagrion diospiri* Risbec 1951a:316-318. 3 ♀, 9 ♂ syntypes, Bambey, Senegal (MNHN).

HOST. - Specimens in the type series were from 7 different lots, but only one lot included reared specimens from *Hoplocorypha* (Mantidae). A female was collected on "Diospiros" (= *Diospyros*; Ebenaceae). Risbec later (1951b:1127) reported the species from eggs of *Solygia sulcatifrons* (Mantidae).

***dispar*** Masi. ORIENTAL: Taiwan.

*Podagrion dispar* Masi 1926a:19 (Figs. 11 a-e). Holotype ♂, Anping, Formosa (IPAL).

***echthrus*** Crawford. NEOTROPICAL: Mexico.

*Podagrion echthrus* Crawford 1912b:163-164 (Figs. 1, 2). Lectotype ♀, herein designated, Santa Lucrecia, Vera Cruz, Mexico (USNM, examined); 31 ♀, 2 ♂ paralectotypes, same as lectotype.

***enei*** Bakkendorf. AFROTROPICAL: Nigeria.

*Podagrion enei* Bakkendorf 1960:364-368 (Figs. 1-7). Holotype ♀, Ibadan, Nigeria, W. Africa (ZMC); 5 ♂ paratypes, same as holotype; 8 ♀, 7 ♂ paratypes, same as holotype except host known (see Host).

HOST. - The holotype was reared from a mantid "ootheca." One series of paratypes was reared from ootheca of *Sphodromantis lineola* (Mantidae).

**epibulum** Masi. ORIENTAL: Taiwan; Sri Lanka (Narendran 1994).

*Podagrion epibulum* Masi 1926a:10-12 (Figs. 3 a-d, 4 a,b). 11 ♀, 5 ♂ syntypes, Taiberin, Formosa (IPAL and/or MCSN).

TAXONOMY. - Narendran (1994) redescribed the species from material taken in Sri Lanka.

**epichiron** Masi. ORIENTAL: Taiwan.

*Podagrion epichiron* Masi 1926a:18-19 (Figs. 10 a,b). Holotype ♀, Kosempo, Formosa (IPAL or MCSN).

**flabellatum** Girault. AUSTRALIAN: Australia (Tasmania).

*Podagrion flabellatum* Girault 1929/431:342. 2 ♀, 1 ♂ syntypes, Launceston, Tasmania (SAM).

TAXONOMY. - Dahms (1984:599) discussed the types of this species.

HOST. - The types were reared from "what appeared to be galls."

**fraternum** (Westwood). AFTROTROPICAL: Mauritius, Reunion.

*Palmon fraternum* Westwood 1847:260. ♀, ♂ syntypes (number unstated), Ile de France [Mauritius] (OUM).

*Priomerus insidiosus* Coquerel 1856:507-508 (Pl. 15, Fig. 1a). ♀, ♂ syntypes (number unstated), Ile Bourbon [Reunion] (depository unknown). [Apparently synonymized by Dalla Torre 1898:369.]

*Coquerelia insidiosa* (Saussure) 1890:Pl. 20, Fig. 7. [New combination.]

*Coquereliana insidiosa* (Saussure): Gahan and Fagan 1923:39. [New combination.]

TAXONOMY. - *Priomerus insidiosus* was placed in the new genus *Coquerelia* by Saussure (1890) but this name was preoccupied and was replaced by *Coquereliana* in Gahan and Fagan (1923). Dalla Torre (1898) synonymized *insidiosus*.

HOST. - The types of *P. insidiosus* were reared from *Mantis pustulata* (now = *Polyspilota aeruginosa*) (Mantidae).

**fulvipes** (Holmgren). PALEARCTIC: "China." ORIENTAL: India (Kerala, Tamil Nadu, Assam: Narendran and Sureshan 1988)

*Blephonira fulvipes* Holmgren 1869:438 (Pl. VIII Fig. 6). ♀ (number unstated), "China" (SMNH, examined).

TAXONOMY. - Narendran and Sureshan 1988 redescribed and illustrated (Figs. III:1-5) the female of this species, based upon the "lectotype" and specimens from India. Narendran (1994) repeated this with figures (Figs. 119-121).

**galeatae** Fischer. AFROTROPICAL: Ethiopia.

*Podagrion galeatae* Fischer 1961:1-2 (Figs. 1-2). Holotype ♀, Konso, SW Ethiopia (Staatlichen Mus. Naturkunde, Stuttgart); 1 ♂ paratype, same as holotype.

HOST. - The types were reared from *Hoplocorypha galeata* (now = *saussurii*) (Mantidae).

**hayati** Narendran. ORIENTAL: India (Uttar Pradesh).

*Podagrion hayati* Narendran 1994:74-75 (Figs. 107-109). Holotype ♀, Aligarh, Uttar Pradesh, India (UCK).

**helictoscela** (Masi). ORIENTAL: Taiwan.

*Pachytomoidella helictoscela* Masi 1926a:173-175 (Figs. 14 a-d). Holotype ♀, Kankau, Formosa (IPAL or MCSN).

**holbeini** Girault. AUSTRALIAN: Australia (Victoria).

*Podagrion holbeini* Girault 1923/372:7. [2 ♀, 1 ♂ syntypes, Bright, Victoria, Australia (QM).]  
TAXONOMY. - Girault (1923) provided little information with the description. The type data above are from Dahms (1984:694). According to Bouček (1988:141) this is probably a synonym of *P. koebelei*.

**hyalinum** (Girault). AUSTRALIAN: Australia (Queensland).

*Podagrionella hyalina* Girault 1913/175:80. Holotype ♀, Longreach, Queensland, Australia (SAM).  
TAXONOMY. - Dahms (1984:702) discussed the type of this species. Girault (1915/243:292) transferred the species.

**idomena** (Walker). AFROTROPICAL: Sierra Leone.

*Palmon idomene* Walker 1850:130-131. ♀, ♂ syntypes (number unstated), Sierra Leone ("Mr. Clear's collection;" now ?BMNH).

**indicum** Girault. *Nomen nudum*.

*Podagrion indicum* Girault, in Ramakrishna Ayyar 1919:935. India.  
TAXONOMY. - This name was published in a list by Ramakrishna Ayyar and has no validity.

**indiensis** Narendran. ORIENTAL: India (Kerala).

*Podagrion indiensis* Narendran 1994:72-73 (Figs. 95-97). Holotype ♀, Silent Valley, Kerala, India (UCK).

**instructum** (Walker). ORIENTAL: Hong Kong, "Port Natal."

*Palmon instructum* Walker 1862:387. ♀ (number unstated), Hong Kong and "Port Natal" (BMNH).

**insulare** Westwood. AFROTROPICAL: Mauritius.

*Palmon insularis* Westwood 1847:259. ♀ (number unstated), Ile de France [Mauritius] (OUM).

**isos** Grissell and Goodpasture. NEARCTIC: USA (Florida).

*Podagrion isos* Grissell and Goodpasture 1981:234 (Fig. 18). Holotype ♀, Gainesville, Florida, USA (USNM, examined); 1 ♀ paratype, same as holotype; 8 ♀ paratypes, Longwood, Florida; 1 ♀ paratype, Orange County, Florida.

***ivorensis*** Risbec. AFROTROPICAL: Ivory Coast.

*Podagrion ivorensis* Risbec 1953:597-599 (Fig. 9c). 1 ♀, 2 ♂ syntypes, Adiopodoume, Ivory Coast (MNHN).

***judas*** Fernando. ORIENTAL: Sri Lanka.

*Podagrion judas* Fernando 1957a:216-217 (Pl. XLIV Figs. 2, 5; Pl. XLV Figs. 2, 5). 21 ♀, 5 ♂ syntypes, Kotte, Ceylon (UC).

***julia*** (Girault). AUSTRALIAN: Australia (South Australia).

*Podagrionella julia* Girault 1927/416:330. [Holotype ♀, Adelaide, South Australia, Australia (SAM)].

TAXONOMY. - The type data is cited from Dahms (1984:733). Bouček (1988:141) transferred the species.

***keralensis*** Narendran. ORIENTAL: India (Kerala).

*Podagrion keralensis* Narendran 1994:69-70 (Figs. 82-85). Holotype ♀, Silent Valley, Kerala, India (UCK); 12 ♀ paratypes same locality as holotype; 13 ♀ paratypes, Feroke, Kerala; 1 ♀ paratype, Agali, Kerala; 2 ♀ paratypes, Coimbatore, Tamil Nadu.

***koebeleri*** Crawford. AUSTRALIAN: Australia (South Australia, Queensland; ACT and Victoria: Bouček 1988); New Caledonia.

*Podagrion koebeleri* Crawford 1912a:4-5 (Fig. 2). ♀ [6] and ♂ [8] syntype series, South Australia, Australia (USNM, examined).

*Podagrion grotii* Girault 1915/245:291-292. 1 ♀, 1 ♂ syntypes, Gordonvale, Queensland, Australia (QM, but see below). [Synonymized by Bouček 1988:141.]

*Podagrion dolichurum* Cockerell 1930:2-3 (Figs. 1-5). Holotype ♀, Noumea, New Caledonia (AMNH); 2 ♀, 1 ♂ paratypes same data as holotype (at least one paratype in BMNH according to Bouček 1988:141). [Synonymized by Bouček 1988:141.]

TAXONOMY. - Although the number of specimens of *koebeleri* was unstated in the original description, the numbers quoted above are based upon specimens in the USNM. The type situation for *grotii* was discussed by Dahms (1984:665), but it needs further clarification. Bouček (1988) discussed the identity of *koebeleri*.

HOSTS. - The types of *grotii* were taken from a mantid "eggmass" and those of *dolichurum* were reared from mantid "egg-cases".

***klugianum*** (Westwood). PALEARCTIC: Egypt.

*Palmon (Pachytomus) klugianum* Westwood 1847:261. Sexes, number unstated, Egypt (OUM, ♂ lectotype examined).

HOST. - Graham designated a lectotype for this taxon although he did not publish. This paper validates Graham's selection. The type(s) were supposedly associated with figs, but there is no label data to indicate this. Masi (1935) discussed this species and questioned the association.

***libycum*** Masi. PALEARCTIC: Libya.

*Podagrion libycum* Masi 1929:221-222 (Figs. V 1-n). Holotype ♀ [= ♂], Giarabub, Libya (MCSN).

TAXONOMY. - Although Masi labelled the description as being of a female, he stated after the description that the female was unknown. In the figure, the caption was for a male, and he compares the male of *libycum* to that of *pachymerum*.

***longicaudum*** Masi. AFROTROPICAL: Somalia.

*Podagrion longicaudum* Masi 1940:252-254 (Figs. Ia-i). 6 ♀, 3 ♂ syntypes, Villaggio Duca [Jawhar], Somalia (?MCSN).

***macrurum*** Schrottky. NEOTROPICAL: Argentina.

*Podagrion macrurum* Schrottky 1902:109-110. Lectotype ♀, herein designated, Buenos Aires, Argentina (Universidade de Sao Paulo, Brasil); ♂ paralecotype same as lectotype.

HOST. - The types were reared from *Coptopteryx argentina* (Mantidae).

***magniclavus*** (Girault). AUSTRALIAN: Australia (Queensland).

*Pachytomoidella magniclavus* Girault 1913/172:40-41. Holotype ♀, Nelson, Queensland, Australia (lost).

TAXONOMY. - Dahms (1984:785) discussed the type, which is apparently lost. Girault (1915/243:293) repeated the description of this species. Baltazar (1966:137) transferred the species by implication.

***malabarensis*** Narendran. ORIENTAL: India (Kerala).

*Podagrion malabarensis* Narendran 1994:72 (Figs. 92-94). Holotype ♀, Calicut, Kerala, India (UCK).

***manii*** Narendran. ORIENTAL: India (Kerala).

*Podagrion manii* Narendran 1994:70-71 (Figs. 86-88). Holotype ♀, Kannur District, Kerala, India (UCK).

***mantidiphagum*** Girault. NEOTROPICAL: Trinidad; Mexico (Morelos), Panama Canal Zone. NEARCTIC: USA (Arizona, Texas) (records from Grissell and Goodpasture (1981) except type locality).

*Podagrion mantidiphagum* Girault 1917/303:37-38. Lectotype ♀ [designated by Grissell and Goodpasture 1981:235], Palo Seco, Trinidad, West Indies (USNM, examined); 2 ♀, 1 ♂ paralecotypes same as holotype.

TAXONOMY. - Grissell and Goodpasture (1981) redescribed and illustrated this species.

HOST. - The type series was reared from an "egg mass" of a mantid.

***mantis*** Ashmead. NEARCTIC: USA (Florida; Hawaii, Washington, California, Nevada, Arizona, New Mexico, Texas, Kansas, Missouri, Arkansas, Mississippi, Alabama, Georgia, North and South Carolina). NEOTROPICAL: Mexico: Baja California Norte as far south as Morelos. Argentina (Parker *et al.* 1953, De Santis 1968) (records, except as noted, from Grissell and Goodpasture (1981)).

*Podagrion mantis* Ashmead 1886a:57. Holotype ♀, Jacksonville, Florida, USA (USNM, examined).

*Podagrion mantidis* Riley and Howard 1892:243-244, 414. [Invalid emendation.]

TAXONOMY. - Grissell and Goodpasture (1981) redescribed and illustrated this



species, including the male.

HOSTS. - All rearings are from mantid egg cases. The type specimen was reared from an "egg mass" of *Mantis* (now = *Stagmomantis*) *carolina*. Additional rearings include *Stagmomantis limbata* and *Tenodera angustipennis* (introduced into the United States from eastern Asia).

BIOLOGY. - Peck (1963) gave a list of references (mostly notes) to the hosts and biology of *P. mantis*. Breland (1941) presented a fairly complete account of this species as an ectoparasite of single eggs within the mantid egg case. Grissell and Goodpasture (1981) discussed and illustrated the mating behavior of this species, pointing out that behavior differed depending upon whether mating took place in a natural environment or an artificial one.

***mantisiphagum*** (Mani). ORIENTAL: India (Orissa; Delhi: Narendran 1994).

*Pachytomus mantisiphagum* Mani 1936:126. Holotype ♂, Barkuda Island, Chilka Lake, India (Zoological Survey of India, Calcutta).

HOST. - The type was reared from "eggs of mantid".

[*mantoidae* of Pruthi and Mani 1940:3 (Fig.2), nec Motschulsky.

Motschulsky (1859) described *Anastatus mantoidae* [= Eupelmidae] which is the type of the genus. Dalla Torre (1898) incorrectly transferred the species to *Podagrion*. Gahan and Fagan (1923) transferred it back to *Anastatus*, where it belongs. Pruthi and Mani (1940) referred to "*Podagrion mantoidae* Motschulsky", giving a good habitus illustration of a species of *Podagrion*. Obviously this cannot be *mantoidae*, which is in a different genus and family.]

***melleum*** (Westwood). NEOTROPICAL: Brazil (Ashmead 1904a)

*Palmon melleus* Westwood 1847:260. ♀ (number unstated), locality unstated (OUM).

TAXONOMY. - Westwood did not state a locality with the description, but listed Brazil as one of several localities for material he described in the paper. Dalla Torre (1898) listed Brazil as the type locality apparently based upon the host name.

HOST. - The type(s) was reared from eggs of "*Mantidis Brasiliae*", but this name cannot be verified (pers. comm. D. A. Nickle).

***meridionale*** Masi. PALEARCTIC: Egypt, Cyprus, Mauritania.

*Podagrion meridionale* Masi 1935:69-71. ♀, ♂ syntypes (number unstated), Mauritania, Aegyptus, Cyprus (?MCSN).

HOST. - Gerling (1969) reared the species from egg cases of *Sphodromantis viridis* (Mantidae).

BIOLOGY. - Gerling discussed and illustrated the oviposition of this species. It attacks mature or old egg cases but not fresh ones. It took females about 45 minutes to drill into the egg case, and they would then remain motionless for 0.5 to nearly 1 hour after which they would leave. Multiple parasites emerged from a single egg case.

***metatarsum*** Girault. AUSTRALIAN: Australia (Victoria).

*Podagrion metatarsum* Girault 1929/431:341-342. 1 ♀, 2 ♂ syntypes, Melbourne, Victoria, Australia (SAM).

TAXONOMY. - Dahms (1984:811-812) discussed the types of this species. Bouček (1988) suggested that this might be a synonym of *P. koebelei*.

HOST. - The type series was reared from "eggs" of *Orthodera* sp. (Mantidae).

***micans*** Strand. ORIENTAL: Sri Lanka.

*Podagrion micans* Strand 1911c:157. Holotype ♀, Ceylon (ZMB).

TAXONOMY. - Mani (1989) redescribed the female.

***minus*** Strand. PALEARCTIC: Italy.

*Podagrion minus* Strand 1911c:158-159. ♀ syntype(s) (number unstated), Lucca, Italy (ZMB).

***nigriclava*** Dodd. AUSTRALIAN: Australia (Northern Territory).

*Podagrion nigriclava* Dodd 1917:360. 1 ♀, 1 ♂ syntypes, Darwin, Northern Territory, Australia (QM)

HOST. - The types were reared from mantid "ootheca."

***nipponicum*** Habu. PALEARCTIC: Japan; People's Republic of China (Liao *et al.* 1987), Korea (Paik 1978).

*Podagrion chinensis* Ashmead: Ishii 1932:353 (Fig. 686). [*?Nomen nudum.*]

*Podagrion nipponicum* Habu 1962:183-193 (Figs. 341-365, 373, Pl. IV Fig. 2, Pl. VIII Figs. 1, 2). Holotype ♀, Kurokawa, Japan (NIAS); 100's of ♀, ♂ paratypes from 30 localities throughout Japan.

TAXONOMY. - Ishii (1932), in a handbook to Japanese insects, illustrated and discussed the species "*chinensis* Ashmead." Ashmead never described such a taxon, and Ishii created a *nomen nudum*. Habu later (1962) described the species *nipponicum* and cited "*chinensis* [Ashmead]: Ishii" as a synonym of it. It is possible to attribute the name *chinensis* to Ishii with *nipponicum* as a junior synonym, but I defer such a case to the first reviser to correct. I use Habu's name because it is obvious that Ishii was not describing the species in the taxonomic sense. Liao *et al.* (1987:38-39) discussed the species "*chinensis* Ashmead" and gave a colored illustration (Fig. 11) but this does not agree entirely with the color illustration given by Habu. There is obviously some confusion with these names. Even Habu (1962) suggested that *nipponicum* might be a synonym of *sinense* Walker and that both *opisthacanthum* and *quinquedentatum* might also be synonyms. He presented a detailed study of variation found in the hind femora of males and females and the ratio of ovipositor length of females reared from different hosts.

HOSTS. - The type series was reared from *Tenodera aridifolia* and *T. angustipennis* (Mantidae). The former was host to the holotype.

BIOLOGY. - Habu (1962) briefly discussed the biology, including emergence and oviposition. Adult females could live up to 59 days. Habu observed one female insert her ovipositor into the egg case from which she had emerged.

***noyesi*** Narendran. ORIENTAL: India (Kerala).

*Podagrion noyesi* Narendran 1994:73 (Figs. 998-100). Holotype ♀, Silent Valley, Kerala, India (UCK); 5 ♀ paratypes, same data as holotype; 2 ♀ paratypes, Calicut, Kerala; 1 ♀ paratype, Malampuzha, Kerala.

**obscurum** (Westwood). AUSTRALIAN: Australia (Western Australia).

*Palmon obscurum* Westwood 1847:260. Lectotype ♀ (number unstated) [designated by Bouček 1988:141], King George's Sound, Western Australia, Australia (OUM).

TAXONOMY. - This species was transferred by Dalla Torre (1898:370).

**okinawense** Habu. PALEARCTIC: Okinawa Islands.

*Podagrion okinawense* Habu 1962:198-199 (Figs. 367, 370, 372, Pl. IV Fig. 3, Pl. VIII Fig. 5).

Holotype ♀, Loochoos, Okinawa Islands (HU); 1 ♀ paratype, same as holotype.

**olenus** (Walker). AUSTRALIAN: Australia (New South Wales).

*Palmon olenus* Walker 1839:7-8. Lectotype ♀ [designated by Bouček 1988:141], Sydney, New South Wales, Australia (BMNH).

TAXONOMY. - The species was transferred by Dalla Torre (1898:370).

**oon** Grissell and Goodpasture. NEARCTIC: USA (Florida).

*Podagrion oon* Grissell and Goodpasture 1981:234-235 (Figs. 22, 25). Holotype ♀, Orange County, Florida, USA (USNM, examined); 2 ♀, 1 ♂ paratypes, Allenhurst, Florida, USA; 2 ♀ paratypes, Pasco County, Florida, USA; 1 ♀ paratype, Lake County, Florida.

HOST. - The paratypes from Allenhurst were reared from egg cases of *Stagmomantis carolina* (Mantidae).

**ophthalmicum** Strand. NEOTROPICAL: Colombia; Trinidad (Callan 1978).

*Podagrion ophthalmicum* Strand 1911c:157-158. Holotype ♀, "Columbia" (ZMB, examined).

DISTRIBUTION. - Columbia is presumably a misspelling for Colombia.

HOST. - Callan (1978) reared this species from mantid oothecae in Trinidad.

**opisthacanthum** Masi. ORIENTAL: Taiwan; India (Tamil Nadu: Mani and Kaul 1972; Kerala: Narendran 1994).

*Podagrion opisthacanthum* Masi 1926a:14-16 (Figs. 7 a-e). 9 ♀ syntypes, Taihorin, Formosa (IPAL and/or MCSN).

TAXONOMY. - Masi (1926a) questioned whether this might be a synonym of *sinensis* Walker. Mani (1989) and Narendran (1994) redescribed the female.

**pachymerum gibba** Bernard. PALEARCTIC: France.

*Podagrion pachymerum gibba* Bernard 1938:42-45 (Fig. B). ♀, ♂ syntypes (number unstated), Banyuls-sur-Mer, France (depository unknown).

HOST. - The syntype series was reared from *Mantis religiosa* (Mantidae).

**pachymerum pachymerum** (Walker). PALEARCTIC: France; CIS (the Caucasus and western Europe (Nikol'skaya and Zerova 1978)). ORIENTAL: India (Tamil Nadu: Mani 1938).

*Priomerus pachymerus* Walker 1833:118. Lectotype ♀ [designated by Eady 1959:270], South of France (BMNH, examined).

*Palmon religiosus* Westwood 1847:259 (Pl. 10, Figs. 23, a-e). ♀ (number unstated), locality unstated (?OUM). [Synonymized apparently by Mayr 1874:63.]

*Podagrion splendidum* of Walker 1871a:19 (Fig. 2). [Lapsus for *splendens* Spinola 1811.]

TAXONOMY. - Walker (1871a:28) synonymized his own species *pachymerus* under

*Podagrion splendens* Spinola (which he wrongly labelled in Fig. 2, page 19 as *Podagrion splendidum*). [Walker repeated the illustration again in 1872a, but the drawings actually were first published by Haliday 1841 (Pl. F, Fig. 3) labelled as *Priomerus pachymerus*.] Mayr (1874) and Dalla Torre (1898) believed that *splendens* Spinola (published in a key) was without a description and thus gave Walker's name, *pachymerus*, priority, based upon the previous synonymy. While some workers considered the two names synonyms (e.g., Gahan and Fagen 1923, Hoffmeyer 1931, Mani 1938), others recognized both *pachymerus* and *splendens* as valid (e.g., Eady 1959, Nikol'skaya and Zerova 1978). Mani (1989) redescribed and figured the female.

HOST. - The type(s) of *religiosus* Westwood was reared from *Mantis religiosa* (Mantidae). Others (e.g., Andre 1877, Sellenschlo 1984b) have also reported it from this host.

BIOLOGY. - (Considering the taxonomic confusion, some of these papers might refer to *splendens*.) Williams (1914) demonstrated that females could oviposit into hardened oothecae. Chopard (1922:265-271) reviewed the known biology of the species. Ramaswamayya (1923:55-57) discussed oviposition. Andre (1877:138) described and illustrated the larva. Other less inclusive papers include Picard (1933), Bonnamour (1936), Bertrand (1937), and Sellenschlo (1984b).

MORPHOLOGY - Picard (1936a) discussed and illustrated variation in the hindleg. Domenichini (1953) illustrated and described abdominal morphology. Sellenschlo discussed and illustrated larval (1982) and antennal morphology (1983).

***pachymerus rufiventre* (Giraud). PALEARCTIC: ?Austria.**

*Palmon pachymerus rufiventre* Giraud 1863:1311. ♀, ♂ syntypes (number unstated), locality and depository unknown.

TAXONOMY. - Dalla Torre (1898) listed the type locality as "Austria inf."

***parvulum* Masi. AFROTROPICAL: Somalia.**

*Podagrion parvulum* Masi 1940:257-258 (Figs. IIIa-d). Holotype ♀, Villaggio Duca [Jawhar], Somalia (?MCSN).

***pavo* Girault. AUSTRALIAN: Australia (Victoria).**

*Podagrion pavo* Girault 1915/243:291. 4 ♀, 2 ♂ syntypes, Melbourne, Victoria, Australia (NMV).

TAXONOMY. - Dahms (1988:391-392) discussed the types of this species.

HOST. - The type series was reared from "*Tinodera australiana*" (= *Tinodera australasiae*) (Mantidae).

***pax* Girault. AUSTRALIAN: Australia (Queensland).**

*Podagrion pax* Girault 1913/156:47. Holotype ♀, Nelson, Queensland, Australia (QM).

TAXONOMY. - Dahms (1988:395) discussed the type of this species. Bouček (1988:141) listed the date of description for this species as Girault 1915/156, but this was simply a redescription.

HOST. - The type was reared from an "eggmass of a mantid".

***philippinense cyanonigrum*** Habu. PALEARCTIC: Japan. ORIENTAL: Taiwan.

*Podagrion philippinense cyanonigrum* Habu 1962:195-198 (Fig. 368, 371, 374, Pl.IV Fig. 1, Pl.VIII Fig. 3). Holotype ♀, Nagasaki, Japan (NIAS); 1 ♀ paratype, Toroen, Taiwan; 8 ♀ paratypes each from different locality in Japan.

***philippinense philippinense*** Crawford. ORIENTAL: Philippine Islands. PALEARCTIC: People's Republic of China (Zhejiang, Bakkendorf 1960; Jiangxi, Sheng and Xu 1989).

*Podagrion philippinensis* Crawford 1910a:128. [1 ♀, 1 ♂ syntype], Manila, Philippine Islands (USNM).

TAXONOMY. - Crawford did not state the number of specimens examined. The above numbers are based upon USNM material.

HOSTS. - This species was reared from egg cases of *Tenodera aridifolia sinensis* and *Hierodula patellifera* (Mantidae) (Sheng and Xu 1989).

BIOLOGY. - Sheng and Xu (1989) reported that this species overwintered as late-stage larvae inside the host eggs (perhaps meaning egg cases; information taken from abstract provided by National Agricultural Library, Beltsville, Maryland; article not seen). One to two generations were produced per year (May/June and October). Up to 70% of progeny were female.

***prionomerum*** Masi. ORIENTAL: Taiwan, India (Kerala, Karnataka, Narendran 1994).

*Podagrion prionomerum* Masi 1926a:12-14 (Figs. 5 a,b, 6). Holotype ♀, Kankau, Formosa (IPAL or MCSN).

TAXONOMY. - Narendran (1994) redescribed this species based upon material from India.

***quinquedentatus*** Ashmead. ORIENTAL: Hong Kong.

*Podagrion quinquedentatus* Ashmead 1904b:84. Holotype ♂, Hong Kong, "China" (USNM).

***quinquis*** Hoffmeyer. NEOTROPICAL: Paraguay.

*Podagrion quinquedentatum* Schrottky 1911:2. ♀ (number unstated), Puerto Bertoni, Paraguay (depository unknown). [Preoccupied by Ashmead 1904b:84.]

*Podagrion quinquis* Hoffmeyer 1929:334. [New Name for *quinquedentatum* Schrottky 1911, nec Ashmead 1904b:84.]

*Podagrion zapiolai* E. Blanchard 1942:13. [*Nomen nudum*.] ["Synonymized" by De Santis 1968:8.]

***repens*** (Motschulsky). ORIENTAL: Sri Lanka.

*Priomerus repens* Motschulsky 1859:118. Lectotype ♀ [designated by Narendran 1994:76], Sri Lanka (Zoological Museum of Moscow).

TAXONOMY. - Crawford (1912a:5) redescribed the female of this species based upon the "type-material." He did not state where that material was deposited.

***risbeci*** (Cockerell). AUSTRALIAN: New Caledonia.

*Pachytomus risbeci* Cockerell 1930:4-5 (Figs. 11-15). Holotype ♂, Noumea, New Caledonia (AMNH); 2 ♂ paratypes same data as holotype.

TAXONOMY . - Bouček (1988:141) transferred this species.

HOST . - The type series was reared from mantid "egg-cases".

***scylla*** Fernando. ORIENTAL: Sri Lanka.

*Podagrion scylla* Fernando 1957a:215-216 (Pl. XLIV Fig. 3, 6; Pl. XLV Figs. 1, 4). 12 ♀, 8 ♂ syntypes, Ratnapura, Sri Lanka (UC).

***sensitivus*** De Santis and Diaz. NEOTROPICAL: Brasil.

*Podagrion sensitivus* De Santis and Diaz 1975:197-198 (Figs. 1, 2). Holotype ♀, Isla Fernando de Noronha, Brasil (FCNM).

***shirakii*** Crawford. ORIENTAL: Taiwan.

*Podagrion shirakii* Crawford 1913:245. 3 ♀, 3 ♂ syntypes, Taihoku, Formosa (USNM, examined).

TAXONOMY . - The original number of specimens was not given in Crawford's paper. The numbers cited above are based upon the USNM collection.

HOST . - The type series was reared from "egg masses" of *Paratenodera* (now = *Tenodera*) *aridifolia* (Mantidae).

***sinensis*** (Walker). ORIENTAL: Hong Kong. PALEARCTIC: People's Republic of China (Shanxi: Li 1985; Jiangxi: Sheng and Xu 1989).

*Palmon sinensis* Walker 1852:42-43. ♀, ♂ syntypes (number unstated), Hong Kong (BMNH).

HOST . - Li (1985) reported this species as a parasite of *Paratenodera sinensis* (now = *Tenodera aridifolia sinensis*) (Mantidae) stating that it attacked 15 to 32% of egg cases placed in cotton fields (this information taken from abstract in Review of Applied Entomology, Ser. A, 1988, vol. 76; article seen, but parasite name not found). Sheng and Xu (1989) listed the same host, as well as *Hierodula patellifera* (Mantidae) (information taken from abstract provided by National Agriculture Library, Beltsville, Maryland; article not seen).

BIOLOGY . - Sheng and Xu (1989) reported that this species overwintered as late-stage larvae inside the host eggs (perhaps meaning egg cases; information taken from abstract provided by National Agriculture Library, Beltsville, Maryland; article not seen). One to two generations were produced per year (May/June and October). Up to 65% of progeny were female.

***splendens*** Spinola. PALEARCTIC: CIS (the Caucis) and western Europe (Nikol'skaya and Zerova 1978).

*Podagrion splendens* Spinola 1811:147. ♀, ♂ syntypes (number unstated), locality unstated (depository unknown).

*Bactyrishion bicoloratum* Costa 1857:226-227 (Fig. 4). Sex and number unstated, locality unstated (UN, confirmed by G. Tomasetta). [Synonymized apparently by Mayr 1874:63.]

TAXONOMY . - *Podagrion splendens* was named and described by Spinola in a generic key. Walker (1871a:28) synonymized his own species *pachymerum* (which see) under *Podagrion splendens* but it is now considered a valid taxon. There is considerable confusion surrounding these two taxa. Mayr (1874) and Dalla Torre (1898) believed that *splendens* was published without description,

and following Walker's synonymy gave *pachymerum* priority (see also the discussion by Gahan and Fagan (1923:119)). While some workers considered the two names synonyms (e.g., Hoffmeyer 1931), others recognized both *pachymerum* and *splendens* as valid taxa (e.g., Mani 1938, Eady 1959, Nikol'skaya and Zerova 1978). It is quite likely that some literature for this species is reported under the name *pachymerum*.

MORPHOLOGY - Ferrière (1955) illustrated the hindleg, wing, and antenna.

***tainanicum*** Masi. ORIENTAL: Taiwan.

*Podagrion tainanicum* Masi 1926a:16-18 (Figs. 8 a,b, 9). 2 ♀ syntypes, Tainan, Formosa (IPAL and/or MCSN).

***tarachodesi*** Risbec. AFROTROPICAL: Senegal, Ivory Coast.

*Podagrion tarachodesi* Risbec 1951a:312-313. 32 ♀, 9 ♂ syntypes, Bambey, Senegal; 24 ♀, 15 ♂ syntypes, Abengourou, Ivory Coast (all MNHN).

TAXONOMY. - Risbec (1956:170-171) redescribed and illustrated the male of this species.

***terebrator*** Masi. AFROTROPICAL: Seychelles.

*Podagrion terebrator* Masi 1917:126-127 (Figs. 4-1, 2). ♀ (number unstated), Silhouette, Seychelles (BMNH).

***terebratum*** Strand. ORIENTAL: People's Republic of China (Guandong).

*Podagrion terebratum* Strand 1911c:156. Holotype ♀, Canton, China (ZMB).

***texanus*** Ashmead. *Nomen nudum*.

*Podagrion texanus* Ashmead, in Wolcott 1950:47. Puerto Rico.

TAXONOMY. - This name was listed by De Santis (1979), who cited it from Wolcott (1950). Ashmead did not publish this name, and Wolcott simply cited it, based upon material from Puerto Rico reared from *Gonatista reticulata* (Mantidae).

***variabilis*** Risbec. AFROTROPICAL: Ivory Coast.

*Podagrion variabilis* Risbec 1953:599-600 (Figs. 9e-f). 1 ♀, 1 ♂ syntypes, Adiopodoume, Ivory Coast (MNHN).

***viduum*** Masi. ORIENTAL: Taiwan.

*Podagrion viduum* Masi 1926a:170-173 (Figs. 12 a-e, 13). Holotype ♂, Anping, Formosa.

***virescens*** Strand. AUSTRALIAN: Papua New Guinea.

*Podagrion virescens* Strand 1911c:156. Holotype ♀, Nova Hollandia (= Papua New Guinea) (ZMB).

Distribution. - Bouček (1988:141) reported this species from Western Australia.

***washingtoni*** Girault. AUSTRALIAN: Australia (Queensland).

*Podagrion washingtoni* Girault 1915/243:290. Holotype ♀, Pentland, Queensland, Australia (QM).

TAXONOMY. - Dahms (1986:650-651) discussed the type of this species.

**worcesteri** Girault. AUSTRALIAN: Australia (Queensland).

*Podagrion worcesteri* Girault 1913/159:97-98. Holotype ♀, Nelson, Queensland, Australia (QM, examined).

TAXONOMY. - Dahms (1986:655) discussed the type specimen. Girault (1915/243) redescribed the species and transferred it to *Propodagrion* (now = *Podagrion*.).

***Podagrionella*** Girault (text, p. 151)

*Podagrionella* Girault 1913/159:96-97. Type-species: *Podagrionella bella* Girault (monotypic).

*Iridophaga* Picard 1933:237-239. Type-species: *Iridophaga lichtensteini* Picard (monotypic). [Synonymized by Bouček 1988:141.]

*Tarachodiphaga* Ferrière 1955:214-215. Type-species: *Podagrion senegalensis* Risbec (orig. desig.). [Synonymized earlier in the present work.]

*Iridophagoides* Erdős 1964:93. Type-species: *Iridophagoides petiolatus* Erdős (orig. desig. and monotypic). [Synonymized earlier in the present work.]

***bella*** Girault. AUSTRALIAN: Australia (Queensland).

*Podagrionella bella* Girault 1913/159:96-97. Holotype ♀, Nelson (= Gordonvale), Australia (QM, examined).

TAXONOMY. - Dahms (1983:121) discussed the type.

***caudata*** Narendran. ORIENTAL: India (Tamil Nadu).

*Podagrionella caudata* Narendran 1994:83 (Fig. 133). Holotype ♀, Coimbatore, Tamil Nadu, India (UCK); 2 female paratypes, same locality.

***empusae*** (Risbec). AFROTROPICAL: Senegal.

*Podagrion empusae* Risbec 1951a:313-315. 20 ♀ syntypes, Bambey, Senegal (MNHN).

TAXONOMY. - Ferrière (1955:214, Fig. 5) transferred this species from *Podagrion* to *Iridophaga*. Bouček (1988:142) transferred it to *Podagrionella*.

HOSTS. - Part of the syntype series was reared from eggs of *Empusa guttula* (Mantidae) and part from eggs of an unknown mantid.

***indarbela*** Narendran and Sureshan. ORIENTAL: India (Kerala).

*Podagrionella indarbela* Narendran and Sureshan 1988:42-43. Holotype ♀, Chettiyarmad, Kerala, India (reported in UCK, transferred to USNM 1991); 1 ♂ paratype same as holotype.

HOST. - Emerged from eggs of *Indarbela tetraonis* (Arbelidae). According to Narendran (in litt.) there were no praying mantid egg cases associated with the rearing. This host, the only reported instance of a podagrionine reared from Lepidoptera “eggs,” is discussed further under the Biology and Phylogenetics section, p. 59.

***korsakowi*** (Picard). PALEARCTIC: Algeria. AFROTROPICAL: Senegal.

*Podagrion* sp. Korsakoff 1934:273-274.

*Iridophaga korsakowi* Picard 1936b:76. 7 ♀ syntypes, southern Algeria (MNHN).

*Podagrion blepharodesi* Risbec 1951a:306-308 (Fig. 152b). 16 ♀, 7 ♂ syntypes, Bambey, Senegal (MNHN). [Synonymized by Ferrière 1958:291.]

TAXONOMY. - Korsakoff redescribed the species in 1949. Ferrière (1955:214) transferred *blepharodesi* from *Podagrion* to *Iridophaga*. Bouček (1988:142) transferred it to *Podagrionella*.



HOST. - The syntype series of *blepharodesi* was reared from an egg case of *Blepharodes* (now = *Phlaebarodes*) *sudanensis* and that of *korsakowi* from *Blepharopsis mendica* (all Mantidae).

***lamborni*** (Ferrière). AFROTROPICAL: Malawi.

*Iridophaga lamborni* Ferrière 1958:290-291 (Fig. V). 21 ♀, 1 ♂ syntypes, Fort Johnston, Nyasaland (BMNH, examined, in part).

HOST. - The syntype series was reared from a mantid ootheca.

***lichtensteini*** (Picard). PALEARCTIC: France.

*Iridophaga lichtensteini* Picard 1933:237-239 (Figs. 1-4). 4 ♀, 3 ♂ syntypes, Sete (=Cette), France (MNHN, examined in part).

TAXONOMY. - Bouček (1988:142) transferred this species to *Podagrionella*.

HOST. - The syntype series was reared from an ootheca of *Iris oratoria* (Mantidae).

***petiolatus*** (Erdős). PALEARCTIC: Algeria. **New combination.**

*Iridophagoides petiolatus* Erdős 1964:93 (Fig. 3). Holotype ♀, Oran, Algeria (MNHN, examined).

TAXONOMY. - Bouček (1976a) redescribed and illustrated (Fig. 1) the species, based on the holotype.

***senegalensis*** (Risbec). AFROTROPICAL: Senegal. **New combination.**

*Podagrion senegalensis* Risbec 1951a:315-316 (Fig. 153). 16 ♀, 2 ♂ syntypes Bambey, Senegal (MNHN, examined).

*Tarachodiphaga senegalensis* (Risbec): Ferrière 1955:214-215. [New generic combination.]

TAXONOMY. - The specimens I examined from MNHN were purportedly syntypes (Steffan, personal communication) and were labeled "*Podagrion senegalensis* Risbec, ex *Tarachodes*." There were 7 females mounted on a slide with the coverslip sealed in wax as was Risbec's method. There is no certainty that these are syntypes.

HOSTS. - The syntype series was reared from egg cases of *Tarachodes saussurei* (= *saussurii*) (Mantidae).

***tatiana*** (Bouček). PALEARCTIC: Spain. **New combination.**

*Iridophagoides tatiana* Bouček 1976a:182-183 (Figs. 2-3). Holotype ♀, La Herradura, Spain (BMNH, examined); 1 ♀ paratype, Santa Elena, Spain; 1 ♂ paratype, nr. Nerja, Spain.

### ***Pradontomerus* Bouček (text, p. 127)**

*Pradontomerus* Bouček 1978:120-121. Type-species: *Pradontomerus hyper* Bouček (orig. desig. and monotypic).

***hyper*** Bouček. AFROTROPICAL: Tanzania, Zimbabwe.

*Pradontomerus hyper* Bouček 1978:121 (Figs. 53, 54). Holotype ♀, Rongai, Kilimanjaro, Tanzania (BMNH, examined); 4 ♀ paratypes same as holotype; 2 ♂ paratypes, Salisbury, Rhodesia (= Zimbabwe) (PPRI).

HOST. - Specimens from Tanzania reared from *Gelis* sp. (Ichneumonidae) cocoons on plants infested with *Dasychira* sp. I have also seen specimens reared from *Meteorus* sp. (Braconidae) cocoons (new record) from Zimbabwe (in USNM).

***Propachytomoides* Girault (text, p. 156)**

- Podagrionella* Girault 1914/201:47. Type-species: *Podagrionella fasciatipennis* Girault (orig. desig. and monotypic). [Preoc. by *Podagrionella* Girault 1913e.] [Synonymized by Bouček 1988:142.]  
*Propachytomoides* Girault 1917/334:152. Type-species: *Propachytomoides semialbiclavus* Girault (orig. desig. and monotypic).

***fasciatipennis* (Girault).** AUSTRALIAN: Australia (Queensland).

- Podagrionella fasciatipennis* Girault 1914/201:47. 3 ♀ syntypes Nelson (= Gordonvale), Australia (QM, examined).  
*Propachytomoides semialbiclavus* Girault 1917/334:152. Holotype ♀, Brooklyn, Australia (USNM, examined). **New synonymy.**

TAXONOMY. - Dahms (1984) discussed the syntypes of *P. fasciatipennis*. Bouček (1988) transferred the species to *Propachytomoides*. According to Girault (1917/334) the type of *P. semialbiclavus* is supposed to be in the Queensland Museum. Dahms (1986) stated that the type was not there. For some reason it was placed in the USNM many years ago and is still there. I have seen the types of both species, as well as a number of specimens from the QM, and they are conspecific, in my opinion.

***pentlandensis* (Girault).** AUSTRALIAN: Australia (Queensland).

- Podagrionella pentlandensis* Girault 1913/170:427-428. Holotype ♀, Pentland, Australia (QM).  
 TAXONOMY. - Dahms (1986) discussed the type. Bouček (1988) transferred the species to *Propachytomoides*.

***spilopteron* (Cameron).** AUSTRALIAN: Australia (New South Wales; West Australia, Bouček 1988; Tasmania, Girault 1927/416).

- Podagrion spilopteron* Cameron 1912:645. Lectotype ♀ [designated by Bouček 1988:142], Cooma, Australia (BMNH).  
 TAXONOMY. - The original number of specimens was unspecified, but Bouček (1988) selected the lectotype from "two syntypes." Girault (1918) transferred the species to *Propodagrion*. Bouček (1988) transferred it to *Propachytomoides*.

***Propalachia* Bouček (text, p. 138)**

*Propalachia* Bouček 1978:101. Type-species: *Propalachia infumata* Bouček (orig. desig.).

***beaveri* Bouček.** ORIENTAL: Malaysia; Thailand (Bouček 1978).

- Propalachia beaveri* Bouček 1978:103 (Fig. 19). Holotype ♀, Penang, Malaysia (BMNH, examined); 5 ♀, 3 ♂ paratypes same as holotype.

***infumata* Bouček.** AFTROTROPICAL: Zimbabwe, South Africa.

- Propalachia infumata* Bouček 1978:102-103. Holotype ♀, Salisbury, Zimbabwe (BMNH,

examined); 1 ♂ paratype same as holotype; 1 ♀ paratype Pondoland, South Africa; 1 ♀ Natal, South Africa.

**intermedia** Narendran. ORIENTAL: India.

*Propalachia intermedia* Narendran 1994:63-64 (Figs. 80-81). [Data for types omitted from paper.]

***Pseuderimerus*** Gahan (text, p. 90)

*Pseuderimerus* Gahan 1919:124. Type-species: *Pseuderimerus mayetiolae* Gahan (orig. desig. and monotypic).

*Lochitimorpha* Szelenyi 1957b:382. Type-species: *Lochitimorpha semiaenea* Szelenyi (orig. desig. and monotypic). [Synonymized earlier in the present work.]

**femoratus** Gahan. NEARCTIC: USA (California).

*Pseuderimerus femoratus* Gahan 1933:32. Holotype ♀, Altamont, California, USA (USNM, examined).

**flavus** (Nikol'skaya). PALEARCTIC: CIS (Tadzhikistan: Bouček 1965).

*Ditropintous flavus* Nikol'skaya 1952:140 (described in key with no further information).

TAXONOMY. - Bouček (1965) transferred the species and compared it to *luteus*.

Zerova and Seregina (1990, Figs. 2, 4-6) illustrated *flavus* and included it in a key.

HOSTS. - The original description cited the species from isosome (= *Tetramesa*: Eurytomidae) pupae in wheat stems.

**indicus** (Subba Rao and Bhatia). ORIENTAL: India (Delhi). PALEARCTIC: Sudan (Bouček 1978).

*Liodontomerus indicus* Subba Rao and Bhatia 1962:125-127 (Figs. 1-5). Holotype ♀, Delhi, India (Indian Agricultural Research Institute, New Delhi); unspecified number of paratypes same as holotype.

TAXONOMY. - Earlier in this paper I transferred this species from *Liodontomerus* to *Pseuderimerus* and explained the reasons. Mani (1989) and Narendran (1994) redescribed females and males.

HOST. - The type series was reared from seeds of *Foeniculum vulgare* infested with *Systole albipennis*. Bouček (1978) reported it from "yansoon" seed in Sudan.

**luteolus** Zerova and Seregina. PALEARCTIC: CIS (Tadzhikistan).

*Pseuderimerus luteolus* Zerova and Seregina 1990:146-148 (Figs. 1, 1-8). Holotype ♀, Kondara, Tadzhikistan (?IZU); 17 ♀, 1 ♂ paratypes same as holotype.

HOSTS. - The holotype was reared from "cells of gall makers" living in stems of *Cousinia radians* (Asteraceae) and paratypes from stems of *C. refracta*. The gall makers were all Cynipidae, and a list of 6 potential host species were given: *Asiocynips cousinia*, *A. caulina*, *Phanacis compactus*, *P. cousinia*, *Aulacidea sicolor* and *A. parvula*.

***luteus*** Bouček. PALEARCTIC: Czechoslovakia, Hungary; Morocco (Bouček 1978), CIS (Ukraine: Zerova and Seregina 1990).

*Pseuderimerus luteus* Bouček 1954a:70 (Fig. 4). Holotype ♀, Lysa Labem, Czechoslovakia (NMP); 1 ♂ paratype Budapest, Hungary.

TAXONOMY. - Zerova and Seregina (1990, Figs. 2, 1-3) illustrate *luteus* and included it in a key.

HOST. - Bouček (1978) reported this species from barley stubble containing *Mayetiola* (as *Phytophaga*) *destructor* (Cecidomyiidae) in Morocco.

***mayetiolae*** Gahan. NEARCTIC: USA (California).

*Pseuderimerus mayetiolae* Gahan 1919a:125-126 (Fig. 2). Holotype ♀, Altamont (= Altamont), California, USA (USNM, examined); 2 ♀, 2 ♂ paratypes same as holotype; 3 ♀, 1 ♂ paratypes Concord, California, USA; 2 ♀, 2 ♂ paratypes Benecia, California, USA.

TAXONOMY. - Gahan (1933) redescribed and illustrated this species.

HOST. - The type series was reared from *Mayetiola destructor* (Cecidomyiidae).

MORPHOLOGY - Hill and Pinckney (1940) illustrated the larval and pupal exuvium of this species. They also present a key to parasites of the hessian fly, based upon remains left in the host puparium.

***semiaenea*** (Szelenyi). PALEARCTIC: Hungary.

*Lochitomorpha semiaenea* Szelenyi 1957b:386-387 (Fig. A). Holotype ♀, Somlovasarhely, Hungary (HNHM, examined).

TAXONOMY. - Earlier in this paper I transferred *semiaenea* to *Pseuderimerus*.

***semiflavus*** Gahan. NEARCTIC: USA (California).

*Pseuderimerus semiflavus* Gahan 1933:33. Holotype ♀, Birdsw Landing, California, USA (USNM, examined).

HOST. - The type was taken from a puparium of *Mayetiola* (as *Phytophaga*) *destructor* (Cecidomyiidae).

### ***Pseudotorymus*** Masi (text, p. 107)

*Holaspis* Mayr 1874:83. Type-species: *Torymus militaris* Boheman (desig. by Ashmead 1904a:242, 377). [Preocc. by Gray 1863 (Reptilia).]

*Eridontomeroidella* Girault in Ramakrishna Ayyar 1919:935. Type-species: "*Eridontomeroidella gibboni* Girault" (monotypic). [*Nomen nudum.*] [Earlier in the present work I explained the placement of this name.]

*Pseudotorymus* Masi 1921b:235. Objective replacement name for *Holaspis* Mayr nec Gray 1863.

*Senegalella* Risbec 1951a:289. Type-species: *Senegalella acythopeusi* Risbec (desig. by Bouček 1976b:347). [Synonymized earlier in the present work.]

*Thiesia* Risbec 1951a:292. Type-species: *Thiesia gallephila* Risbec (monotypic). [Synonymized earlier in the present work.]

***acythopeusi*** (Risbec). AFROTROPICAL: Senegal; Ruanda (Republic of the Congo; Risbec 1957), Madagascar (de Luca 1965a). **New combination.**

*Senegalella acythopeusi* Risbec 1950:265. [*Nomen nudum.*]

*Senegalella acythopeusi* Risbec 1951a:290-291 (Figs. 147 a,c,d.). Lectotype ♀, herein designated, Bambey, Senegal (MNH, examined); 9 ♀, 3 ♂ paralectotypes same as lectotype.

*Senegalella acthopoensi* Auriv. [sic]: de Luca, 1965a. [*Lapsus profundus.*]

TAXONOMY. - Bouček (1976b:347) stated that this species had been confused with the Nearctic species *Microdontomerus anthonomi*. I have seen the types of both species and the overall similarity is striking. Their differences, however, are equally striking: *Senegalella acythopeusi* has an occipital carina, an asetose frenal area, and hindcoxa with dorsal setae; *Microdontomerus anthonomi* has no occipital carina, a setose frenal area, and the hindcoxa without dorsal setae.

HOSTS. - All records are from Bruchidae. The lectotype was reared from the pupa of *Acythopeus traghardi*. de Luca (1965a:75) listed also *Callosobruchus maculatus* and questionably *Bruchidius albosparsus* as hosts of this species.

***africanus*** (Crosby). AFROTROPICAL: Mozambique; Senegal (Etienne and Delvare 1987). **New combination.**

*Hemitorymus africanus* Crosby 1909:80-81. Lectotype ♀ [designated by Bouček 1978], Zumbo, East Africa [= Mozambique] (Cornell University, Ithaca); 4 ♀, 13 ♂ paralectotypes same as lectotype (1 ♀, 1 ♂ paralectotype examined, BMNH).

TAXONOMY. - Bouček (1978) transferred this species from *Hemitorymus* (= *Torymus*) to *Antistrophoplex*. This transfer, however, was incorrect. Based upon the presence of an occipital carina, a single anellus, a sessile stigma, and emarginate metasomal terga this species should be placed as *Pseudotorymus*. Etienne and Delvare (1987) included the species in a key to hymenopterous parasites of diakhatou fruit (*Solanum aethiopicum*) (Solanaceae) in Senegal.

HOST. - The type series was reared from *Tetraspondylia terminaliae* (as *Asphondylia*: Cecidomyiidae). Etienne and Delvare (1987) reported it as a hyperparasite of *Eurytoma* sp. (Eurytomidae) and *Catolaccus* sp. (Pteromalidae) attacking *Asphondylia* and of *Bracon* sp. (Braconidae) attacking *Scrobipalpa* (Gelechiidae), all in the fruit of *Solanum aethiopicum* (Solanaceae).

***amethystinus*** Steffan. PALEARCTIC: Algeria.

*Pseudotorymus amethystinus* Steffan 1962a:183-184 (Fig. 5). Holotype ♀, Collo, Algeria (NMHN); 1 ♀ paratype, El Kantour, Algeria.

***amuthae*** Narendran. ORIENTAL: India (Tamil Nadu).

*Pseudotorymus amuthae* Narendran 1994:50-51 (Figs. 732-733). Holotype ♀, Padappai, Tamil Nadu, India (UCK).

HOST. - The type was associated with *Jasminum sambac*.

***arvernicus*** (Walker). PALEARCTIC: France.

*Callimome arvernicus* Walker 1833:134. Lectotype ♀ [designated by Eady 1959:269], "S. of France," (BMNH).

TAXONOMY. - Eady (1959:269) transferred this species.

***australis*** (Risbec). AFROTROPICAL: Madagascar. **New combination.**

*Senegalella australis* Risbec 1956:159-160. 2 ♀ syntypes, Ankaratra, Manjakatempo (MHNH, examined).

TAXONOMY. - A lectotype needs to be selected for this species.

HOSTS. - Reared from a gall on a liana stem and from galls on the root of an orchid.

**brassicae** Ruschka. PALEARCTIC: Czechoslovakia, Germany, Austria; Italy (Solinas and Bucci 1982).

*Pseudotorymus brassicae* Ruschka 1923:404-406 (Figs. 3-6). ♀, ♂ syntypes (number unstated), Prague, Czechoslovakia; Vienna, Austria; Naumburg, Germany (?NMW).

HOSTS. - All records are from Cecidomyiidae. The type series was reared from *Dasineura brassicae* on *Brassica napus oleifera* (Cruciferae) in Czechoslovakia and *Dasineura sisymbrii* in Austria. Solinas and Bucci (1982) reported the species as an ectoparasite of *Gephyraulus* (as *Paragephyraulus*) *diplotaxis* and *Contarina* sp. in flowers of *Diplotaxis muralis* (Cruciferae) in Italy.

**brevicaudis** Erdős. PALEARCTIC: Hungary.

*Pseudotorymus brevicaudis* Erdős 1956:186-187 (Fig. 4). Holotype ♀, Szigetszentmiklos, Hungary (lost).

TAXONOMY. - According to Thuroczy (1992:131) the type is lost.

**capreae** (Walker). PALEARCTIC: France.

*Callimome capreae* Walker 1833:132. Lectotype ♀ [designated by Eady 1959:269], "vicinity of Paris", France (BMNH).

TAXONOMY. - Eady (1959) transferred this species and believed that *krygeri* Hoffmeyer might be a synonym of it.

**cupreus** Erdős. PALEARCTIC: Hungary; Mongolia (Szelenyi 1973).

*Pseudotorymus cupreus* Erdős 1955:287-288 (Figs. 2f-g). Holotype ♀, Tompa, Hungary (HNHM, confirmed by Thuroczy 1992:131).

**dubius** (Nees). PALEARCTIC: Austria, Italy (Masi 1933), Mongolia (Szelenyi 1973), CIS (Ukraine: Nikol'skaya and Zerova 1978).

*Torymus dubius* Nees 1834:72. Lectotype ♀ [designated by Graham 1988:24], Germany (OUM).

*Holaspis apionis* Mayr 1874:84. ♀, ♂ syntypes (number unstated), Austria (?NMW). [Synonymized by Graham 1988:24.]

HOST. - The type series of *apionis* was reared from seed heads of *Trifolium pratense* (Fabaceae) containing *Apion apricans* (Curculionidae). Nikol'skaya and Zerova (1978) listed *Apion craccae* as a host (for *apionis*).

**frontinus** (Walker). PALEARCTIC: England, Austria.

*Callimome frontinus* Walker 1851:214-215. Lectotype ♀, [designated by Eady 1959:269], England (OUM).

*Holaspis carinata* Mayr 1874:85-86. Unknown number of ♀ syntypes, Austria (?NMW, see Rushka 1923:403). [Synonymized by Eady 1959:269.]

TAXONOMY. - Ruschka (1923:403) apparently was the first to transfer *carinata* to *Pseudotorymus*. Eady (1959:269) transferred *frontinus*.

***gallephila* (Risbec). AFROTROPICAL: Senegal, Madagascar. New combination.**

*Thiesia gallephila* Risbec 1951a:293-294 (Figs. 136c, 138c). 2 ♀ syntypes, Bambey, Senegal (MNHN, examined).

*Thiesia gallephila madagascariensis* Risbec 1956:151-152 (Fig. 3e). Syntype series from Manakambahiny, Mandraka, and Mitsingo (MNHN, examined, exact numbers not stated). **New synonymy.**

**TAXONOMY.** - I have seen the 2 female syntypes of *T. gallephila* from Senegal, and 2 female, 1 male syntypes of *T. g. madagascariensis* from Madagascar. These specimens show no morphological differences, and I consider them to be synonyms. Lectotypes should be chosen for both subspecies, but I have not done so because of their poor condition and because I have not seen all of the type material. Risbec (1954a:535) synonymized *Thiesia* with *Lochitites* (now = *Idiomacromerus*), but this is incorrect.

**HOST.** - The type series of *gallephila gallephila* was reared from galls on *Guiera senegalensis* (Combretaceae). The type series of *gallephila madagascariensis* was reared from leaf galls on "Hazotokana" (common name for *Brachylaena ramiflora*; Asteraceae), a leaf gall on *Dalbergia* sp. (Fabaceae), and a leaf gall on "*Mantalia (terminalis)*" (= *Mantalania* sp.). [There is no plant genus "*Mantalia*," but *Mantalania* was described from near the type locality of Mitsingo (Wasshausen, pers. comm.) and is undoubtedly what Risbec was referring to when he gave the host. There is no species "*terminalis*," which Risbec gave italicized in parentheses, and he may have meant that the leaf galls were at the terminals of branches.]

***harithavarnus* Nardendran. ORIENTAL: India (Kerala, Karnataka).**

*Pseudotorymus harithavarnus* Nardendran 1994:48-49. Holotype ♀, University of Calicut, Kerala, India (UCK); 3 ♀ paratypes, same data as holotype; 6 ♀ paratypes, Kayamkulam, Kerala, India; 1 ♀ paratype, Kundukadu, Kerala, India; 3 ♀, 2 ♂ paratypes, Bangalore, Karnataka, India.

**HOST.** - The specimens from Bangalore were reared from a caterpillar boring into pods of *Cajanus indicus* (Fabaceae).

***hirsuticornis* Szelenyi. PALEARCTIC: Mongolia.**

*Pseudotorymus hirsuticornis* Szelenyi 1973:200-201 (Fig. 4d). Holotype ♀, 12 km se Zentrum, Mongolia (HNHM, confirmed by Thuroczy 1992:131).

***ignisplendens* Szelenyi. PALEARCTIC: Mongolia.**

*Pseudotorymus ignisplendens* Szelenyi 1973:198-200. Holotype ♀, 14 km sw Somon Bajan-dalaj, Mongolia (HNHM, confirmed by Thuroczy 1992:132); 3 ♀, 26 ♂ paratypes same as holotype; 1 ♀ paratype, 47 km e Grenzposten Caganbulag, Mongolia; 1 ♀ paratype, 11 km s Pass Zosijn, Mongolia; 2 ♀ paratypes, 2-3 km se Salzee Dund, Mongolia.

***indicus* (Mani). ORIENTAL: India (Uttar Pradesh; Tamil Nadu, Kerala: Mani 1989).**

*Holaspis indicus* Mani 1944:153-154 (Figs. 8-11). Holotype ♀, Dehra Dun, India (IARD); ♀, ♂ paratypes (number unspecified) same as holotype.

TAXONOMY. - Farooqi (1986:272) transferred the species, and Mani (1989) re-described and illustrated the females and males. Narendran (1994) also re-described the species.

HOST. - The type series was reared from "flower bud galls" on *Dalbergia sissoo* (Fabaceae). Mani (1989) listed the host as "leafcutting bee."

**krygeri** Hoffmeyer. PALEARCTIC: Denmark.

*Pseudotorymus krygeri* Hoffmeyer 1931:261-262 (Fig. 9). 4 ♀, 4 ♂ syntypes, Korsor Skov, Denmark (ZMC).

TAXONOMY. - Eady (1959) suggested that species could be a synonym of *P. capreae* Walker.

HOST. - The type series is from *Dasyneura terminalis* (Cecidomyiidae) on *Salix* (Salicaceae).

**lazulellus** (Ashmead). NEARCTIC: USA (Colorado; Connecticut: Viereck 1916). Canada (Ontario: Putman 1935; New Brunswick, Quebec: Burks 1967).

*Syntomaspis lazulella* Ashmead 1890:26. Holotype ♀, "Colorado", USA (USNM, examined).

TAXONOMY. - Peck (1951:530) transferred the species.

HOST. - The type was reared from a gall on *Rudbeckia* sp. (Asteraceae). Additional records summarized by Peck (1963) and Grissell (1979) are: Eurytomidae: *Tetramesa albomaculatum*, *Tetramesa* sp. in *Secale cereale* (Poaceae); Cecidomyiidae: *Dasyneura leguminicola*; and unknown insects in *Quercus* (Fagaceae) galls and *Trifolium* (Fabaceae) heads. Some of these hosts are probably incorrect and need verification.

**leguminosae** (Risbec). AFROTROPICAL: Senegal; Mali (Risbec 1955), Sudan (Risbec 1950), Nigeria (Bouček 1976b), Ivory Coast (Rasplus 1990), Mozambique (Risbec 1955). ORIENTAL: India (Tamil Nadu: Ramakrishna Ayyar 1919). **New combination.**

*Eridontomeroidella gibboni* Girault in Ramakrishna Ayyar 1919:935. [*Nomen nudum.*]

*Senegalella leguminosae* Risbec 1950:330 (Fig. 1230a). [*Nomen nudum.*]

*Senegalella leguminosae* Risbec 1951a:292 (Fig. 147b). 10 ♀, 2 ♂ syntypes, Bambey, Senegal (MNHN, examined).

*Antistrophoplex leguminosae* (Risbec); Bouček 1976b:347. [New combination.]

TAXONOMY. - As explained earlier in this paper (p. 109), I discovered specimens of *E. gibboni* in the USNM collection. They are identical to *S. leguminosae*, but because *E. gibboni* was never described, it holds no place in priority, even though it is an older name. Bouček (1976b:347) placed *S. leguminosae* in the genus *Antistrophoplex* (and in 1982 in *Microdontomerus*) but this was in error as I explained earlier (p. 79).

HOSTS. - Originally, 2 females were reared in Senegal from pods of *Acacia arabica* (Fabaceae) and were possibly parasitic on *Bruchidius albosparsus* (Bruchidae; cited as *albospassus*) which lived in the pods (Risbec 1951a). Risbec (1950) also reported rearing this species from the bruchid *Bruchidius baudoni* on *Acacia seyal* in Mali and the French Sudan and from this *Acacia* in Senegal (1951b). Also he reported it (1951b) from "graines de Niebe" (= *Vigna sinensis*; Fabaceae) "without doubt parasites of bruchids". De Luca (1964, 1965a,



1965b) repeated these citations in various lists of bruchid parasites. Rasplus (1990) added the following bruchids as hosts from Ivory Coast: *Bruchidius akaensis*, *B. albizziarum*, *B. ineaci*, *B. leonensis*, *B. mabwensis*, *B. submaculatus*, and *B. uberatusz* as well as the eurytomid *Risbecoma capensis*. [Hosts given in the same paper as *Bruchidius securiger*, *B. dichrostachydis*, and *B. lamtoensis* are unpublished names, Rasplus in *litt.*.]

**leguminus** Ruschka. PALEARCTIC: Czechoslovakia; ?Austria, CIS (Ukraine: Nikol'skaya and Zerova 1978).

*Pseudotorymus leguminum* Ruschka 1923:404. 2 ♀, 1 ♂ syntypes, "Mayr Collection," 1 ♀ syntype, nr Eisenstadt and Turnau, Czechoslovakia (NMW).

HOSTS. - The host of the Mayr material was "most likely" *Contarinia silvestris* (Cecidomyiidae) on *Lathyrus silvestris* (Fabaceae) and of the single female syntype, *Contarinia onobrychidis* on *Onobrychis sativa* (Fabaceae).

**medicaginis** (Mayr). PALEARCTIC: Austria, CIS (Ukraine: Nikol'skaya and Zerova 1978), Mongolia (Szelenyi 1973).

*Torymus medicaginis* Mayr 1874:127. Unknown number of ♀ syntypes, Austria (NMW).

TAXONOMY. - The transfer was first made by Ruschka (1923:404) who commented on the type.

HOSTS. - The type series was reared from galls on *Medicago falcata* (Fabaceae) from which *Contarinia* (as *Cecidomyia*) *loti* emerged (Cecidomyiidae) (Hoffmeyer (1930d) gave the host as *Dasineura* sp.). Szelenyi (1973) reported this species reared from *Vicia cracca* pods and *Vicia tenuifolia* (Fabaceae) root galls in Mongolia.

**mesembryanthemumi** (Cameron). AFROTROPICAL: South Africa. **New combination.**

*Torymus mesembryanthemumi* Cameron 1904:109. Lectotype ♀ [designated by Bouček 1976b:348], Pearston, South Africa (BMNH, examined).

*Antistrophoplex mesembryanthemumi* (Cameron). [Valid emend. by Bouček 1976b:348.]

TAXONOMY. - Bouček (1976b) transferred this species to *Antistrophoplex* (= *Microdontomerus*). The occipital carina, single anellus, sessile stigma, and emarginate abdominal terga place this as a species of *Pseudotorymus*.

HOST. - The type was reared from a bud gall on *Mesembryanthemum* (Aizoaceae).

**metallicus** (Risbec). AFROTROPICAL: Republic of the Congo. **New combination.**

*Senegalella metallica* Risbec 1957:213-215. Holotype ♀, Ruhengeri, Kagogo, Ruanda (MRCB).

TAXONOMY. - Risbec (1957:216) described a "variation" of *metallica* also from Ruanda, but he did not give this variation a name.

**militaris** (Boheman). PALEARCTIC: Sweden; CIS (Ukraine: Nikol'skaya and Zerova 1978), Turkey (Doganlar 1984).

*Torymus militaris* Boheman 1834:338-339. ♀ syntype(s) (number unknown), Sweden (depository unknown).

TAXONOMY. - Thomson (1876) transferred the species to *Holaspis*, and Ruschka

(1923:404) transferred it to *Pseudotorymus*.

HOST. - The type series was associated with grasses. Nikol'skaya and Zerova (1978) associate the species with *Salix*.

**napi** (Amerling and Kirchner). PALEARCTIC: Czechoslovakia.

*Torymus napi* Amerling and Kirchner, in Kirchner 1860:72. ♀ syntype(s), Prague, Czechoslovakia (depository unknown).

TAXONOMY. - Hoffmeyer (1931:261) was apparently the first to use this combination.

HOST. - The type(s) were reportedly reared from "*Diplosis ochracea*" (Cecidomyiidae) apparently in rape seed (*Brassica napus*: Cruciferae). According to R. Gagne (pers. comm.) it is highly likely that the true host is the cecidomyiid *Dasineura brassicae*.

**nepthys** (Walker). PALEARCTIC: England.

*Callimome nepthys* Walker 1848a:219. Lectotype ♀ [designated by Eady 1959:269], nr. Newcastle, England (BMNH).

TAXONOMY. - Eady (1959:269) transferred the species.

**pannonicus** (Mayr). PALEARCTIC: Hungary; CIS (Ukraine: Nikol'skaya and Zerova 1978), Turkey (Doganlar 1984).

*Holaspis pannonica* Mayr 1874:86. Holotype ♀, Hungary (?NMW).

TAXONOMY. - Ruschka (1923:406) transferred the species but could not find the Mayr types in NMW.

**papaveris** Thomson. PALEARCTIC: Sweden; Spain (Nieves Aldrey and Chicote 1986), CIS (Ukraine: Nikol'skaya and Zerova 1978), Mongolia (Szelenyi 1973).

*Holaspis papaveris* Thomson 1876:100. Syntype(s) sexes and numbers unknown, [? ♂ syntype, Oland, Sweden, MZL].

TAXONOMY. - Hansson (1991:11) stated that a possible male syntype was in the MZL.

HOSTS. - Nikol'skaya and Zerova (1978) reported the species from the cecidomyiids *Dasineura papaveris* and *Lestodiplosis callida*. Nieves Aldrey and Chicote (1986) reported the species from the cynipid *Aylax papaveris* in *Papaver* sp.

**parellinus** (Boheman). PALEARCTIC: Sweden.

*Torymus parellinus* Boheman 1834:372-373. ♂ syntype(s), Sweden (depository unknown).

**pulchellus** Masi. PALEARCTIC: Libya.

*Pseudotorymus pulchellus* Masi 1929:219-221 (Figs. 5i,k). Holotype ♀, Giarabub, Libya (MCSN).

**reticulatus** Szelenyi. PALEARCTIC: Mongolia.

*Pseudotorymus reticulatus* Szelenyi 1973:201-201. Holotype ♀, 15 km n Somon Galuut, Mongolia, CIS (HNHM, confirmed by Thuroczy 1992:132); 18 ♀, 14 ♂ paratypes from numerous localities in Mongolia.

**rosarum** (Zerova and Seregina). PALEARCTIC: CIS (Tadzhikistan). **New combination.**

*Adontomerus rosarum* Zerova and Seregina 1992:460-462 (Pl. 2, Figs. 1-6). Holotype ♀, Kandara, Tadzhikistan, CIS (IZU); 7 ♀, 9 ♂ paratypes same data (examined, in part).

TAXONOMY. - I examined a paratype female loaned by Zerova. Based upon wing veins (marginal vein 7 times length of stigmal vein and 4 times length of post-marginal vein), the well developed occipital carina (reaching midway to hypostomal carina), and straight anterior metapleural margin, this species is a member of the Torymoidini. I place it in the genus *Pseudotorymus*, based upon the single anellus. The hindfemur is not toothed but is ventrally barely serrate.

HOST. - The type series was reared from galls of *Diplolepis fructuum* (Cynipidae).

**salemensis** Narendran. ORIENTAL: India (Tamil Nadu).

*Pseudotorymus salemensis* Narendran 1994:50-51 (Figs. 732-733). Holotype ♀, North Salem, Tamil Nadu, India (BMNH).

**salicinus** Erdős. PALEARCTIC: Hungary.

*Pseudotorymus salicinus* Erdős 1956:185-186 (Figs. 3a-c, e). Lectotype ♀ [designated by Thuroczy 1992:132], Vac, Hungary (HNHM, confirmed by Thuroczy 1992:132); 3 ♂ paralectotypes same as lectotype (HNHM, part).

**salicis** Ruschka. PALEARCTIC: Germany, Austria.

*Pseudotorymus salicis* Ruschka 1923:403. 3 ♀ syntypes, Vienna, Austria; 1 ♀ syntype, Germany (NMW).

HOST. - The type series was reared from *Dasineura* (as *Rhabdophaga*) *rosaria* (Cecidomyiidae) on *Rosa* (Rosaceae) and from *Nematus vallisnerii* (now = *Pontania proxima*; Tenthredinidae). Nikol'skaya and Zerova (1978) list also *Pontania capreae* (now = *proxima*; Tenthredinidae) as host.

**salviae** Ruschka. PALEARCTIC: Germany.

*Pseudotorymus salviae* Ruschka 1923:403-404. ♀, ♂ syntypes (number unspecified), Naumburg, Germany (Biologischen Reichsanstalt für Land- und Forstwirtschaft, Naumburg, Germany).

HOSTS. - The type series was reared from cecidomyiid galls on *Salvia pratensis* (Lamiaceae).

**sanguinalis** Erdős. PALEARCTIC: Hungary.

*Pseudotorymus sanguinalis* Erdős 1957:349-350 (Fig. 3a). Holotype ♀, Peszer, Hungary (not in HNHM, confirmed by Thuroczy 1992:132); 2 ♀, 1 ♂ paratypes same as holotype.

TAXONOMY. - Thuroczy (1992:132) stated that no type material is at HNHM.

HOST. - The types were reared from *Pyrausta sanguinalis* (Pyrilidae).

**sapphyrinus sapphyrinus** (Fonscolombe). PALEARCTIC: France.

*Cinips sapphyrina* Fonscolombe 1832:285. Syntype(s) sexe(s) and number unknown, France (depository unknown).

TAXONOMY. - Fonscolombe (1840:191) transferred *sapphyrinus* to *Callimome*. Mayr (1874:109) moved it to *Torymus*. Hoffmeyer (1930d:239) treated it as

*Callimome*. To my knowledge, Szelenyi (1973) was the first to treat this species as a *Pseudotorymus*.

HOST. - The type(s) was reared from galls on "*Eryngii campestris*" (= *Eryngium campestre*; Umbelliferae) and galls on *Rosa eglanteriae* (Rosaceae). Bouček (1977) gave the host on *Eryngium* as the cecidomyiid *Thomasiella* (now = *Lasioptera*) *eryngii*.

***saphyrinus mongolicus*** Szelenyi. PALEARCTIC: Mongolia.

*Pseudotorymus saphyrinus mongolicus* Szelenyi 1973:198. Holotype ♀, 12 km w Somon Lun, Mongolia, CIS (HNHM, confirmed by Thuroczy 1992:133).

HOST. - The types were reared from *Lasioptera* (as *Thomasiella*) *eryngii* (Cecidomyiidae).

***semicarinatus*** Erdős. PALEARCTIC: Hungary.

*Pseudotorymus semicarinatus* Erdős 1956:184-185 (Fig. 11). Holotype ♀, Budapest, Hungary (HNHM, confirmed by Thuroczy 1992:133).

TAXONOMY. - Erdős (1956:184) cited Figure 2 for this species but this is a mistake. It should be Figure 11.

***stachidis*** (Mayr). PALEARCTIC: Austria.

*Holaspis stachidis* Mayr 1874:84-85. 1 ♀, 5 ♂ syntypes, Austria, (NMV, see Ruschka 1923:403).

*Holaspis stachys* Mayr. Dalla Torre 1898:291. [Invalid spelling.]

TAXONOMY. - Hoffmeyer (1930d:260) was the first to transfer this species to *Pseudotorymus*.

HOST. - The type series was reared from galls on *Stachys sylvatica* (Lamiaceae). Hoffmeyer (1930d) listed *Wachtliella stachydis* (Cecidomyiidae) as a host.

***verbasci*** Erdős. PALEARCTIC: Hungary.

*Pseudotorymus verbasci* Erdős 1955:287 (Figs. 2d-e). Holotype ♀, Hogyesz, Hungary (HNHM, confirmed by Thuroczy 1992:133).

HOST. - The type was reared from *Asphondylia* (as *Ischnonyce*) *verbasci* (Cecidomyiidae) in flowers of *Verbascum asutriaci* (Schrophulariaceae).

***vittiger*** Ruschka. PALEARCTIC: Austria.

*Pseudotorymus vittiger* Ruschka 1923:406. 2 ♀ syntypes, Modling, Austria, 1 ?♂ syntype, Pfaffstatten, Austria [?NMW].

***Rhynchodontomerus*** Novicky and De Santis (text, p. 122)

*Rhynchodontomerus* Novicky and De Santis 1961:25-26. Type-species: *Monodontomerus inclusus* Kiefer and Jorgensen (monotypic).

***inclusus*** (Kieffer and Jorgensen). NEOTROPICAL: Argentina.

*Monodontomerus inclusus* Kieffer and Jorgensen 1910:384-385. ♀, ♂ (numbers and depository not given), Prov. Mendoza, Argentina.

TAXONOMY. - Novicky and De Santis (1961) illustrated this species (Figs. 1-4).

HOST. - The type series was reared from *Clistoses artifex*: (now = *Cecidoses eremia*, Cecidosidae).

***Rhynchotocida* Bouček (text, p. 131)**

*Rhynchotocida* Bouček 1978:116. Type-species: *Rhynchotocida ovivora* Bouček (orig. desig.).

***caudata* Bouček.** ORIENTAL: Philippines. AUSTRALIAN: Indonesia (Irian Jaya), Papua New Guinea.

*Rhynchotocida caudata* Bouček 1978:119 (Figs. 50-52). Holotype ♀, Bomberi, Vogelkop, New Guinea (BPBM); 1 ♂ paratype, Maprik, New Guinea; 1 ♂ paratype, near Kokoda, Papua; 1 ♀ paratype, Jacmal Bunhian, Ifugao Prov., Philippines.

***frenalis* Bouček.** ORIENTAL: Laos.

*Rhynchotocida frenalis* Bouček 1978:120 (Figs. 48,49). Holotype ♀, de Tha Ngnone, Gi Siop Village, Vientiane Prov., Laos (BPBM).

***maai* Bouček.** ORIENTAL: Malaysia (Sarawak, Sabah), Singapore, Laos, Vietnam, Philippine Islands.

*Rhynchotocida maai* Bouček 1978:118-119 (Figs. 46, 47). Holotype ♀, Lake Area, Bau, Sarawak, Malaysia (BPBM); 1 ♀ paratype, Wapi, Laos; 2 ♂ paratypes, Fyan, Vietnam; 1 ♂ paratype, Singapore; 1 ♂ paratype, Bidi, Sarawak, Malaysia; 1 ♂ paratype, Sandakan, Borneo, Malaysia; 1 ♂ paratype, Pili, Luzon, Philippine Islands (BMNH, BPBM).

***ovivora* Bouček.** ORIENTAL: Malaysia (Peninsular Malaysia).

*Rhynchotocida ovivora* Bouček 1978:117-118 (Figs. 43-45). Holotype ♀ Trengganu, Malaysia (BMNH, examined); 1 ♂ paratype same as holotype.

HOST. - Reared from heteropterous eggs on cocoa.

***tridens* Bouček.** ORIENTAL: India (Karnataka).

*Rhynchotocida tridens* Bouček 1978:120 (Figs. 41, 42). Holotype ♀, near Mysore, India (BMNH, examined); 2 ♀ paratypes same as holotype.

TAXONOMY. - Narendran (1994) redescribed this species based upon the type female.

***Stenotorymus* Masi (text, p. 170)**

*Stenotorymus* Masi 1938:207. Type-species: *Stenotorymus linearis* Masi (monotypic).

I have seen apparently undescribed species from Malaysia (Borneo, Pahang: USNM), India (Tamil Nadu: CNC) and Thailand (BPBM).

***linearis* Masi.** AFROTROPICAL: Somalia.

*Stenotorymus linearis* Masi 1938:208-210 (Figs. a-f). Holotype ♀, Belet Amin, Somalia (MCSN, examined).

***Thaumatomyus* Ferrière and Novicky (text, p. 172)**

*Thaumatomyus* Ferrière and Novicky 1954:34. Type-species: *Thaumatomyus notanisoides* Ferrière and Novicky (orig. desig. and monotypic).

***notanisoides*** Ferrière and Novicky. PALEARCTIC: Tunisia, Yugoslavia; Algeria, Bulgaria, Azerbaijan, and Spain (Bouček 1977).

*Thaumatomyrmus notanisoides* Ferrière and Novicky 1954:35-37 (Figs. 1-5). 4 ♀, 2 ♂ syntypes, Tunisia; 1 ♀ syntype, Damatia, Yugoslavia (MHNG, MNHN).

TAXONOMY. - Ferrière and Novicky (1954) described this species from a type and cotypes, but did not state which specimen (male or female) or which locality referred to the type. Besuchet (per. comm.) confirmed that the "types and paratypes" of this species are in MHNG. HOST. - The types were reared from cynipid galls on *Hypochoeris* sp. (Asteraceae) (see also Wall 1984). Bouček (1977) listed the host as *Phanacis hypochoeridis* (Cynipidae).

### ***Torymoidellus*** Bouček (text, p. 113)

*Torymoidellus* Bouček 1988:136. Type-species: *Torymoidellus reticulatus* Bouček (orig. desig. and monotypic).

***reticulatus*** Bouček. AUSTRALIAN: Australia (Queensland).

*Torymoidellus reticulatus* Bouček 1988:137 (Figs. 194). Holotype ♀, Mt. Glorious, Queensland, Australia (BMNH, examined); 1 ♀ paratype same as holotype.

### ***Torymoides*** Walker (text, p. 110)

*Torymoides* Walker 1871b:37-38. Type-species: *Torymoides amabilis* Walker (monotypic).

*Dimeromicrus* Crawford 1910a:127. Type-species: *Dimeromicrus ashmeadi* Crawford (orig. desig. and monotypic). [Synonymized by Bouček 1988:135.]

*Macrodontomerus* Girault 1913/158:84 [September]. Type-species: *Macrodontomerus unimaculatus* Girault (monotypic). [Synonymized by Bouček 1988:135.]

*Macrodontomerus* Girault 1913/175:100 [December]. Type-species: *Macrodontomerus triangularis* Girault (orig. desig.). [Synonymized by Bouček 1988:135.]

*Didactyliocerus* Masi 1916:69. Type-species: *Didactyliocerus dispar* Masi (monotypic). [Synonymized by Bouček 1988:135.]

*Ameromicrus* Nikol'skaya, in Nikol'skaya and Kjaø 1954:411-412. Type-species: *Ameromicrus violaceus* Nikol'skaya (monotypic). [Synonymized earlier in the present work.]

*Pondorymus* Bouček 1978:124. Type-species: *Pondorymus latus* Bouček (orig. desig. and monotypic). [Synonymized earlier in the present work.]

***acaciae*** (Cameron). AUSTRALIAN: Australia (New South Wales).

*Callimone* [sic] *acaciae* Cameron 1912:643. Lectotype ♀ [designated by Bouček 1988:136], Erina, New South Wales, Australia (BMNH).

TAXONOMY. - Bouček (1988:136) transferred this species to *Torymoides*.

HOSTS. - Cameron described this species from small, "berry-like" galls on the foliage of *Acacia* (Fabaceae).

***affinis*** (Masi). ORIENTAL: Taiwan.

*Dimeromicrus affinis* Masi 1926a:7-8. 7 ♀ syntypes, "Tainan and Pollaha", Formosa (IPAL and/or MCSN).

***akdenizeus*** (Doganlar). PALEARCTIC: Turkey. **New combination.**

*Ameromicrus akdenizeus* Doganlar 1989:144-145 (Fig. 3). Holotype ♀, Yumurtalik, Adana, Turkey (Doganlar Collection); 6 ♀, 4 ♂ paratypes same as holotype (2 ♀, 1 ♂ in BNHM).

***aligherini*** (Girault). AUSTRALIAN: Australia (New South Wales; South Australia (Bouček 1988)).

*Macrodontomerus aligherini* Girault 1927/416:329-330. Holotype ♀, Sydney, New South Wales, Australia (SAM); 11 ♀, ♂ paratypes, Sydney and Melrose, New South Wales, Australia (Macleay Museum, SAM, ANIC and QM).

TAXONOMY. - Dahms (1983) discussed the rather complex type situation. Bouček (1988:37) transferred this species to *Torymoides*.

HOSTS. - Dahms (1983) gave paratype host information that Girault did not publish in his original description. According to paratype labels, this species was reared "from oval fleshy galls on leaves of *E. [Eucalyptus] haemastoma* [Myrtaceae] in inquilines".

***amabilis*** Walker. ORIENTAL: Sri Lanka; India (Kerala: Narendran 1984a).

*Torymoides amabilis* Walker 1871b:38. Holotype ♀, Sri Lanka (BMNH, examined).

TAXONOMY. - Narendran (1984a:114-116, Fig. III) described the male of *amabilis* for the first time and redescribed the female based upon specimens from India (deposited in Department of Zoology, University of Calicut, Kerala, India).

***anamalaianus*** (Mani and Kaul). ORIENTAL: India (Kerala, Tamil Nadu).

*Holaspis anamalaianus* Mani and Kaul 1972:313-316 (Figs. 1A-H, 2A-E). Holotype ♀, Anamalai Hills, Devikulam, India (School of Entomology, Agra); ♀, ♂ paratypes (number unspecified) same as holotype (some in USNM).

TAXONOMY. - Mani and Kaul (1972) listed many Indian localities of non-type material. Farooqi (1986) transferred this species to *Pseudotorymus*. Narendran (1994) transferred the species to *Torymoides* and I agree. I believe it is a synonym of *T. kiesenwetteri* but hesitate to formally synonymize the names without a complete study of the species of *Torymoides*.

***antipoda*** (Kirby). AUSTRALIAN: New Zealand.

*Callimome antipoda* Kirby 1883:202. Lectotype ♀ [designated by Bouček 1988:136], Lindis, New Zealand (BMNH).

TAXONOMY. - Bouček (1988:136) transferred this species to *Torymoides*.

HOST. - Noyes and Valentine (1989) reported this species as a parasite of a gall-forming cecidomyiid on *Carmichaelia* sp. (Fabaceae) and Hunt (1992) reported it from an undescribed cecidomyiid on *Carpodetus serratus* (Grossulariaceae).

BIOLOGY. - According to Hunt (1992) this species is both a primary and secondary ectoparasitoid. Oviposition takes place when the gall is immature, with up to 6 parasitoids on each host (2 was more commonly seen). Sex ratios were nearly 1:1. Adults emerge in spring (probably from galls initiated the previous spring and autumn) and summer (from galls initiated the previous autumn).

***ashmeadi*** (Crawford). ORIENTAL: Philippine Islands.

*Dimeromicrus ashmeadi* Crawford 1910a:128. 1 ♀, 1 ♂ syntypes, Manila, Philippine Islands (USNM, examined).

***asphondyliarum*** (Kieffer and Jorgensen). NEOTROPICAL: Argentina. **New combination.**

*Lochites asphondyliarum* Kieffer and Jorgensen 1910:366. Syntype ♂ (s), Chacras de Coria, Argentina (depository unknown).

TAXONOMY. - Earlier in this paper (p. 89) I explained the reasons for transferring Kieffer and Jorgensen species from *Lochites* (now = *Idiomacromerus*).

HOST. - The type was reared from *Asphondylia crassipalpis* (Cecidomyiidae) on *Baccharis salicifolia* (Asteraceae).

***atricornis*** (Girault). AUSTRALIAN: Australia (New South Wales).

*Macrodonotomerus atricornis* Girault 1915/243:278. 3 ♀, 2 ♂ syntypes, Melbourne, New South Wales, Australia (NMV).

TAXONOMY. - Dahms (1983:65) discussed the type material and confirmed that they are in NMV. Bouček (1988:136) transferred this species to *Torymoides*.

HOST. - "Galls on wattle" (Fabaceae).

***australiensis*** (Girault). AUSTRALIAN: Australia (New South Wales).

*Dimeromicrus australiensis* Girault 1913/175:98. 8 ♀ syntypes, Lawson and Forest Reefs, Australia (SAM).

TAXONOMY. - Dahms (1983:99) discussed the type situation, and, according to him, only 2 female syntypes are now extant (SAM). *Dimeromicrus australiensis* was redescribed by Girault in 1915/243:277. It was transferred to *Torymoides* by Bouček (1988:136).

***bipunctatus*** (Szelenyi). PALEARCTIC: Mongolia. **New combination.**

*Liodontomerus bipunctatus* Szelenyi 1973:191-192 (Fig. 2b). Holotype ♀, 50 km se Cojbalsan, Mongolia (HNHM, confirmed by Thuroczy 1992:131).

TAXONOMY. - Szelenyi (1982:379) transferred this species to *Ameromicrus*. The present combination is a result of my earlier synonymy of *Ameromicrus*.

***bouceki*** (Zerova and Seregina). PALEARCTIC: CIS (Kazakhstan). **New Combination.**

*Ameromicrus bouceki* Zerova and Seregina 1993:26 (Figs. 2-1, 2-2, 2-3). Holotype ♀, nr Dzhanipek, nw Kazakhstan; 27 ♀, 3 ♂ paratypes, same data as holotype.

TAXONOMY. - Earlier in this work, I synonymized *Ameromicrus* and its species with *Torymoides*.

HOST. - The type series was reared from a gall-former on *Salsola laricina* (Chenopodiaceae).

***breviventris*** (Girault). AUSTRALIAN: Australia (Queensland).

*Dimeromicrus breviventris* Girault 1915/243:277. Holotype ♂, Brisbane, Australia (QM).

TAXONOMY. - In Girault's 1915 paper it is not clear whether *breviventris* is being described as a new species or is merely a redescription. Girault in 1939/457



referred to his 1915 paper and specified that *breviventris* was described as a "new species". Dahms (1983:151-152) confirmed the holotype. Bouček (1988) missed this species in his list.

***capricornis*** (Girault). AUSTRALIAN: Australia (Queensland).

*Macrodonotomerus capricornis* Girault 1915/243:279. Holotype ♂, Gordonvale (Cairns), Queensland (QM).

TAXONOMY. - Dahms (1983:164) discussed the type and confirmed the type depository. Bouček (1988:136) transferred this species to *Torymoides*.

***cinctiventris*** (Girault). AUSTRALIAN: Australia (Queensland).

*Macrodonotomerus cinctiventris* Girault 1915/243:279. Holotype ♀, Kuranda, Queensland, Australia (QM).

TAXONOMY. - Dahms (1983:179) discussed the type specimen and confirmed the type depository. Bouček (1988:136) transferred this species to *Torymoides*.

***confluens*** (Bouček). PALEARCTIC: CIS (Azerbaijan, Georgia). **New combination.**

*Ameromicrus confluens* Bouček 1970a:32-33 (Figs. II, 1-3). Holotype ♀, Baku, Azerbaijan, CIS (NMP); 1 ♀ paratype, Tbilisi-Xanisi, Georgia.

TAXONOMY. - The present new combination is a result of my earlier synonymy of *Ameromicrus* with *Torymoides*. Zerova and Seregina (1993) illustrated the female habitus, antenna, and forewing of this species.

***daonus*** (Walker). AUSTRALIAN: Australia (Western Australia).

*Callimome daonus* Walker 1838:474. ?1 ♀, King George's Sound, Australia. [Type material lost according to Bouček 1988:136.]

TAXONOMY. - Bouček (1988:136) transferred this species to *Torymoides*.

***dispar*** (Masi). PALEARCTIC: Italy (Masi 1926b, Steffan 1962b); Austria (Masi 1926b), Yugoslavia, Albania, Syria (Ruschka 1923), Turkey (Doganlar 1984).

*Didactyliocerus dispar* Masi 1916:69-71 (Figs. 5-1, 5-2). Lectotype ♂, herein designated, Giglio Island, Toscano Archipelago, Italy (MCSN, examined); 4 ♂ paralectotypes same as lectotype.

TAXONOMY. - The 5 males from MCSN are marked as "typus" and "syntypus". No type or holotype was designated in the original description, and I take this opportunity to select and label the specimen marked as "typus" to be lectotype. This specimen bears a unique label reading "Is. Giglio, VIII.1901, G. Doria". Masi (1926a:161) described the female from specimens collected near Modena, Italy.

***eltonicus*** (Zerova and Seregina). PALEARCTIC: CIS (Kazakhstan). **New Combination.**

*Ameromicrus eltonicus* Zerova and Seregina 1993:28 (Figs.3-1, 3-2, 3-3). Holotype ♀, Elton Lake, Kazakhstan; 2 ♀ paratypes, same data as holotype.

TAXONOMY. - Earlier in this work, I synonymized *Ameromicrus* and its species with *Torymoides*.

HOST. - The type series was reared from a cecidomyiid gall-former on *Salsola* sp. (Chenopodiaceae).

***erythromma*** (Kieffer and Jorgensen). NEOTROPICAL: Argentina. **New combination.**

*Lochites erythromma* Kieffer and Jorgensen 1910:376. ♀, ♂ syntypes (number unstated), Chacras de Coria, Argentina (depository unknown).

TAXONOMY. - Earlier in this paper (p. 89) I explained the reasons for transferring Kieffer and Jorgensen species from *Lochites* (now = *Idiomacromerus*).

HOST. - The syntypes were reared from *Lasioptera* (now = *Neolasioptera*) *interrupta* (Cecidomyiidae) on *Baccharis subulata* (Asteraceae).

***eucalypti*** (Ashmead). AUSTRALIAN: Australia (New South Wales).

*Torymus eucalypti* Ashmead 1900a:331-332. 3 ♀, 2 ♂ syntypes, Sydney, New South Wales, Australia (USNM, examined).

TAXONOMY. - There are 7 labelled syntypes in USNM. Huber (1927:107) transferred *eucalypti* to *Dimeromicrus*, and Bouček (1988:136) transferred it to *Torymoides*.

HOST. - Reared from "a soft red gall on *Eucalyptus*" (Myrtaceae).

***festiva*** (Kieffer and Jorgensen). NEOTROPICAL: Argentina. **New combination.**

*Lochites festiva* Kieffer and Jorgensen 1910:391-392. ?Holotype ♀, Province of Mendoza, Argentina (depository unknown).

TAXONOMY. - Earlier in this paper (p. 89) I explained the reasons for transferring Kieffer and Jorgensen species from *Lochites* (now = *Idiomacromerus*).

HOST. - The holotype was reared from *Allodiplosis crassa* (Cecidomyiidae) on *Gourliaea decorticans* (Papilionaceae).

***gifuensis*** (Ashmead). PALEARCTIC: Japan (also Kamijo 1963). **New combination.**

*Torymus gifuensis* Ashmead 1904b:83. Lectotype ♀, here designated, Gifu, Japan (USNM).

*Torymus japonicus* Ashmead 1904b:82. Holotype ♂, Gifu, Japan (USNM, examined). **New synonymy.**

TAXONOMY. - In 1904b, Ashmead described *Torymus japonicus* and *Torymus gifuensis* in the same paper. Both species were from Gifu, Japan. *Torymus japonicus* was described from "one specimen" (= male holotype, USNM). *Torymus gifuensis* was stated to be described from "one male and two female specimens" (but description disagrees) of which only one male and one female syntype now remain in the USNM collection. Huber (1927:108) transferred "*gifuensis*" from the genus *Torymus* to *Dimeromicrus* (now *Torymoides*), but he did not realize that the syntypes of *gifuensis* are not congeneric; the female syntype is in the genus *Torymoides*, while the male syntype is in the genus *Torymus*. Huber did not select a lectotype, so his generic transfer is not completely correct. I studied all the available type material of both species, and it is evident that the holotype male of *Torymus japonicus* should be transferred to

*Torymoides* (new combination) and is conspecific with the female syntype of *Torymoides gifuensis*. The situation thus produces two choices: 1) if the female syntype was chosen as lectotype for *gifuensis*, then the names *gifuensis* and *japonicus* must be synonymized, and the male "syntype" of *gifuensis* remains in *Torymus*, its species identity unknown, 2) if the male syntype was chosen as lectotype, however, then the two species names would remain valid, and the female syntype of *gifuensis* would be placed as the opposite sex of *japonicus*. I preferred to select the female specimen of *gifuensis* as lectotype, and thus synonymize the two names. The systematics of Torymidae are based almost entirely on females, and if the male is chosen as lectotype, there is a good chance it (and its name) may never be correctly associated with a female. Also, there is the very likely possibility that the female has already been described under another name, either older or younger, which would require yet more name changes in the future. By resolving this nomenclatural problem in favor of the synonymy of *japonicus* and *gifuensis*, there will be no need to worry about the name of a single male specimen among the hundreds of names already available in *Torymus*. For the preceding reasons I select and label the female syntype of *Torymus gifuensis* Ashmead 1904b as lectotype, place the name *Torymus japonicus* Ashmead 1904b as a junior subjective synonym of *Torymus gifuensis* Ashmead 1904b, and transfer both names to the genus *Torymoides*.

***hyalipennis* (Szelenyi). PALEARCTIC: Mongolia. New combination.**

*Liodontomerus hyalipennis* Szelenyi 1973:193-194. Holotype ♀, 25 km wsw Quelle, Mongolia (HNHM, confirmed by Thuroczy 1992:132).

TAXONOMY. - Szelenyi (1982:379) transferred this species to *Ameromicrus*. The present new combination is a result of my earlier synonymy of *Ameromicrus* with *Torymoides*.

***iole* (Girault). AUSTRALIAN: Australia (Queensland).**

*Macrodontomerus iole* Girault 1915/243:279. Holotype ♂, Gordonvale (Cairns), Queensland, Australia (QM).

TAXONOMY. - Dahms (1984:728) discussed the holotype and confirmed the type depository. Bouček (1988:136) transferred this species to *Torymoides*.

***justitia* (Girault). AUSTRALIAN: Australia (Queensland).**

*Macrodontomerus justitia* Girault 1915/243:278. Holotype ♂, Gordonvale (Cairns), Queensland, Australia (QM).

TAXONOMY. - Dahms (1984:735) discussed the holotype and confirmed the type depository. Bouček (1988:136) transferred this species to *Torymoides*.

***keralensis* Narendran. ORIENTAL: India (Kerala).**

*Torymoides keralensis* Narendran 1994:44-45 (Fig. 48). Holotype ♀, Kalkandi, Kerala, India (UCK); 1 ♀ paratype, same data as holotype; 5 ♀ paratypes, Malampuzha, Kerala, India; 17 ♀ paratypes, Agali, Kerala, India; 1 ♀ paratype, Wayanad, Kerala, India.

***kiesenwetteri*** (Mayr). PALEARCTIC: Italy (also Masi 1916, 1919, Rivosecchi 1960, Steffan 1962b); Hungary (Erdős 1956), Poland (Szczepanski 1983), Andorra (Compton and Cripps 1984), Spain, Yugoslavia, and Egypt (Ferrière 1960), Turkey (Doganlar 1984). ORIENTAL: "Apparently widespread through South Asia" (Bouček 1988), India (Kerala: Narendran 1994).

*Holaspis kiesenwetteri* Mayr 1874:83. 3 ♀ syntypes, Trieste [Italy] (NMW, Ruschka 1923:402).

*Dimeromicrus longicauda* Masi 1916:67-68 (Fig. 4). 19 ♀ syntypes, "Giglio" [Italy] (depository unknown). [Synonymized by Erdős 1956:188.]

TAXONOMY. - Erdős (1956:188) first described the male of *kiesenwetteri* (specimens in HNHM). He also illustrated the female (Figs. 6 b,c,d) and male (Fig. 6 e). He synonymized *longicauda* with *kiesenwetteri* and transferred the latter to *Dimeromicrus*. Bouček (1988:135) transferred the species to *Torymoides*. Masi (for *longicauda*) cited new locality records for Italy (1919:128) and discussed variation among female specimens (1933:218). Ruschka (1923:407) redescribed the female of *longicauda* but provided no new information. Ferrière (1960:3-4) compared *kiesenwetteri* with *lindbergi* and summarized the distribution of the former. Steffan (1962b:30) reported additional locations from Italy. Narendran (1994) redescribed the female.

HOSTS. - Rivosecchi (1960) gave a detailed account of the hosts and biology of *kiesenwetteri*. In Italy it is reported to successfully parasitize 3 species of Tephritidae on 3 species of Asteraceae: *Myopites inulaedysentericae* (reported as *blotii*) on *Pulicaria dysenterica*, *M. longirostis* (reported as *frauenfeldi*) on *Inula crithmoides*, and *M. stylatus* on *Inula viscosa*. Szczepanski (1983) reported this species from the undergrowth of *Carpinus* forest in Poland. Kapoor and Agarwal (1983) and Agarwal and Kapoor (1989) reported it from India in the pupae of *Chetostoma completum* (Tephritidae). Also in India, Narendran (1994) reported the species from the tephritids *Acanthophilus helianthi* and *Procecidochares utilis* (on *Eupatorium adenophorum*) and from galls on *Eupatorium glandulosum* (Asteraceae).

***latus*** (Bouček). AFROTROPICAL: South Africa. **New combination.**

*Pondorymus latus* Bouček 1978:125 (Fig. 57). Holotype ♀, Port St. Johns, Pondoland, South Africa (BMNH, examined); 1 ♀ paratype same as holotype.

***lindbergi*** (Ferrière). PALEARCTIC: Cape Verde Island.

*Dimeromicrus lindbergi* Ferrière 1960:4-5. 34 ♀, 20 ♂ syntypes, Cape Verde Island (numerous localities) (MHNG).

TAXONOMY. - According to Besuchet (pers. comm.) the type and paratypes of this species are in MHNG.

***maculiventris*** (Szelenyi). PALEARCTIC: Mongolia. **New combination.**

*Liodontomerus maculiventris* Szelenyi 1973:192-193. Holotype ♀, 6 km wnw Somon Tosongengel, Mongolia (HNHM, confirmed by Thuroczy 1992:132).

TAXONOMY. - Szelenyi (1982:379) transferred this species to *Ameromicrus*. The present new combination is a result of my earlier synonymy of *Ameromicrus* with *Torymoides* (see p. 110).

***nikolskayae*** (Zerova and Seregina). PALEARCTIC: CIS (Kazakhstan). **New Combination.**

*Ameromicrus nikolskayae* Zerova and Seregina 1993:26-27 (Figs. 3-4, 3-5, 3-6). Holotype ♀, Alam-Ata, Kazakhstan; 2 ♀ paratypes, same data as holotype.

TAXONOMY. - Earlier in this work, I synonymized *Ameromicrus* and its species with *Torymoides*.

HOST. - The type series was reared from a cecidomyiid gall-former on *Ceratoides* sp. (Chenopodiaceae).

***osinius*** (Walker). AUSTRALIAN: Australia (Western Australia).

*Callimome osinius* Walker 1839:6-7. Number of specimens unknown, King George's Sound, Australia (remnants of one specimen ?BMNH, see Bouček 1988).

TAXONOMY. - Bouček (1988:136) transferred this species to *Torymoides*.

***piceae*** (Kamijo). PALEARCTIC: Japan. **New combination.**

*Ameromicrus piceae* Kamijo 1963:90-92 (Figs. 1-4). Holotype ♀, Toikambetsu, Teshio Prov., Hokkaido, Japan (HU); 47 ♀, 38 ♂, paratypes, Hokkaido and Honshu, Japan.

TAXONOMY. - The present new combination is a result of my earlier synonymy of *Ameromicrus* with *Torymoides*.

HOSTS. - The type series was reared from Pinaceae seeds of *Picea glehnii*, *P. jezoensis*, and *P. polita*. It is possible that the species is parasitic on *Megastigma* sp. (Torymidae) in the seed (Kamijo 1963).

***semisanguineus*** (Girault). AUSTRALIAN: Australia (Queensland).

*Macrodotomermes semisanguineus* Girault 1915/243:280. Holotype ♀, Cloncurry, Queensland, Australia (QM).

TAXONOMY. - Dahms (1986:521) discussed the type specimen and confirmed the depository. Bouček (1988:136) transferred this species to *Torymoides*.

***smithi*** (Schread). NEARCTIC: USA (Connecticut).

*Lochites smithi* Schread 1937:103. Lectotype ♀, herein designated, Stamford, Connecticut, USA (USNM, examined); 1 ♀, 1 ♂ paralectotypes same as lectotype.

TAXONOMY. - Peck (1951:528) transferred this species to *Dimeromicrus*.

HOST. - Reared from *Caryomyia* (Cecidomyiidae) gall (Schread 1937:104).

***sulcius*** (Walker). NEOTROPICAL: Brazil, Grenada, St. Vincent, Nicaragua; Mexico, St. Kitts, Montserrat, Peru, Argentina (De Santis 1978, 1979). NEARCTIC: USA (Florida; Texas: Peck 1951). **New combination.**

*Callimome sulcius* Walker 1839:64. Holotype ♀, Bahia, Brazil (BMNH, examined).

*Callimome caburus* Walker 1839:63-64. Holotype ♂, Bahia, Brazil (BMNH, examined). **New synonymy.**

*Megastigma cecidomyiae* Ashmead 1887:185-186. Lectotype ♀, herein designated, Florida (USNM, examined); 6 ♀ paralectotypes, same as lectotype. **New synonymy.**

*Lochites auriceps* Ashmead 1894:153. 12 ♀, ♂ syntypes St. Vincent, West Indies (2 ♀ syntypes USNM, examined; remainder ?BMNH). [Synonymized with *cecidomyiae* by Milliron 1949:347.]

*Torymus ventralis* Howard 1897:135. 2 ♂ syntypes, Mount Gay, Grenada (1 syntype BMNH, 1

syntype USNM, both examined). **New synonymy.**

*Torymus howardii* Dalla Torre 1898:307. [Objective replacement name for *Torymus ventralis* Howard 1897:135 nec Fonscolombe 1832:286.]

*Megastigmus fulvus* Cameron 1904b:58. Holotype ♀, San Marcos, Nicaragua (BMNH, examined). [Synonymized with *cecidomyiae* by Milliron 1949:347.]

**TAXONOMY.** - Crosby (1913:168) transferred *cecidomyiae* from *Megastigmus* to the genus *Lochites* (now = *Idiomacromerus*), but this was incorrect. *Torymus ventralis* was transferred to *Dimeromicrus* by Huber (1927:107). In large part the coloration and widespread nature of *Torymoides sulcius* has caused problems in its recognition as a single taxon. In general, the overall body color is orange to yellow with occasional white markings. However, males have a metallic green head, thus creating the original difficulty in associating males and females (i.e., male *caburus* and female *sulcius* described in same paper). Also, both sexes have differing amounts of smokey grey infusion on the legs and this has caused confusion.

**HOSTS.** - All of the rearings have been from cecidomyiid galls as follows: on *Baccharis halimifolia* (Asteraceae) in Florida Ashmead 1887); on *Manihot glaziovii* (Euphorbiaceae) in Argentina and galls of *Iatrophobia brasiliensis* on *Manihot tripartita* in Brazil (De Santis 1978); and *Hyperdiplosis* sp. from an unknown locality (De Santis 1979).

***sureshani*** Narendran. **ORIENTAL:** India (Kerala).

*Torymoides sureshani* Narendran 1994:45 (Fig. 49). Holotype ♀, Malampuzha, Kerala, India (UCK); 1 ♀ paratype (?same as holotype); 2 ♀ paratypes, Agali, Kerala, India.

***swaedicola*** (Kieffer and Jorgensen). **NEOTROPICAL:** Argentina. **New combination.**

*Lochites swaedicola* Kieffer and Jorgensen 1910:437. ♀, ♂ syntypes (number unstated), Chacras de Coria, Argentina (depository unknown).

**TAXONOMY.** - Earlier in this paper (p. 89) I explained the reasons for transferring Kieffer and Jorgensen species from *Lochites* (now = *Idiomacromerus*).

**HOST.** - The type series was reared from an unknown cecidomyiid on *Suaeda divaricata* (Chenopodiaceae).

***testacea*** (Kieffer and Jorgensen). **NEOTROPICAL:** Argentina. **New combination.**

*Lochites testacea* Kieffer and Jorgensen 1910:391-392. ?Holotype ♀, Province of Mendoza, Argentina (depository unknown).

**TAXONOMY.** - Earlier in this paper (p. 89) I explained the reasons for transferring Kieffer and Jorgensen species from *Lochites* (now = *Idiomacromerus*).

**HOST.** - The type(s) was reared from *Allodiplosis crassa* (Cecidomyiidae) on *Gourliaea decorticans* (Papilionaceae).

***transrugosus*** (Szelenyi). **PALEARCTIC:** Hungary. **New combination.**

*Ameromicrus transrugosus* Szelenyi 1982:380-381. Holotype ♀, Doghalom, Hungary (HNHM, confirmed by Thurocz 1992:133).

**TAXONOMY.** - The present new combination is a result of my earlier synonymy of *Ameromicrus* with *Torymoides*.

**triangularis** (Girault). AUSTRALIAN: Australia (New South Wales).

*Macrodonotomerus triangularis* Girault 1913/175:100. Holotype ♀, Mittagong, New South Wales, Australia (SAM).

TAXONOMY. - Dahms (1986:593) discussed the type specimen and confirmed the depository. Bouček (1988:136) transferred this species to *Torymoides*.

**unguttatipennis** (Girault). AUSTRALIAN: Australia (Queensland).

*Macrodonotomerus unguatipennis* Girault 1915/243:280. Holotype ♀, Caloundra (Brisbane), Queensland, Australia (QM).

TAXONOMY. - Dahms (1986:611) discussed the type and confirmed its depository. Bouček (1988:136) transferred this species to *Torymoides*.

**unimaculatus** (Girault). AUSTRALIAN: Australia (Queensland).

*Macrodonotomerus unimaculatus* Girault 1913/158:84. Holotype ♀, Ingham, Queensland, Australia (QM, examined).

TAXONOMY. - Dahms (1986:614-615) discussed the type and confirmed its depository. Bouček (1988:136) transferred this species to *Torymoides*.

**vibidia** (Walker). AUSTRALIAN: Australia (New South Wales). PALEARCTIC: Nepal (Kapoor and Malla 1979).

*Callimome vibidia* Walker 1839:7. Lectotype (sex not known) [designated by Bouček 1988:136], Sydney, New South Wales, Australia (BMNH, examined).

TAXONOMY. - This species was transferred to *Dimeromicrus* (by implication) by Kapoor and Malla 1979:932. Bouček (1988:136) transferred this species to *Torymoides*. The metasoma is missing so that the sex cannot be determined.

HOST. - Reared from larvae of *Procecidochares utilis* (Tephritidae) in *Eupatorium adenophorum* (Asteraceae) (Kapoor and Malla 1979, Kapoor and Agarwal 1983).

**violaceus** (Nikol'skaya). PALEARCTIC: CIS ("SW Soviet Republic"; Georgia, Azerbaijan: Bouček 1970a; Moldavia: Bouček 1961), Mongolia (Szelenyi 1973), Bulgaria (Bouček 1970a). **New combination.**

*Ameromicrus violaceus* Nikol'skaya (in Nikol'skaya and Kyao) 1954:412 (Figs. 3a, b). Holotype ♀, 13 ♀ and 1 ♂ paratypes from "sw Soviet Republic" (Stavropol, Janvartzevo, and Kharkino) (ZIAN, examined in part).

*Liodontomerus bifasciatus* Szelenyi 1973:190-191 (Figs. 2a, 3a, 4a). Holotype ♀, 25 km e Somon Lun, Mongolia (HNHM, confirmed by Thuroczy 1992:131); 4 ♀ paratypes Mongolia (various localities). [Synonymized by Szelenyi 1982:379.]

TAXONOMY. - The present new combination is a result of my earlier synonymy of *Ameromicrus* with *Torymoides* (see p. 110). Zerova and Seregina (1993) illustrated the female and male habitus and the forewing and female antenna.

HOST. - Some of the type specimens of *violaceus* were taken from galls of *Asphondylia miki* (Cecidomyiidae) on *Medicago*. Rzaeva (1971) also reported rearing this from the same host. Zerova and Seregina (1993) added the cecidomyiid host *Dasineura loewi* from galls on *Euphorbia stepposa* (Euphorbiaceae).

***yumurtalikiensis* (Doganlar). PALEARCTIC: Turkey. New combination.**

*Ameromicrus yumurtalikiensis* Doganlar 1989:142-144 (Figs. 1-2). Holotype ♀, Yumurtalik, Adana, Turkey (Doganlar Collection); 5 ♀, 3 ♂ paratypes same as holotype (2 ♀, 1 ♂ paratypes in BMNH).

***Torymus* Dalman (text, p. 103)**

*Callimome* Spinola 1811:146-148. Type-species: *Ichneumon bedeguaris* Linnaeus (desig. by Curtis 1835:552). [Suppressed by Int. Comm. Zool. Nomen., Opinion 155, 1944.]

*Misocampe* Latreille 1818:213. Type-species: *Ichneumon bedeguaris* Linnaeus (desig. by Gahan and Fagan 1923:91). [Suppressed by Int. Comm. Zool. Nomen., Opinion 155, 1944.]

*Torymus* Dalman 1820:135, 178. Type-species: *Ichneumon bedeguaris* Linnaeus (desig. by Ashmead 1904a:242).

*Misocampus*: Stephens 1829:395. [Emendation of *Misocampe*.]

*Syntomaspis* Förster 1856:43-44. Type-species: *Torymus eurynotus* Förster (desig. by Gahan and Fagan 1923:139). [Apparently synonymized by Huber 1927:2-4; treated as subgenus by Bouček and Graham 1978a:226.]

*Lioterphus* Thomson 1876:60, 99. Type-species: *Torymus pallidicornis* Boheman (desig. by Ashmead 1904a:241). [Synonymized by Grissell 1976:10; treated as subgenus by Bouček and Graham 1978a:226.]

*Callimomus* Thomson 1876:60, 77. Type-species: *Callimomus scaposus* Thomson (desig. by Ashmead 1904a:241). [Apparently synonymized by Schmiedeknecht 1914:209, who included the type species under *Torymus*.]

*Nannocerus* Mayr 1885:159, 195. Type-species: *Nannocerus biarticulatus* Mayr (monotypic). [Synonymized by Bouček 1993:209 and treated as subgenus.]

*Hemitorymus* Ashmead 1904a:243. Type-species: *Hemitorymus thoracicus* Ashmead (monotypic). [Synonymized by Gahan 1948:244.]

**Checklist:** To compile this list, I used my own card file (developed from Zoological Record and computer searches of the National Agricultural Library), that of the USNM, the various catalogs by De Santis (1967, 1979, 1980, 1983, 1989), and taxonomic papers and catalogs of Mayr (1874), Dalla Torre (1898), Hoffmeyer (1930d), Nikol'skaya and Zerova (1978), Eady (1959), Graham (1969), and Bouček and Graham (1978a, 1978b). While I am confident that most (if not all) names have been uncovered, I am also certain this list is not entirely accurate for European species. There is still much confusion concerning Palearctic nomenclature. A list of European species recently produced by Wall (1984), for example, does not reflect the many nomenclatural changes made after Eady 1959, nor does it appear to be complete, nor entirely accurate even to that date. Therefore, I have relied only marginally upon it to compile my own list.

Numerous misidentifications have been made over the past century, and an attempt is made to trace some of the more important names that appear in the literature. Similarly, I have tried to trace the authority for names placed in synonymy, but neither of these tasks has proven easy. In the list below, I document the authority for synonymy when I have been able to locate it. The results are not to my satisfaction, but to resolve the list entirely would require much additional study of the Palearctic fauna and literature.



In the following list, valid names are in **bold italic**, invalid names in *italic*, and names preceded by asterisk (\*) are *nomina nuda*. Synonyms are listed both alphabetically and under the valid name.

- abbreviatus* Boheman see ***chloromerus*** (Walker)  
*abdominalis* Boheman see ***cingulatus*** Nees  
*abdominalis* Walker see ***chloromerus*** (Walker)  
*abortus* Crosby see ***xanthopus*** (Schulz)  
***aceris*** Bouček 1994a:69-71 (*Torymus*): PALEARCTIC  
***acrophilae*** (Ruschka) 1921:341 (*Torymus*): PALEARCTIC  
*admirabilis* Förster see ***affinis*** (Fonscolombe)  
***advenus*** (Osten Sacken) 1870:59-60 (*Callimome*): NEARCTIC  
***aea*** (Walker) 1843c:104 (*Callimome*): NEARCTIC  
*amelanchieris* Cushman 1918:82-83 (*Syntomaspis*) synonymized by Burks 1975:151  
***aeneoscapus*** (Huber) 1927:35 (*Callimome*): NEARCTIC  
*aeneus* Ashmead see ***lissus*** (Walker)  
*aeneus* Nees see ***cingulatus*** Nees  
*aequalis* Walker see ***auratus*** (Geoffroy)  
***aereus*** (Huber) 1927:71 (*Callimome*): NEARCTIC  
***aerope*** (Walker) 1844b:182 (*Callimome*): PALEARCTIC  
*pulchellus* Thomson 1876:98 (*Torymus*) synonymized by Eady 1959:268  
***affinis*** (Fonscolombe) 1832:283-284 (*Cinips*): PALEARCTIC  
*apicalis* Walker 1833:133 (*Callimome*) synonymized by Bouček and Graham 1978a:226  
*fuscipennis* Walker 1833:137 (*Callimome*) synonymized by Bouček and Graham 1978a:226  
*littoralis* Walker 1833:134 (*Callimome*) synonymized by Bouček and Graham 1978a:226  
*tarsalis* Walker 1833:134 (*Callimome*) synonymized by Bouček and Graham 1978a:226  
*saphyrinus* Boheman 1834:371-372 (*Torymus*) synonymized by Bouček and Graham 1978a:226  
 (who used the misspelling *sapphyrinus*)  
*caudatus* Nees 1834:60-61 (*Torymus*) synonymized by Bouček and Graham 1978a:226  
*sapphyrinus* of Nees 1834:418 (*Torymus*) nec ***sapphyrinus*** Fonscolombe (***Pseudotorymus***) according to Hoffmeyer 1930d:245  
*admirabilis* Förster 1840:32 (*Torymus*) synonymized by Bouček and Graham 1978a:226  
*crinicaudis* Ratzeburg 1844:179 (*Torymus*) synonymized by Bouček and Graham 1978a:226  
*affinis* Förster see ***ventralis*** (Fonscolombe)  
***africanum*** (Hoffmeyer) 1929:333 (*Callimome*): PALEARCTIC  
*chlorocopes* Boheman of Masi 1921a:172-177 (*Torymus*) [Hoffmeyer (1929) named this species based upon the description given by Masi (1921a) of a misidentification of ***chlorocopes*** Boheman]  
*alamedensis* Huber see ***fagopirum*** (Provancher)  
***alaskensis*** (Huber) 1927:31-32 (*Callimome*): NEARCTIC  
*cecidomyiae* of Ashmead 1902:143 (*Torymus*) nec ***cecidomyiae*** (Walker) according to Huber 1927:31-32  
*albitarsus* Huber see ***capillaceus albitarsus*** (Huber)  
***alegrensis*** (Brèthes) 1927:333 (*Syntomaspis*): NEOTROPICAL  
*alpinus* Thomson see ***nigritarsus*** (Walker)  
*amelanchieris* Cushman see ***aea*** (Walker)  
*amethystinus* Boheman see ***juniperi*** (Linnaeus)

- amurensis* (Walker) 1874:312 (*Callimome*): PALEARCTIC  
*amoenus* Boheman see *formosus* Walker  
*amyrius* Walker see *nitens* (Walker)  
*anastatorus* Fahringer 1944:580-581 (*Torymus*): PALEARCTIC  
*angelicae* Walker see *cingulatus* Nees  
*annellus* Thomson see *varians* (Walker)  
*antennatus* Walker see *ventralis* (Fonscolombe)  
*anthobiae* Ruschka 1921:338 (*Torymus*): PALEARCTIC  
*anthomyiae* Ashmead 1887:189 (*Torymus*): NEARCTIC  
*antipai* Andriescu 1971:431 (*Torymus*): PALEARCTIC  
*anularius* Szelenyi 1973:185-186 (*Torymus*): PALEARCTIC  
*apicalis* Walker see *affinis* (Fonscolombe)  
*apiomyiae* Bouček and Mihajlovic 1986:447-449 (*Torymus*): PALEARCTIC  
*appropinquans* Ratzeburg see *auratus* (Geoffroy)  
*approximatus* Förster 1840:32-33 (*Torymus*): PALEARCTIC  
*aprilis* (Ashmead) 1904a:397 (*Syntomaspis*): NEOTROPICAL  
*arcticus* (Thomson) 1876:80 (*Callimomus*): PALEARCTIC  
*cupratus* of Mayr 1874:127-128 (*Torymus*) nec *cupratus* Boheman according to Thomson 1876:80  
*argei* Bouček 1994a:71-72 (*Torymus*): PALEARCTIC  
*arrogans* Schrottky 1907:74-75 (*Torymus*): NEOTROPICAL  
*artemisiae* Mayr 1874:105 (*Torymus*): PALEARCTIC  
*arundinis* (Walker) 1833:124 (*Callimome*) [attributed to Curtis by Walker 1833]: PALEARCTIC  
*lasiopterae* Giraud 1863:1270-1271 (*Callimome*) synonymized by Hoffmeyer 1929:334  
*asphondyliae* Kieffer and Jorgensen 1910:467 (*Torymus*): NEOTROPICAL  
*asphondyliae* Gahan see *hainesi* Ashmead  
*associatus* Förster 1840:32 (*Torymus*): PALEARCTIC  
*asteridis* (Huber) 1927:43-44 (*Callimome*): NEARCTIC  
*ater* Walker see *auratus* (Geoffroy)  
*atheatus* Grissell 1976:63-64 (*Torymus*): NEARCTIC, NEOTROPICAL  
*atropicis* (Huber) 1927:44 (*Callimome*): NEARCTIC  
*aucupariae* (Rodzianko) 1908:602-608 (*Syntomaspis*): HOLARCTIC  
*auratus* (Geoffroy) 1785:380 (*Cynips*): PALEARCTIC  
*aequalis* Walker 1833:129 (*Callimome*) synonymized by Eady 1959:266  
*aer* Walker 1833:138 (*Callimome*) synonymized by Eady 1959:266  
*autumnalis* Walker 1833:125-126 (*Callimome*)  
*bicolor* Walker 1833:130 (*Callimome*) synonymized by Eady 1959:266  
*chlorinus* Walker 1833:129 (*Callimome*) synonymized by Eady 1959:266  
*dauci* Walker 1833:124-125 (*Callimome*) [attributed to Curtis by Walker 1833] synonymized by Dalle Torre 1898:304  
*exilis* Walker 1833:138 (*Callimome*) synonymized by Eady 1959:266  
*flavipes* Walker 1833:124 (*Callimome*) synonymized by Eady 1959:266  
*gracilis* Walker 1833:137 (*Callimome*) synonymized by Bouček and Graham 1978a:226  
*latus* Walker 1833:128 (*Callimome*) synonymized by Eady 1959:266  
*leptocerus* Walker 1833:129-130 (*Callimome*)  
*leucopterus* Walker 1833:130-131 (*Callimome*) synonymized by Eady 1959:266

- meridionalis* Walker 1833:131-132 (*Callimome*) synonymized by Eady 1959:266  
*minutus* Walker 1833:137 (*Callimome*)  
*mutabilis* Walker 1833:127 (*Callimome*)  
*stramineitarsus* Walker 1833:135 (*Callimome*) synonymized by Eady 1959:266  
*terminalis* Walker 1833:132-133 (*Callimome*) synonymized by Eady 1959:266  
*euchlorus* Boheman 1834:359-360 (*Torymus*) synonymized by Eady 1959:266  
*viridissimus* Boheman 1834:358-359 (*Torymus*)  
*propinquus* Förster 1840:32 (*Torymus*) synonymized by Mayr 1874:115  
*nanus* Förster 1840:33 (*Torymus*) synonymized by Mayr 1874:115  
*appropinquans* Ratzeburg 1844:179 (*Torymus*)  
*contractus* Ratzeburg 1848:180 (*Torymus*) synonymized by Mayr 1874:126  
*gallarum* Ratzeburg 1852:223 (*Torymus*) synonymized by Mayr 1874:115  
*hibernans* Mayr 1874:111 (*Torymus*) synonymized by Eady 1959:266  
*sodalis* Mayr 1874:120 (*Torymus*) synonymized by Eady 1959:266  
***auronitens*** Förster 1840:32 (*Torymus*): PALEARCTIC  
*aurulentus* Nees see ***erucarum*** (Schrank)  
***austriacus*** Graham 1994a:31-32 (*Torymus*): PALEARCTIC  
*autumnalis* Walker see ***auratus*** (Geoffroy)  
*axillaris* Ashmead see ***biorhizae*** (Ashmead)  
***aztecus*** Cameron 1904b:59 (*Torymus*): NEOTROPICAL  
***azureus*** Boheman 1834:369-370 (*Torymus*): HOLARCTIC  
*chalybaeus* Ratzeburg 1844:179-180 (*Torymus*) synonymized by Mayr 1874:100  
*azureus* of Mayr 1874:100 (in part) (see Graham 1969:63)  
***baccharidis*** (Huber) 1927:46-47 (*Callimome*): NEARCTIC  
*pilularidis* Huber 1927:45-46 (*Callimome*) synonymized by Grissell 1976:18  
*baccharicidis* of Doult 1961:51 (erroneous spelling)  
*baccharicidis* of Doult see ***baccharidis*** (Huber)  
*bakeri* Cameron see ***hainesi*** Ashmead  
*bakkendorfi* Hoffmeyer see ***impar*** Rondani  
***ballestrerii*** (Rondani) 1877:204-205 (*Trogocarpus*): PALEARCTIC  
***basalis*** Walker 1833:125 (*Callimome*): PALEARCTIC  
*confinis* var  $\beta$  Walker 1833:125 (*Callimome*) synonymized by Eady 1959:263  
*viridiaeneus* Walker 1833:131 (*Callimome*) synonymized by Eady 1959:263  
***baudysi*** (Bouček) 1954b:60-62 (*Syntomaspis*): PALEARCTIC  
***bedeguaris*** (Linnaeus) 1758:567 (*Ichneumon*): HOLARCTIC  
*viridis* Geoffroy 1785:380 (*Cynips*) synonymized by Graham 1994c:122  
*elegans* Boheman 1834:352-353 (*Torymus*)  
*divisus* Walker 1871a:34 (*Callimome*)  
*forsteri* Ratzeburg 1844:178 (*Torymus*) synonymized by Ratzeburg 1848:179  
*chrysochlora* of Huber 1927:38-39 (*Callimome*) misidentification in part of *chrysochlora* Osten Sacken  
\****beneficus*** Yasumatsu see ***beneficus*** Yasumatsu and Kamijo  
***beneficus*** Yasumatsu and Kamijo 1979:94-97 (*Torymus*): PALEARCTIC  
\****beneficus*** Yasumatsu 1955:100 (*Torymus*) [*nomen nudum*]  
*bicolor* Walker see ***auratus*** (Geoffroy)  
***biarticulatus*** (Mayr) 1885:52 (*Nannocerus*): NEOTROPICAL  
***bicoloratus*** (Huber) 1927:73 (*Callimome*): NEARCTIC

- bifasciipennis*** (Gahan) 1936:481-482 (*Callimome*): NEOTROPICAL  
***biorhizae*** (Ashmead) 1887:186 (*Diomrous*): NEARCTIC  
*axillaris* Ashmead 1894b:333 (*Torymus*) synonymized by Grissell 1992a:273  
***boharti*** Grissell 1976:65-66 (*Torymus*): NEARCTIC  
***bohemanii*** Thomson 1876:89 (*Torymus*): PALEARCTIC  
***boops*** Graham 1994a:24-25: PALEARCTIC  
***borealis*** Thomson 1876:83 (*Torymus*): PALEARCTIC  
***brachyurus*** Boheman 1834:354-355 (*Torymus*): PALEARCTIC  
*brevicauda* Osten Sacken see ***fagopirum*** (Provancher)  
 \**brevicauda* Spinola see ***difficilis*** Nees  
*brevicauda* Walker see ***microstigma*** (Walker)  
*brevis* Breland see ***helianthi*** Brodie  
*brevisimicauda* Ashmead see ***fagopirum*** (Provancher)  
*britannicus* Dalla Torre see ***chloromerus*** (Walker)  
***brodiei*** (Ashmead) 1887:187 (*Syntomaspis*): NEARCTIC  
***bruesi*** (Huber) [new name] 1927:19 (*Callimome*): NEARCTIC (fossil)  
*sackenii* [*sackenii*] Brues 1910:17-18 (*Torymus*) nec *sackenii* Ashmead [Brues used the correct spelling *sackenii* in his Fig. 10]  
***budensis*** Erdős 1956:183 (*Torymus*): PALEARCTIC  
*caburus* Walker see ***Torymoides sulcius*** (Walker)  
***californicus*** (Ashmead) 1886b:127 (*Syntomaspis*): NEARCTIC  
*californica subdolum* Huber 1927:85-86 (*Callimome*) synonymized by Grissell 1976:47  
***campanulae*** Cameron 1880:40 (*Torymus*): PALEARCTIC  
***canariensis*** Hedqvist 1977:235-237 (*Torymus*): PALEARCTIC  
***capillaceus albitarsis*** (Huber) 1927:80-81 (*Callimome*): NEARCTIC  
***capillaceus capillaceus*** (Huber) 1927:74-75 (*Callimome*): NEARCTIC  
*medicaginis* Gahan 1919b:162 (*Syntomaspis*) nec *Torymus medicaginis* Mayr (= ***Pseudotorymus***)  
*sativae* Huber 1927:77-78 (*Callimome*) new name for *medicaginis* Gahan, synonymized by Grissell 1976:66  
***capite*** (Huber) 1927:32-33 (*Callimome*): NEARCTIC  
*castanopsidis* Huber see ***tubicola*** (Osten Sacken)  
***caudatus*** Boheman 1834:365-366 (*Torymus*): PALEARCTIC  
*azureus* of Mayr 1874:100 (in part) (see Graham 1969:63)  
*caudatus* Nees see ***affinis*** (Fonscolombe)  
***cecidomyiae*** (Walker) 1844a:15-16 (*Callimome*): NEARCTIC  
*strobiloides* Huber 1927:40-41 (*Callimome*) synonymized by Burks 1975:151  
*cecidomyiae* of Ashmead see ***alaskensis*** (Huber)  
***centuareae*** (Hoffmeyer) 1930d:251 (*Callimome*): PALEARCTIC  
*cerri* Mayr see ***notatus*** (Walker)  
***ceylonicus*** (Motschulsky) 1863:47 (*Callimome*): ORIENTAL  
*chalybaeus* Ratzeburg see ***azureus*** Boheman  
***chapadae*** Ashmead 1904a:398 (*Torymus*): NEOTROPICAL  
***chaubattiensis*** Bhatnagar 1952:155-156 (*Torymus*): ORIENTAL  
***chilensis*** (Brèthes) 1916c:88-89 (*Callimome*): NEOTROPICAL  
*chlorinus* Förster see ***chloromerus*** (Walker)  
*chlorinus* Walker see ***auratus*** (Geoffroy)

- chlorocopes*** Boheman 1834:377-378 (*Torymus*): PALEARCTIC  
*chlorocopes* of Masi see ***africanum*** (Hoffmeyer)
- chloromerus*** (Walker) 1833:128 (*Callimome*): PALEARCTIC  
*abdominalis* Walker 1833:126 (*Callimome*) nec *abdominalis* Boheman, synonymized by Eady 1959:236  
*euphorbiae* Walker 1833:132 (*Callimome*) synonymized by Eady 1959:263  
*micropterus* Walker 1833:130 (*Callimome*) synonymized by Bouček and Graham 1978a:226  
*abbreviatus* Boheman 1834:357-358 (*Torymus*)  
*cyanimus* Boheman 1834:367-369 (*Torymus*) synonymized by Bouček and Graham 1978a:226  
*chlorinus* Förster 1840:32 (*Torymus*) synonymized by Mayr 1874:105  
*hieracii* Mayr 1874:112-113 (*Torymus*) synonymized by Eady 1959:263  
*britannicus* Dalla Torre 1898:301 (*Torymus*)  
*euphorbiae* Ruschka 1921:339 (*Torymus*) synonymized by Eady 1959:263
- chrysis*** (Fabricius) 1804:150 (*Diplolepis*): PALEARCTIC  
*\*crassipes* Spinola 1811:148 (*Diplolepis*) synonymized by Dalla Torre 1898:303 [*nomen nudum*]  
*chrysis* of Nees see ***fastuosus*** Boheman
- chrysocephalus*** Boheman 1834:340-342 (*Torymus*): PALEARCTIC  
***chrysochlorus*** (Osten Sacken) 1870:63-64 (*Callimome*): NEARCTIC  
*chrysochlora* of Huber see ***bedeguaris*** (Linnaeus), ***solitarius*** (Osten Sacken)  
*cinerosum* Huber see ***warreni*** (Cockerell)
- cingulatus*** Nees 1834:62 (*Torymus*): PALEARCTIC  
*abdominalis* Boheman 1834:343 (*Torymus*) nec *abdominalis* Walker  
*aeneus* Nees 1834:64 (*Torymus*) synonymized by Mayr 1874:91  
*geranii* Curtis 1835:552 (*Callimome*) nec ***geranii*** (Walker)  
*angelicae* Walker 1836:25 (*Callimome*) synonymized by Graham 1969:66  
*medius* Förster 1840:31-32 (*Torymus*) synonymized by Hoffmeyer 1930d:247  
*lusitanicus* Tavares 1901:45 (*Torymus*) synonymized by Hoffmeyer 1930d:246
- cissus* Walker of Dalla Torre see ***lissus*** (Walker)  
*citriformis* Ashmead see ***tubicola*** (Osten Sacken)
- citripes*** (Huber) 1927:48 (*Callimome*): NEARCTIC  
***coccineus*** (Huber) 1927:68-69 (*Callimome*): NEARCTIC  
***coccorum*** (Hoffmeyer) 1930a:23-24 (*Callimome*): PALEARCTIC  
*coerulea* Fullaway see ***fullawayi*** (Huber)  
***coeruleus*** (Ashmead) 1881:xxxiii (*Callimome*): NEARCTIC  
*cognata* Breland see ***mexicanus*** Ashmead  
***coloradensis*** (Huber) 1927:49 (*Callimome*): NEARCTIC  
***compactus*** (Walker) 1834:161 (*Callimome*): PALEARCTIC  
*compressus* Förster see ***formosanus*** (Walker)
- condaliae*** Kieffer and Jorgensen 1910:379 (*Torymus*): NEOTROPICAL  
***confinis*** (Walker) 1833:125 (*Callimome*): PALEARCTIC  
*curtus* Walker 1833:131 (*Callimome*) synonymized by Eady 1959:264  
*inconspectus* Walker 1833:133 (*Callimome*) synonymized by Eady 1959:264  
*confinis* var  $\beta$  Walker see ***basalis*** Walker
- confluens*** Ratzeburg 1852:224 (*Torymus*): PALEARCTIC  
***confusus*** (Walker) 1834:161 (*Callimome*): PALEARCTIC  
***congener*** Förster 1840:33 (*Torymus*): PALEARCTIC

- congruens* Förster see *laetus* (Walker)  
*conjunctus* Nees see *nobilis* Boheman  
*contractus* Ratzeburg see *auratus* (Geoffroy)  
*contractus* (Walker) 1874:313 (*Callimome*): PALEARCTIC  
*contubernalis* Boheman 1834:362-363 (*Torymus*): PALEARCTIC  
*corni* Mayr 1874:121 (*Torymus*): PALEARCTIC  
*crassa* (Breland) 1939a:87-89 (*Callimome*): NEOTROPICAL  
*\*crassipes* Spinola see *chrysis* (Fabricius)  
*cribratus* Kieffer and Jorgensen 1910:410 (*Torymus*): NEOTROPICAL  
*crinicaudis* Ratzeburg see *affinis* (Fonscolombe)  
*cruentatus* (Huber) 1927:50-51 (*Callimome*): NEARCTIC  
*cultriventris* Ratzeburg 1844:179 (*Torymus*): PALEARCTIC  
*nordlingeri* Ratzeburg 1844:179 (*Torymus*) synonymized by Mayr 1874:113  
*cumelis* Walker of Ashmead see *eumelis* (Walker)  
*cupratus* Boheman 1834:375-377 (*Torymus*): PALEARCTIC  
*cupratus* of Mayr see *articus* (Thomson)  
*cuprigaster* Szelenyi 1973:184-185 (*Torymus*): PALEARCTIC  
*curtus* Walker see *confinis* (Walker)  
*cyaneus* Walker 1847:227 (*Torymus*): PALEARCTIC  
*eurynotus* Walker 1850:126-127 (*Callimome*)  
*eurynotus* Förster 1859:99-100 (*Syntomaspis*)  
*cyanimus* Boheman see *chloromerus* (Walker)  
*cynipedis* Boheman see *geranii* (Walker)  
*cynipedis* of Walker see *erucarum* (Schrank)  
*cyniphidum* Ratzeburg see *geranii* Walker  
*dasyneurae* (Huber) 1927:56-57 (*Callimome*): NEARCTIC  
*dauci* Walker see *auratus* (Geoffroy)  
*dennoi* Grissell 1976:26 (*Torymus*): NEARCTIC  
*denticulatus* (Breland) 1939a:85-87 (*Callimome*): NEARCTIC, NEOTROPICAL  
*devoniensis* Parfitt see *nitens* (Walker)  
*diabolus* Moser 1965:26-27 (*Torymus*): NEARCTIC  
*difficilis* Nees 1834:61 (*Torymus*): PALEARCTIC  
*\*brevicauda* Spinola 1811:148 synonymized by Dalla Torre 1898:303 [*nomen nudum*]  
*discolor* Thomson see *ventralis* (Fonscolombe)  
*distinctus* Förster 1840:32 (*Torymus*): PALEARCTIC  
*divisus* Walker see *bedeguaris* (Linnaeus)  
*dorynicola* (Müller) 1870:77 (*Callimome*): PALEARCTIC  
*druparum* Boheman 1834:361-362 (*Torymus*): PALEARCTIC, ?NEOTROPICAL  
 [found in imported fruit (De Santis 1983); removed from synonymy with *varians* (Walker) by Bouček and Graham 1978a:226]  
*druparum* of Mayr see *rosarum* (Hoffmeyer)  
*dryophantae* (Ashmead) 1887:187 (*Syntomaspis*): NEARCTIC  
*dryorrhizoxeni* Ashmead see *lissus* (Walker)  
*dubiosus* (Huber) 1927:24-25 (*Callimome*): NEARCTIC  
*duplicatus* (Huber) 1927:27-28 (*Callimome*): NEARCTIC  
*durus* (Osten Sacken) 1870:59 (*Callimome*): NEARCTIC  
*ebrius* (Osten Sacken) 1870:58-59 (*Callimome*): NEARCTIC

- eglanteriae** Mayr 1874:100 (*Torymus*): PALEARCTIC  
*elegans* Boheman see **bedeguaris** (Linnaeus)  
**elegantissimus** (Ashmead) 1881:xxxiv (*Callimome*): NEARCTIC  
*\*elegantulus* Yasumatsu see **geranii** (Walker)  
**erdosi** (Györfi) 1945:6-7 (*Callimome*): PALEARCTIC  
**erucarum** (Schrank) 1781:375 (*Ichneumon*): PALEARCTIC  
*purpurascens* Olivier 1790:780 (*Cynips*)  
*fulgens* Fabricius 1798:230 (*Ichneumon*) synonymized by Graham 1969:65  
*fuliginosus* Spinola 1808:214 (*Diplolepis*) synonymized by Graham 1994b:99  
*cynipidis* of Walker 1833:119-120, misidentification  
*fulgidus* Boheman 1834:345-347 (*Torymus*)  
*aurulentus* Nees 1834:146 (*Torymus*) synonymized by Dalla Torre 1898:311  
*rasaces* Walker 1844b:181 (*Callimome*) synonymized by Eady 1959:262  
*rubripes* Ratzeburg 1844:179 (*Torymus*) synonymized by Mayr 1874:87  
**euchlorus** Boheman see **auratus** (Geoffroy)  
**eumelis** (Walker) 1843b:114 (*Callimome*): NEOTROPICAL  
*cumelis* Walker of Ashmead 1904a:398 [misspelling]  
*euphorbiae* Ruschka see **chloromerus** (Walker)  
*euphorbiae* Walker see **chloromerus** (Walker)  
*eurynotus* Walker see **cyaneus** Walker  
*eurynotus* Förster see **cyaneus** Walker  
**eurytomae** (Puzanova-Malyshева) 1936:604 (*Syntomaspis*): PALEARCTIC  
*exilis* Walker see **auratus** (Geoffroy)  
**fagi** (Hoffmeyer) 1930a:24 (*Callimome*): PALEARCTIC  
**fagineus** Graham 1994a:22-24 (*Torymus*): PALEARCTIC  
*fulgens* Fabricius of Mayr 1874:88-89 (*Torymus*)  
*fulgens* Fabricius of Thomson 1876:81-82 (*Torymus*)  
**fagopirum** (Provancher) 1881[August]:291 (*Callimome* [sic]): NEARCTIC  
*brevicauda* Osten Sacken 1870:62 (*Callimome*) nec *brevicauda* Walker  
*sackenii* Ashmead 1881[October]:xxxii (*Callimome*) new name for *brevicauda* Osten Sacken  
*[fagopirum* was synonymized with *sackenii* by Huber 1927:31 who failed to note that  
*fagopirum* had priority by two months]  
*brevissimicauda* Ashmead 1881:xxxiii-xxxiv (*Callimome*) synonymized with by Ashmead  
1887:188  
*virentis* Ashmead 1881:xxxiv (*Callimome*) ?synonymized by Huber 1927:29  
*ostensackenii* Dalla Torre 1898:311 (*Torymus*) new name for *brevicauda* Osten Sacken  
*alamedensis* Huber 1927:28-29 (*Callimome*) synonymized by Grissell 1976:56  
*\*ribesii* Huber 1927:31 (*Callimome*) [*nomen nudum*]  
**fastuosus** Boheman 1834:347-348 (*Torymus*): PALEARCTIC  
*chrysis* of Nees 1834:67 (*Torymus*) [misidentification according to Mayr 1874:78]  
*robustus* Ratzeburg 1852:225 (*Torymus*) synonymized by Mayr 1874:78  
**favardi** Steffan 1962a:186-188 (*Torymus*): PALEARCTIC  
**femoralis** (Perez) 1895:199 (*Callimome*): PALEARCTIC  
**ferrugineipes** (Huber) 1927:33-34 (*Callimome*): NEARCTIC  
**festivus** Hobbs 1950:173-175 (*Torymus*): NEARCTIC  
*fischeri* Ruschka see **hormomyiae** Kieffer  
**flavicollis** (Ashmead) 1904a:398 (*Syntomaspis*): NEOTROPICAL

- flavicoxa** (Osten Sacken) 1870:61 (*Callimome*): HOLARCTIC  
*?glechomae* Mayr 1874:90 (*Torymus*) synonymized by Grissell 1976:28  
*superbus* Provancher 1888:407 (*Cleonymus*) by Burks 1963:1257
- flavipes** Walker see **auratus** (Geoffroy)
- flavipes** Parfitt see **nitens** (Walker)
- flavipes** Ashmead see **xanthopus** (Schulz)
- flaviventris** Ashmead 1888:iv (*Torymus*): NEARCTIC
- flavocinctus** Kieffer and Jorgensen 1910:391 (*Torymus*): NEOTROPICAL
- flavovariegatus** Gijswijt 1990:44-45 (*Torymus*): PALEARCTIC
- floridensis** Peck 1951:523 (*Torymus*): NEARCTIC  
*robustum* Huber 1927:72-73 (*Callimome*) nec *robustus* Ratzeburg
- formosus** (Walker) 1833:122-123 (*Callimome*): PALEARCTIC  
*amoenus* Boheman 1834:348-349 (*Torymus*)  
*compressus* Förster 1840:32 (*Torymus*)
- forsteri** Ratzeburg see **bedeguaris** (Linnaeus)
- frankiei** Grissell 1973:236 (*Torymus*): NEARCTIC
- frater** Thomson 1876:97 (*Torymus*): PALEARCTIC
- fulgens** Fabricius see **erucarum** (Schrank)
- fulgens** Fabricius of Mayr see **fagineus** Graham
- fulgens** Fabricius of Thomson see **fagineus** Graham
- fulgidus** Boheman see **erucarum** (Schrank)
- fuliginosus** Spinola see **erucarum** (Schrank)
- fullawayi** (Huber) 1927:19 (*Callimome*): NEARCTIC  
*coerulea* Fullaway 1912:274 (*Syntomaspis*) nec *coeruleus* Ashmead
- fulvus** (Huber) 1927:26-27 (*Callimome*): NEARCTIC
- fuscicornis** (Walker) 1833:138 (*Callimome*): PALEARCTIC  
*posticus* Walker 1833:137 (*Callimome*) synonymized by Eady 1959:261  
*moelleri* Thomson 1876:99 (*Lioterphus*) synonymized by Eady 1959:261
- fuscipennis** Walker see **affinis** (Fonscolombe)
- fuscipes** Boheman 1834:374-375 (*Torymus*): PALEARCTIC
- gahani** Huber see **tubicola** (Osten Sacken)
- galii** Boheman 1834:344-345 (*Torymus*): PALEARCTIC
- gallarum** Ratzeburg see **auratus** (Geoffroy)
- genisticola** Ruschka 1921:341 (*Torymus*): PALEARCTIC
- geranii** (Walker) 1833:121 (*Callimome*): PALEARCTIC  
*cynipedis* Boheman 1834:342-343 (*Torymus*) (see Yasumatsu and Kamijo 1979:97)  
*cyniphidum* Ratzeburg 1844:178-179 (*Torymus*) synonymized by Bouček and Graham 1978a:227  
*abdominalis* misidentification [see Bouček and Graham 1978b:71]  
*\*elegantulus* Yasumatsu 1955:100 (*Torymus*) [*nomen nudum*; see Yasumatsu and Kamijo 1979:97]  
*cingulatus* of Eady 1959:265 and of Askew 1961:260 [misidentifications, see Bouček and Graham 1978a:227; Yasumatsu and Kamijo 1979:97]
- gifuensis** Ashmead see **Torymoides gifuensis** (Ashmead)
- giganticum** Huber see **tubicola** (Osten Sacken)
- giraudianus** (Hoffmeyer) 1930a:25 (*Callimome*): PALEARCTIC
- glechomae** Mayr see **flavicoxa** (Osten Sacken)



- globiceps*** (Retizius) 1783:70 (*Ichneumon aeneus*): PALEARCTIC  
***gracilior*** Graham 1994a:21-22 (*Torymus*): PALEARCTIC  
*gracilis* Walker see ***auratus*** (Geoffroy)  
***grahami*** Bouček 1994a:72-74 (*Torymus*): PALEARCTIC  
***guyanaus*** Cameron 1913b:118-119 (*Torymus*): NEOTROPICAL  
***hainesi*** Ashmead 1893b:278 (*Torymus*): NEARCTIC, NEOTROPICAL  
     \**hainesi* Ashmead in Fox 1893:3 (*Torymus*) [*nomen nudum*]  
     *bakeri* Cameron 1904b:58-59 (*Torymus*) synonymized by Grissell 1985:352  
     *asphondyliae* Gahan 1919:161-162 (*Callimome*) nec *asphondyliae* Kieffer and Jorgensen  
 \**haywardi* (E. Blanchard) 1941b:29 (*Syntomaspis*): NEOTROPICAL [*nomen nudum*]  
***hederae*** (Walker) 1833:123 (*Callimome*): PALEARCTIC  
***helianthi*** Brodie 1894:45-46 (*Torymus*): NEARCTIC  
     *brevis* Breland 1948:57-58 (*Torymus*) synonymized by Grissell 1976:30  
***henrikseni*** (Hoffmeyer) 1930d:253-254 (*Callimome*): PALEARCTIC  
***heyeri*** Wachtl 1883b:35-36 (*Torymus*): PALEARCTIC  
*hibernans* Mayr see ***auratus*** (Geoffroy)  
*hieracii* Mayr see ***chloromerus*** (Walker)  
***hircinus*** Ashmead 1894b:333-334 (*Torymus*): NEARCTIC  
***hirsutus*** (Huber) 1927:74 (*Callimome*): NEARCTIC  
***holcaspidea*** (Ashmead) 1904a:397-398 (*Syntomaspis*): NEOTROPICAL  
***hormomyiae*** Kieffer 1899:368-369 (*Torymus*): PALEARCTIC  
     *fischeri* Ruschka 1921:241-242 (*Torymus*)  
***hornigi*** Ruschka 1921:338 (*Torymus*): PALEARCTIC  
***huberi*** (Hoffmeyer) [new name] 1929:333 (*Callimome*): NEARCTIC  
     *tarsale* Huber 1927:76-77 (*Callimome*) nec *tarsalis* Walker  
***hylesini*** Graham 1994a:29-31 (*Torymus*): PALEARCTIC  
***igniceps*** Mayr 1874:103-104 (*Torymus*): PALEARCTIC  
***impar*** Rondani 1877:201-202 (*Torymus*): PALEARCTIC  
     *bakkendorfi* Hoffmeyer 1933:246 (*Callimome*) synonymized by Bouček 1974:252  
*incertus* Förster see ***nitens*** (Walker)  
*inconspectus* Walker see ***confinis*** (Walker)  
*inconstans* Walker see ***nitens*** (Walker)  
*incrassata* Thomson see ***notatus*** (Walker)  
***insolitus*** (Walker) 1874:313 (*Callimome*): PALEARCTIC  
     *liogaster* Thomson 1876:98 (*Torymus*) synonymized by Bouček and Graham 1978a:227  
***inulae*** Wachtl 1884:6-7 (*Torymus*): PALEARCTIC  
***iridis*** (Picard) 1930:89-90 (*Callimome*): PALEARCTIC  
***isajevi*** Dolgin and Zerova 1986:1095-1098 (*Torymus*): PALEARCTIC  
*japonicus* Ashmead see ***Torymoides gifuensis*** (Ashmead)  
***juniperi*** (Linnaeus) 1758:567 (*Ichneumon*): PALEARCTIC  
     *maestus* Walker 1833:133 (*Callimome*) synonymized by Eady 1959:261  
     ? *amethystinus* Boheman 1834:370-371 (*Torymus*)  
     *solinus* Walker 1848b:153 (*Callimome*) synonymized by Eady 1959:261  
***kaltenbachii*** Förster 1840:33 (*Torymus*): PALEARCTIC  
***kiefferi*** (Hoffmeyer) [new name] 1929:333-334 (*Callimome*): NEOTROPICAL  
     *lasiopterae* Kieffer and Jorgensen 1910:376 (*Torymus*) nec *lasiopterae* Giraud  
***kinseyi*** (Huber) 1927:44-45 (*Callimome*): NEARCTIC

- koebeli* (Huber) 1927:52 (*Callimome*): NEARCTIC  
*koreanus* Kamijo 1982:508-509 (*Torymus*): PALEARCTIC  
*laetus* Philippi see *philippii* (Hoffmeyer)  
*laetus* (Walker) 1833:136 (*Callimome*): PALEARCTIC  
     *purpurascens* Boheman 1834:353-354 (*Torymus*) synonymized by Hoffmeyer 1929:334  
     *rufipes* Förster 1840:32 (*Torymus*) synonymized by Mayr 1874:124  
     *congruens* Förster 1840:32 (*Torymus*) synonymized by Mayr 1874:124  
*lampros* Graham 1994a:28-29 (*Torymus*): PALEARCTIC  
*lapsanae* (Hoffmeyer) 1930a:26 (*Callimome*): PALEARCTIC  
*laricis* Bouček 1994a:74-78 (*Torymus*): PALEARCTIC  
*larreae* Grissell 1976:76-77 (*Torymus*): NEARCTIC  
*lasiopterae* Giraud see *arundinis* (Walker)  
*lasiopterae* Kieffer and Jorgensen see *kiefferi* (Hoffmeyer)  
*lateralis* Walker see *nitens* (Walker)  
*latus* Walker see *auratus* (Geoffroy)  
*lazulinus* (Förster) 1859:100-101 (*Syntomaspis*): PALEARCTIC  
*leptocerus* Walker see *auratus* (Geoffroy)  
*leucopterus* Walker see *auratus* (Geoffroy)  
*lini* Mayr 1874:113 (*Torymus*): PALEARCTIC  
*liogaster* Thomson see *insolitus* (Walker)  
*lissus* (Walker) 1843a:150 (*Callimome*): NEARCTIC  
     *aeneus* Ashmead 1881:xxxiii (*Callimome*) synonymized by Burks 1975:152  
     *dryorhizonxeni* Ashmead 1885:xiii (*Callimome*) synonymized by Huber 1927:56  
     *omnivora* Ashmead 1887:188 (*Torymus*) synonymized by Huber 1927:56  
     *cissus* Walker of Dalla Torre 1898:302 [misspelling]  
*littoralis* Walker see *affinis* (Fonscolombe)  
*lividus* (Ashmead) 1885:xiii (*Callimome*): NEARCTIC  
*longicalcar* Graham 1994e:122-124 (*Torymus*): PALEARCTIC  
*longicauda* (Provancher) 1883:34 (*Callimome*): NEARCTIC  
*longicauda* Ratzeburg see *nitens* (Walker)  
 \**longicauda* (Spinola) 1811:148 (*Diplolepis*): PALEARCTIC [*nomen nudum*]  
*longior* Brodie 1894:45-46 (*Torymus*): NEARCTIC  
*longiscapus* Grissell 1976:78-79 (*Torymus*): NEARCTIC  
*longistigmus* (Huber) 1927:47-48 (*Callimome*): NEARCTIC  
*loranthi* (Cameron) 1913b:119 (*Syntomaspis*): NEOTROPICAL  
*lusitanicus* Tavares see *cingulatus* Nees  
*lythri* Bouček 1994a:78-79 (*Torymus*): PALEARCTIC  
*macrocentrus* Ratzeburg see *quercinus* Boheman  
*macropterus* Walker see *rubi* (Schrank)  
*macrura* (Förster) 1859:101-102 (*Syntomaspis*): PALEARCTIC  
*maculipennis* (Cameron) 1884:107 (*Syntomaspis*): NEOTROPICAL  
*maestus* Walker see *juniperi* (Linnaeus)  
*magnificus* (Osten Sacken) 1870:62 (*Callimome*): NEARCTIC  
*mandrakensis* (Risbec) 1956:162-164 (*Syntomaspis*): AFROTROPICAL  
 \**marchali* Ashmead see *ulmariae* Ruschka  
*medicaginis* Gahan see *capillaceus capillaceus* (Huber)  
*mediocris* (Walker) 1874:312-313 (*Callimome*): PALEARCTIC  
*medius* Förster see *cingulatus* Nees

- melanocerae* Ashmead see *tubicola* (Osten Sacken)
- mellipes* (Huber) 1927:23-24 (*Callimome*): NEARCTIC
- memnonius* Grissell 1973:237-238 (*Torymus*): NEARCTIC
- mendocinus* Kieffer and Jorgensen 1910:374 (*Torymus*): NEOTROPICAL
- meridionalis* Walker see *auratus* (Geoffroy)
- mexicanus* Ashmead 1899b:195-196 (*Torymus*): NEARCTIC, NEOTROPICAL  
*cognata* Breland 1939a:82-83 (*Callimome*) synonymized by Grissell 1976:79
- microcerus* (Walker) 1833:128-129 (*Callimome*): PALEARCTIC
- micropterus* Walker see *chloromerus* (Walker)
- microstigma* (Walker) 1833:127 (*Callimome*): PALEARCTIC  
*brevicauda* Walker 1833:126 (*Callimome*) synonymized by Eady 1959:264  
*viridis* Förster 1840:32 (*Torymus*) synonymized by Eady 1959:264  
*pruni* Cameron 1883:196-197 (*Torymus*) synonymized by Eady 1959:264
- micrurus* Bouček 1994a:79-80 (*Torymus*): PALEARCTIC
- millefolii* Ruschka 1921:339 (*Torymus*): PALEARCTIC
- minutissimum* Huber see *tubicola* (Osten Sacken)
- minutus* Walker see *auratus* (Geoffroy)
- minutus* Förster 1840:33 (*Torymus*): PALEARCTIC
- missouriensis* (Huber) 1927:42-43 (*Callimome*): NEARCTIC
- modestus* (Förster) 1840:32 (*Torymus*): PALEARCTIC
- moelleri* Thomson see *fuscicornis* (Walker)
- montanus* Zerova and d'Yakonchuck 1976:133 (*Torymus*): PALEARCTIC
- montserrati* Crawford 1911:441-442 (*Torymus*): NEOTROPICAL
- multicolor* (Huber) 1927:51-52 (*Callimome*): NEARCTIC
- muscarum* (Linnaeus) 1758:567 (*Ichneumon*): PALEARCTIC
- mutabilis* Walker see *auratus* (Geoffroy)
- myrtacearum* (Costa Lima) 1916:198-199 (*Syntomaspis*): NEOTROPICAL
- nanulus* (Walker) 1874:313 (*Callimome*): PALEARCTIC
- nanus* Förster (*Torymus*) see *auratus* (Geoffroy)
- narvikensis* Graham 1994a:26-27 (*Torymus*): PALEARCTIC
- neepalensis* Narendran 1994:21-22 (*Torymus*): ORIENTAL
- nemorum* Bouček 1994a:81-82 (*Torymus*): PALEARCTIC
- neuroterus* Ashmead 1887:188 (*Torymus*): NEARCTIC
- nigricornis* Boheman 1834:355-357 (*Torymus*): PALEARCTIC
- nigricornis* Boheman of authors see *nitens* (Walker)
- nigritarsus* (Walker) 1833:135 (*Callimome*): PALEARCTIC  
*alpinus* Thomson 1876:85 (*Torymus*) synonymized by Bouček and Graham 1978a:227  
*taxi* Ruschka 1921:338 (*Torymus*) synonymized by Bouček and Graham 1978a:227
- nitens* (Walker) 1833:126 (*Callimome*): PALEARCTIC  
*nigricornis* of Boheman 1834:355-356 and authors [misidentification; see Bouček and Graham 1978a:227]  
*regius* Nees 1834:55-56 (*Torymus*) synonymized by Bouček and Graham 1978a:227  
*inconstans* Walker 1834:159-160 (*Callimome*) synonymized by Bouček and Graham 1978a:227  
*lateralis* Walker 1834:160 (*Callimome*) synonymized by Bouček and Graham 1978a:227  
*incertus* Förster 1840:33 (*Torymus*) synonymized by Graham 1994e:122  
*longicauda* Ratzeburg 1844:178 (*Torymus*) synonymized by Bouček and Graham 1978a:227  
*amyrius* Walker 1846a:110-111 (*Callimome*) synonymized by Bouček and Graham 1978a:227  
*flavipes* Parfitt 1856a:5074 (*Callimome*) synonymized by Bouček and Graham 1978a:227

- devoniensis* Parfitt 1856b:5255 (*Callimome*) new name for *flavipes* Parfitt nec *flavipes* Walker, synonymized by Bouček and Graham 1978a:227
- nitidulus*** Walker 1833:138 (*Torymus*): HOLARCTIC  
*pallidicornis* Boheman 1834:363-364 (*Torymus*) synonymized by Walker 1846b:18
- nitidulus*** Nees see ***roboris*** (Walker)
- nobilis*** Boheman 1834:339-340 (*Torymus*): PALEARCTIC  
*onjunctus* Nees 1834:63 (*Torymus*) [lapsus]  
*conjunctus* Nees 1834:418 (*Torymus*) [valid emendation] synonymized by Mayr 1874:92  
*subterraneus* Curtis 1835:552 (*Callimome*)
- nonacris*** (Walker) 1843b:113-114 (*Callimome*): NEOTROPICAL
- nordlingeri*** Ratzeburg see ***cultiventris*** Ratzeburg
- notatus*** (Walker) 1833:134-135 (*Callimome*): PALEARCTIC  
*ceri* Mayr 1874:79 (*Syntomaspis*) synonymized by Eady 1959:260  
*incrassata* Thomson 1876:75 (*Syntomaspis*) synonymized by Eady 1959:260
- novitzkyi*** Graham 1994a:28 (*Torymus*): PALEARCTIC
- nubila*** (Breland) 1939a:84-85 (*Callimome*): NEOTROPICAL
- nuda*** (Breland) 1939a:89-90 (*Callimome*): NEOTROPICAL
- obscuripes*** Förster 1840:32 (*Torymus*): PALEARCTIC
- obscurus*** (Breland) 1939b:721 (*Callimome*): NEARCTIC
- occidentalis*** (Huber) 1927:79-80 (*Callimome*): NEARCTIC
- ochreatus*** Say 1836:275 (*Torymus*): NEARCTIC
- omnivorae*** Ashmead see ***lissus*** (Walker)
- oreiplanus*** Kieffer and Jorgensen 1910:388 (*Torymus*): NEOTROPICAL
- orissaensis*** (Mani) 1936:125 (*Lioterphus*): ORIENTAL
- osborni*** (Huber) 1927:93 (*Callimome*): NEARCTIC
- ostensackenii*** Dalla Torre see ***fagopirum*** (Provancher)
- oviperditor*** (Gahan) 1927:99-100 (*Syntomaspis*): NEARCTIC
- pachypsyllae*** (Ashmead) 1888:iii (*Monodontomerus*): NEARCTIC
- pallidipes*** Ashmead 1894a:153-154 (*Torymus*): NEOTROPICAL
- pallidicornis*** Boheman see ***nitidulus*** Walker
- palliditarsis*** Dalla Torre see ***pallitarsis*** Förster
- pallitarsis*** Förster 1840:31 (*Torymus*): PALEARCTIC  
*palliditarsis* Dalla Torre 1898:311 [invalid emendation]
- paraguayensis*** (Girault) 1913/157:61 (*Syntomaspis*): NEOTROPICAL
- pascuorum*** Bouček 1994a:82-83 (*Torymus*): PALEARCTIC
- pavidus*** Say 1836:275-276 (*Torymus*): NEARCTIC
- perplexus*** (Huber) 1927:49-50 (*Callimome*): NEARCTIC
- \****persicariae*** Mayr see ***polygoni*** (Hoffmeyer)
- persimilis*** Ashmead 1894b:334 (*Torymus*): NEARCTIC
- pertinax*** Förster 1891:452 (*Torymus*) (fossil): PALEARCTIC
- philippii*** (Hoffmeyer) [new name] 1929:334 (*Callimome*): NEOTROPICAL  
*laetus* Philippi 1873:298-299 (*Misocampus*) nec *laetus* (Walker)
- phillyreae*** Ruschka 1921:340-341 (*Torymus*): PALEARCTIC  
*schiodtei* (Hoffmeyer) 1930b:115 (*Callimome*) synonymized by Graham 1994d:121
- tripudians*** Graham 1993:19-21 (*Torymus*) synonymized by Graham 1994d:121
- pilularidis*** Huber see ***baccharidis*** (Huber)

- pleuralis* Thomson see *scutellaris* (Walker)  
*poae* (Hoffmeyer) 1930a:26 (*Callimome*): PALEARCTIC  
*polygoni* (Hoffmeyer) [new name] 1930d:251 (*Callimome*): PALEARCTIC  
   \**persicariae* Mayr 1874:59 (*Torymus*) [*nomen nudum*]  
*posticus* Walker see *fuscicornis* (Walker)  
*potamius* Grissell 1976:34-35 (*Torymus*): NEARCTIC  
*pretiosus* (Walker) 1833:121 (*Callimome*): PALEARCTIC  
*propinquus* Förster see *auratus* (Geoffroy)  
*prospidis* Kieffer and Jorgensen 1910:430 (*Torymus*): NEOTROPICAL  
*pruni* Cameron see *microstigma* (Walker)  
*prunicola* (Huber) 1927:91 (*Callimome*): NEARCTIC  
*pubescens* Förster see *varians* (Walker)  
*pulchellus* Thomson see *aerope* (Walker)  
*pumilus* Ratzeburg see *tipulariarum* Zetterstedt  
*punctifrons* (Ashmead) 1894a:154 (*Syntomaspis*): NEOTROPICAL  
*purpurascens* Boheman see *laetus* (Walker)  
*purpurascens* (Fabricius) 1798:231-232 (*Ichneumon*): PALEARCTIC  
*purpurascens* Olivier see *erucarum* (Schränk)  
*purpureomaculata* (Cameron) 1904b:58 (*Syntomaspis*): NEOTROPICAL  
*pygmaeus* Mayr 1874:120 (*Torymus*): PALEARCTIC  
*quercinus* Boheman 1834:373-374 (*Torymus*): PALEARCTIC  
   *macrocentrus* Ratzeburg 1852:224 (*Torymus*)  
*quadricolor* Walker see *ventralis* (Fonscolombe)  
*racemariae* (Ashmead) 1881 (*Callimome*): NEARCTIC  
   *racemariae* Ashmead 1881:xxxiii (*Callimome*)  
   *racemariae* Ashmead 1887:187 (*Syntomaspsis*) [valid emendation]  
*ramicola* Ruschka 1921:337 (*Torymus*): PALEARCTIC  
*ranomanfanensis* (Risbec) 1956:161-162 (*Syntomaspis*): AFROTROPICAL  
*rasaces* Walker see *erucarum* (Schränk)  
*regalis* (Walker) 1833:119 (*Callimome*): PALEARCTIC  
*regius* Nees see *nitens* (Walker)  
*resinanae* Ratzeburg 1852:224-225 (*Torymus*): PALEARCTIC  
*rhamni* Bouček 1994a:83-85 (*Torymus*): PALEARCTIC  
*rhoditidis* (Huber) 1927:34 (*Callimome*): NEARCTIC  
   \**ribesii* Huber see *fagopirum* (Provancher)  
*ringofushi* Kamijo 1979:6-9 (*Torymus*): PALEARCTIC  
*roboris* (Walker) 1833:120 (*Callimome*): PALEARCTIC  
   [removed from synonymy with *nobilis* Boheman by Graham 1994a:33]  
   *nitidulus* Nees 1834:64 (*Torymus*)  
*robustum* Huber see *floridensis* Peck  
*robustus* Ratzeburg see *fastuosus* Boheman  
*rohweri* Huber see *thalassinus* (Huber)  
*rosae* Huber see *solitarius* (Osten Sacken)  
*rosarum* (Hoffmeyer) [new name] 1929:334 (*Callimome*): PALEARCTIC  
   *druparum* of Mayr 1874:103 nec *druparum* Boheman  
*rubenidis* Huber see *tubicola* (Osten Sacken)  
*rubi* (Schränk) 1781:320-321 (*Cynips*): PALEARCTIC

- macropterus* Walker 1833:124 (*Callimome*) synonymized by Bouček and Graham 1978a:227
- rudbeckiae*** Ashmead 1890:26 (*Torymus*): NEARCTIC
- rubripes* Ratzeburg see ***erucarum*** (Schrank)
- rudis* Walker see ***ventralis*** (Fonscolombe)
- rufipes* Förster see ***laetus*** (Walker)
- rufipes*** (Walker) 1834:160 (*Callimome*): PALEARCTIC
- rugglesi*** Milliron 1959:52 (*Torymus*): NEARCTIC
- rugosipunctatus*** Ashmead 1894a:153 (*Torymus*): NEOTROPICAL
- ruschkai*** (Hoffmeyer) [new name] 1929:334 (*Callimome*): PALEARCTIC
- tubicola* Ruschka 1921:340 (*Torymus*) nec *tubicola* (Osten Sacken)
- sackeni* Brues see ***bruesi*** (Huber)
- sackenii* Ashmead see ***fagopirum*** (Provancher)
- sackenii* Brues see ***bruesi*** (Huber)
- salciperdae*** Ruschka 1921:342 (*Torymus*): PALEARCTIC
- salicis*** Graham 1994a:27-28 (*Torymus*): PALEARCTIC
- saphirinus* Boheman see ***affinis*** (Fonscolombe)
- sapphyrinus* Boheman see ***affinis*** (Fonscolombe)
- sapphyrinus* of Nees see ***affinis*** (Fonscolombe)
- sapporoensis*** Ashmead 1904b:82-83 (*Torymus*): PALEARCTIC
- sarothamni*** Kieffer 1899:369 (*Torymus*): PALEARCTIC
- sativae* Huber see ***capillaceus capillaceus*** (Huber)
- scalaris*** (Huber) 1927:21-22 (*Callimome*): NEARCTIC
- scaposus*** (Thomson) 1876:77-78 (*Callimomus*): PALEARCTIC
- schiodtei* (Hoffmeyer) see ***phillyreae*** Ruschka
- schizothecae*** Ruschka 1921:341 (*Torymus*): PALEARCTIC
- scoparii*** (Hoffmeyer) 1930b:116 (*Callimome*): PALEARCTIC
- scutellaris*** (Walker) 1833:123 (*Callimome*): PALEARCTIC
- pleuralis* Thomson 1876:89-90 (*Torymus*) see Bouček and Graham 1978a:227 (name incorrectly cited to Boheman 1834)
- seminum*** (Hoffmeyer) 1929:332 (*Callimome*): PALEARCTIC
- sinensis*** Kamijo 1982:505-507 (*Torymus*): PALEARCTIC
- smithi*** Ashmead 1904a:398-399 (*Torymus*): NEOTROPICAL
- socius*** Mayr 1874:126 (*Torymus*): PALEARCTIC
- sodalis* Mayr see ***auratus*** (Geoffroy)
- solidaginis*** (Huber) 1927:92-93 (*Callimome*): NEARCTIC
- solinus* Walker see ***juniperi*** (Linnaeus)
- solitarius*** (Osten Sacken) 1870:64 (*Callimome*): NEARCTIC
- rosae* Huber 1927:35-36 (*Callimome*) synonymized by Grissell 1976:37
- tubularis* Huber 1927:39-40 (*Callimome*) synonymized by Grissell 1976:37
- chrysochlora* of Huber 1927:38-39 (*Callimome*) misidentification in part of ***chrysochlorus*** (Osten Sacken) 1870:63, according to Grissell 1976:37
- spaici*** Bouček 1994a:85-86 (*Torymus*): PALEARCTIC
- speciosus*** Boheman 1834:349-350 (*Torymus*): PALEARCTIC: (See Bouček and Graham 1978a:227)
- spilopterus*** Boheman 1834:364-365 (*Torymus*): PALEARCTIC
- \**spinipes* (Spinola) 1811:148 (*Diplolepis*): PALEARCTIC [*nomen nudum*]
- splendidulus*** Dalla Torre 1898:313 (*Torymus*): NEARCTIC

- splendidus* Walker 1844a:14-15 (*Callimome*) nec *splendidus* Förster  
*splendidus* Walker see *splendidulus* Dalla Torre  
*splendidus* Förster 1840:32 (*Torymus*): PALEARCTIC  
*stenus* Graham 1994a:25-26 (*Torymus*): PALEARCTIC  
*stramineitarsus* Walker see *auratus* (Geoffroy)  
*streneuus* (Walker) 1871a:34 (*Callimome*): PALEARCTIC  
*strobiloides* Huber see *cecidomyiae* (Walker)  
*subcalifornicus* Grissell 1976:44-45 (*Torymus*): NEARCTIC  
*subdolum* Huber see *californicus* (Ashmead)  
*subigneus* Szelenyi 1973:186 (*Torymus*): PALEARCTIC  
*subnudus* Bouček 1978:131-132 (*Torymus*): AFROTROPICAL  
*subterraneus* Curtis see *nobilis* Boheman  
*sulcatus* (Huber) 1927:22 (*Callimome*): NEARCTIC  
*superbus* Kieffer and Jorgensen 1910:430 (*Torymus*): NEOTROPICAL  
*superbus* Provancher see *flavicoxa* (Osten Sacken)  
*sylvicola* Ashmead 1904a:399 (*Torymus*): NEOTROPICAL  
*tanaceticola* Ruschka 1921:339 (*Torymus*): PALEARCTIC  
*tarsale* Huber see *huberi* (Hoffmeyer)  
*tarsalis* Walker see *affinis* (Fonscolombe)  
*taxi* Ruschka see *nigritarsus* (Walker)  
*terminalis* Walker see *auratus* (Geoffroy)  
*texanus* (Hoffmeyer) 1930c:213-214 (*Callimome*): NEARCTIC  
*thalassinus* (Crosby) 1908:43-44 (*Syntomaspis*): NEARCTIC  
*rohweri* Huber 1927:58-59 (*Callimome*) synonymized by Grissell 1976:85  
*theon* Walker 1843a:149 (*Torymus*): NEARCTIC  
*thompsoni* Fyles 1967a (*Torymus*): NEARCTIC  
*thomsoni* Fyles 1907a:10-11 (*Torymus*) (also 1904b:106)  
*thompsoni* Fyles 1916:55 (*Torymus*) [valid emendation]  
*thoracicus* (Ashmead) 1904a:401 (*Hemitorymus*): NEOTROPICAL  
*thymi* Ruschka 1921:339 (*Torymus*): PALEARCTIC  
*tiliarum* Ruschka 1921:337 (*Torymus*): PALEARCTIC  
*tilicola* Ruschka 1921:337-338 (*Torymus*): PALEARCTIC  
*tipulariarum* Zetterstedt 1838:420 (*Torymus*): PALEARCTIC  
*viridissimus* var B *Tipulariarum* Zetterstedt 1838:420 (*Torymus*)  
*pumilus* Ratzeburg 1844:180 (*Torymus*) synonymized by Mayr 1874:111  
*triangularis* Thomson 1876:96 (*Torymus*): PALEARCTIC  
*tricolor* Huber see *umbilicatus* (Gahan)  
*tripudians* Graham see *phillyreae* Ruschka  
*truncatus* (Fonscolombe) 1832:287 (*Cinips*): PALEARCTIC  
*tsugae* (Yano), in Yano and Oyama 1918:373 (*Callimome*): PALEARCTIC  
*tubicola* (Osten Sacken) 1870:60 (*Callimome*): NEARCTIC, NEOTROPICAL  
*melanocerae* Ashmead 1885:xiii (*Callimome*) synonymized by Grissell 1976:86  
*citriformi* Ashmead 1885:xiii-xiv (*Callimome*)  
*castanopsidis* Huber 1927:64-65 (*Callimome*) synonymized by Grissell 1976:86  
*giganticum* Huber 1927:65-67 (*Callimome*) synonymized by Grissell 1976:86  
*?gahani* Huber 1927:69-70 (*Callimome*) synonymized by Grissell 1976:86  
*rubendis* Huber 1927:78 (*Callimome*) synonymized by Grissell 1976:86

- minutissimum* Huber 1927:78-79 (*Callimome*) synonymized by Grissell 1976:86
- tubicola* Ruschka see *ruschkai* (Hoffmeyer)
- tubularis* Huber see *solitarius* (Osten Sacken)
- ulmariae* Ruschka 1921:340 (*Torymus*): PALEARCTIC
- \**marchali* Ashmead: Marchal 1900:110 (*Torymus*) [*nomen nudum*; Marchal (1900) cited "*Torymus marchali* Ashmead (nov sp in litteris)" without description. Ashmead did not validate the name. The species was reared from *Cecidomyia ulmariae* (now = *Dasineura ulmaria* (Bremer)) from which only the species *Torymus ulmariae* has been reared. It is reasonable to presume that Marchal's and Ruschka's names refer to the same taxon]
- umbilicatus* (Gahan) 1919:163-164 (*Syntomaspis*): NEARCTIC, NEOTROPICAL
- tricolor* Huber 1927:96 (*Callimome*) synonymized by Grissell 1976:50
- urticae* Perris 1840:404-405 (*Cynips*): PALEARCTIC
- [considered a synonym of *confinis* (Walker) by Bouček and Graham 1978:71 but a valid taxon by Askew in Redfern 1993:40]
- vallisnerii* Cameron 1901:273-274 (*Torymus*): PALEARCTIC
- varians* (Walker) 1833:122 (*Syntomaspis*): HOLARCTIC
- pubescens* Förster 1840:32 (*Torymus*) synonymized by Dalla Torre 1898:294
- annellus* Thomson 1876:76 (*Syntomaspis*) synonymized by Graham 1969:69
- ventralis* (Fonscolombe) 1832:286-287 (*Cinips*): PALEARCTIC
- quadricolor* Walker 1833:120-121 (*Callimome*)
- antennatus* Walker 1833:135-136 (*Callimome*) synonymized by Eady 1959:259
- versicolor* Walker 1833:136 (*Callimome*) synonymized by Eady 1959:259
- rudis* Walker 1836:25 (*Callimome*) synonymized by Eady 1959:259
- affinis* Förster 1840:31 (*Torymus*)
- discolor* Thomson 1876:79 (*Callimomus*)
- verbasci* Ruschka 1921:339-340 (*Torymus*): PALEARCTIC
- veronicae* Ruschka 1921:338-339 (*Torymus*): PALEARCTIC
- versicolor* Walker see *ventralis* (Fonscolombe)
- vesiculi* Moser 1956:58-62 (*Torymus*): NEARCTIC
- "*viatus* Boh" Marchal 1900:110 (*Torymus*) [name appears to be a lapsus of unknown origin]
- violae* (Hoffmeyer) 1944:158 (*Callimome*): PALEARCTIC
- virentis* Ashmead see *fagopirum* (Provancher)
- viridiaeneus* Walker see *basalis* Walker
- viridis* Förster see *microstigma* (Walker)
- viridis* Geoffroy see *bedeguaris* (L.)
- viridissimus* Boheman see *auratus* (Geoffroy)
- viridissimus tipulariarum* Zetterstedt see *tipulariarum* Zetterstedt
- warreni* (Cockerell) 1911:82 (*Syntomaspis*): NEARCTIC
- cinerosum* Huber 1927:84-85 (*Callimome*) synonymized by Grissell 1976:52
- xanthopus* (Schulz) [new name] 1906:147 (*Megalostigmus*): NEARCTIC
- flavipes* Ashmead 1888:III (*Megalostigmus*) nec *flavipes* Walker
- abortus* Crosby 1914:27 (*Torymus*) [new name]



**Zaglyptonotus** Crawford (text, p. 173)

*Zaglyptonotus* Crawford 1914:125-126. Type-species: *Zaglyptonotus schwarzi* Crawford (orig. desig. and monotypic).

*Perissocentroides* E. Blanchard 1938:44. [*Nomen nudum.*] [Earlier in the present work I explained the placement of this name.]

*bosqi* (E. Blanchard). *Nomen nudum.*

*Perissocentroides bosqi* E. Blanchard 1939:24. Argentina.

TAXONOMY. - De Santis (1967:185) cited "Blanchard MS" for this species, indicating that it was simply a manuscript name. The original mimeographed papers were distributed 4 times a year as the "Boletín Informativo de la Dirección de Sanidad Vegetal", and so the name should be considered a published one. It is a *nomen nudum*, however, because no description was given with the name.

*bruchii* (Girault). NEOTROPICAL: (The type locality cannot be ascertained.)

*Perissocentrus bruchii* Girault 1917/316:11-12. Holotype ♀, "Bruchi, P.C." (USNM, examined).

TAXONOMY. - Grissell (1992b) transferred this species from *Perissocentrus* and discussed the lack of information about the type locality.

*bruchophagus* (E. Blanchard). *Nomen nudum.*

*Perissocentroidesbruchophagus* E. Blanchard 1938:44. Argentina.

TAXONOMY. - De Santis (1967:185) cited "Blanchard MS" for this species, indicating that it was simply a manuscript name. The original mimeographed papers were distributed 4 times a year as the "Boletín Informativo de la Dirección de Sanidad Vegetal", and so the name should be considered a published one. It is a *nomen nudum*, however, because no description was given with the name.

*mississippiensis* Breland. NEARCTIC: USA (Mississippi, Alabama). Canada ("mid-western" [= Saskatchewan, Alberta]: Sharkey *et al.* 1987).

*Zaglyptonotus mississippiensis* Breland 1938a:205-206. Holotype sex and type locality not stated (Breland Collection, destroyed); material collected Artesia, Jackson, Meridian, and Tupelo, Mississippi, and Tuscaloosa, Alabama (paratype specimens in USNM, examined).

HOST. - The type series was reared from *Tephritis finalis* (Tephritidae) in *Helianthus* (Asteraceae). Sharkey *et al.* (1987) found this to be the host also in midwestern Canada.

*schwarzi* Crawford. NEARCTIC: USA (Texas; Florida, Kansas, Idaho, Colorado: see state list in Peck 1963).

*Zaglyptonotus schwarzi* Crawford 1914:126. Lectotype ♀, herein designated, San Diego, Texas, USA (USNM, examined); 2 ♀ paralectotypes, same as lectotype.

HOSTS. - This species reportedly has been reared from the following hosts (see Peck 1963, Grissell 1979): *Isophrictis similiella* (Gelechiidae), *Desmoris fulvus* (Curculionidae), and a tephritid seed maggot in *Vernonia* (Asteraceae).

***Zdenekius*** Grissell (text, p. 121)

*Zdenekius* Grissell 1993:264-267. Type-species: *Zdenekius smithi* Grissell (orig. desig. and monotypic).

***smithi*** Grissell. NEARCTIC: USA (Oregon, Illinois, Michigan, New Hampshire, Maryland, Washington, D.C., Virginia); Canada (Ontario, Quebec, New Brunswick).

*Zdenekius smithi* Grissell 1993:268-269 (Figs. 1-5, 8-11, 13). Holotype ♀, near Annandale, Virginia, USA (USNM, examined); 10 ♀ paratypes same as holotype; other paratypes: 3 ♀, nr. Cuckoo, Virginia, USA; 1 ♂, Fairfax County, Virginia, USA; 1 ♂, Ann Arbor, Michigan, USA; 1 ♀, Midland County, Michigan, USA; 2 ♂, Prineville, Oregon, USA; 1 ♂, 1 ♀ Durham, New Hampshire, USA; 1 ♂, Washington, D.C., USA; 1 ♂, Algonquin, Illinois, USA (and 1 ♂, state only); 11 ♀, Hamilton, Ontario, Canada; 5 ♀, 1 ♂, Ottawa, Ontario, Canada; 1 ♂, Mont Royal, Montreal, Quebec, Canada.

HOSTS. - None of the type material was reared. On circumstantial evidence this species probably parasitizes aculeate wasps, but it may be hyperparasitic. Two specimens from Maryland were reared from a "nest of *Symmorphus debilis*" (now = *Symmorphus canadensis*) (Vespidae). Other specimens were reared from stems of *Alnus rubra* (Corylaceae) in Oregon, which produced *Anthrax irrotatus* (Bombyliidae), a dipterous group known to parasite aculeate wasps. Another specimen was reared from willow limbs with larvae thought to be crabronine sphecids.

***Zophodetus*** Grissell (text, p. 75)

*Zophodetus* Grissell 1980:253. Type-species: *Zophodetus woodruffi* Grissell (orig. desig. and monotypic).

***woodruffi*** Grissell. NEOTROPICAL: Dominican Republic (amber).

*Zophodetus woodruffi* Grissell 1980:253-255 (Figs. 1-7). Holotype ♀, nw of Santiago, Dominican Republic (FSCA).

**HOST-PARASITE LIST OF TORYMINAE (EXCEPT *TORYMUS*)**  
**ALPHABETICAL BY HOST ORDER AND FAMILY**  
 (for alphabetical index to hosts see p. 309)

This list represents currently used nomenclature as accurately as I have been able to ascertain. Valid host names are listed below with the parasite species listed after it. Also listed are host names as given in the original literature with the note to "see" the valid name (i.e., there are no parasite names listed under invalid host names). In a few cases in the previous catalog section where a host is given that appears to be highly questionable, I do not list it below in the host list. In this list I give only the insect host but not the plant host with which that host is associated (much of that information is given in the catalog). For example, for a known cynipid host on a known oak I list the cynipid but not also the oak as host. In cases where the host is known simply as a "cecidomyiid" or "cynipid," then the plant host is listed in the insect section under the insect host, for example: "Cecidomyiidae: Undetermined cecidomyiid galls on *X-us albus* stems." If no insect host is known and a rearing stated only that the parasite was reared, for example, from *Xus albus* stems, then I list these under "Plant Hosts" on p. 306. I have omitted the genus *Torymus* from this list for the same reasons given in the catalog introduction, p. 176.

In checking the nomenclature for this list I had the help of many co-workers whom I have listed in the Acknowledgment section (p. 5). Even though these workers have checked the list, I assume full responsibility for any errors that found their way into the compilation.

## ANIMAL HOSTS

### COLEOPTERA

#### **Anthribidae:**

?*Brachytarsus* sp. see *Trigonorhinus* sp.

?*Trigonorhinus* sp.: *Microdontomerus anthonomi*

#### **Bruchidae:**

*Acanthscelides aureolus* (Horn): *Microdontomerus anthonomi*

*Acanthscelides compressicornis* (Schaeffer): *Microdontomerus anthonomi*

*Acanthscelides derifieldi* (Johnson): *Microdontomerus anthonomi*

*Acanthscelides desmanthi* Johnson: *Microdontomerus anthonomi*

*Acanthscelides horni* (Pic): *Microdontomerus anthonomi*

*Acanthscelides mixtus* (Horn): *Microdontomerus anthonomi*

*Acanthscelides pullus* (Fall): *Microdontomerus anthonomi*

*Acythopeus traghardi* Aurivillius: *Pseudotorymus acythopeusi*

*Bruchidius akaensis* (Decelle): *Pseudotorymus leguminosae*

*Bruchidius albizarum* (Decelle): *Pseudotorymus leguminosae*

?*Bruchidius albosparus* (Fahraeus): *Pseudotorymus acythopeusi*,

*Pseudotorymus leguminosae*

*Bruchidius baudoni* Caillol: *Pseudotorymus leguminosae*

*Bruchidius ineaci* (Decelle): *Pseudotorymus leguminosae*

*Bruchidius leonensis* (Pic): *Pseudotorymus leguminosae*

*Bruchidius mabwensis* (Decelle): *Pseudotorymus leguminosae*

*Bruchidius* spp: *Pseudotorymus leguminosae*

*Bruchidius submaculatus* Olivier: Pseudotorymus leguminosae  
*Bruchidius uberatus* (Fahraeus): Pseudotorymus leguminosae  
*Bruchus brachialis* Fahraeus: Microdontomerus anthonomi  
*Bruchus pisorum* (L.): Microdontomerus anthonomi  
*Callosobruchus maculatus* (Fabricius): Pseudotorymus acythopeusi  
*Sennius morosus* (Sharp): Microdontomerus anthonomi  
*Stator limbatus* (Horn): Microdontomerus anthonomi  
*Stator pruininus* (Horn): Microdontomerus anthonomi

**Buprestidae:**

*Steraspis speciosa* Klug: Microdontomerus ovivorus

**Curculionidae:**

*Anthonomus grandis* Boheman: Microdontomerus anthonomi  
 ?*Apion apricans* Herbst: Pseudotorymus apionis  
*Apion craccae* L.: Pseudotorymus apionis  
*Bangastermus orientalis* (Capiomont): Microdontomerus anthonomi  
*Desmoris fulvus* (Leconte): Zaglyptonotus schwarzi  
*Microlarinus lareynii* (Jaquelin du Val): Microdontomerus anthonomi  
*Rhinocyllus conicus* Froelich: Microdontomerus anthonomi

**DIPTERA****Bombyliidae:**

?*Anthrax irroratus* Say: Zdenekius smithi

**Cecidomyiidae:**

*Allodiplosis crassa* Kieffer and Jorgensen: Torymoides festiva, Torymoides testacea  
*Asphondylia crassipalpis* Kieffer and Jorgensen: Torymoides asphondyliarum  
*Asphondylia miki* Wachtl: Torymoides violaceus  
*Asphondylia terminaliae* (Tavares) see *Tetrasphondylia terminaliae* Tavares  
*Asphondylia verbasci* Vallot: Pseudotorymus verbasci  
*Cecidomyia loti* DeGeer see *Contarinia loti* (DeGeer)  
*Clinorhyncha arthemidis* Rübsaamen see *Ozirhincus arthemidis* (Rübsaamen)  
 ?*Contarinia loti* (DeGeer): Pseudotorymus medicaginis  
*Contarina onobrychidis* Kieffer: Pseudotorymus leguminus  
*Contarina silvestris* Kieffer: Pseudotorymus leguminus  
*Contarina* sp.: Pseudotorymus brassicae, Torymoides smithi  
*Dasineura brassicae* Winnertz: Pseudotorymus brassicae  
 ?*Dasineura brassicae* (as *Diplosis ochracea* Winnertz): Pseudotorymus napi  
*Dasineura leguminicola* (Lintner): Pseudotorymus lazulellus  
*Dasineura loewi* (Mik): Torymoides violaceus  
*Dasineura papaveris* (Winnerz): Pseudotorymus papaveris  
*Dasineura rosaria* (Loew): Pseudotorymus salicis  
*Dasineura sisymbrii* (Schrank): Pseudotorymus brassicae  
*Dasineura* sp.: Pseudotorymus medicaginis  
*Dasineura terminalis* (Loew): Pseudotorymus krygeri  
*Diplosis ochracea* Winnertz see ?*Dasineura brassicae* Winnertz  
*Ficiomyia perarticulata* Felt: Physothorax bidentulus  
*Gephyraulus diplotaxis* (Solinas): Pseudotorymus brassicae

- Hyperdiplosis* sp.: *Torymoides sulcius*  
*Iatrophobia brasiliensis* (Rubsamen): *Torymoides sulcius*  
*Lasioptera eryngii* (Vallot): *Pseudotorymus sapphyrinus mongolicus*,  
*Pseudotorymus sapphyrinus sapphyrinus*  
*Lasioptera interrupta* Kieffer and Jorgensen see *Neolasioptera interrupta* (Kieffer and Jorgensen)  
*Lestodiplosis callida* Winnertz: *Pseudotorymus papaveris*  
*Mayetiola destructor* (Say): *Ditropinotus aureoviridis*, *Eridontomerus isosomatis*,  
*Pseuderimerus mayetiolae*, *Pseuderimerus semiflavus*  
? *Mayetiola destructor* (Say): *Pseuderimerus luteus*  
*Neolasioptera interrupta* (Kieffer and Jorgensen): *Torymoides erythromma*  
*Ozirhincus anthemidis* (Rübsamen): *Idiomacromerus balasi*  
*Paragephyraultus diplotaxis* Solinas see *Gephyraultus diplotaxis* (Solinas)  
*Rabdophaga rosaria* Loew see *Dasineura rosaria* (Loew)  
*Tetrasphondylia terminaliae* (Tavares): *Pseudotorymus africanus*  
*Thomasiella eryngii* (Vallot) see *Lasioptera eryngii* (Vallot)  
*Wachtliella stachydis* (Bremi): *Pseudotorymus stachidis*  
Undetermined cecidomyiid galls on:  
*Baccharis halimifolia*: *Torymoides sulcius*  
*Carmichaelia* sp.: *Torymoides antipoda*  
*Carpodetus serratus*: *Torymoides antipoda*  
*Ceratoides* sp.: *Torymoides nikolskayae*  
*Manihot glaziovii*: *Torymoides sulcius*  
*Manihot tripartita*: *Torymoides sulcius*  
*Salsola* sp.: *Torymoides eltonicus*  
*Salvia pratensis*: *Pseudotorymus salviae*  
*Suaeda divaricata*: *Torymoides swaedicola*

### Tachinidae:

- Alsomyia nidicola* Townsend see *Townsendiellomyia nidicola* (Townsend)  
*Blepharipa pratensis* (Meigen): *Monodontomerus aereus*  
*Blepharipa scutellata* (Robineau-Desvoidy) see *Blepharipa pratensis* (Meigen)  
*Carcelia laxifrons* Villeneuve: *Monodontomerus aereus*  
*Compsilura concinnata* (Meigen): *Monodontomerus aereus*  
*Exorista larvarum* (L.): *Monodontomerus aereus*  
*Exorista segregata* (Rondani): *Monodontomerus aereus*  
*Korallomyia portentosa* Mesnil (in vespidae nest): *Amoturoides breviscapus*  
*Masicera sphingivora* (Robineau-Dosvoidy): *Monodontomerus minor*  
*Masicera zimini* Kolomiets see *Masicera sphingivora* (Robineau-Dosvoidy)  
*Sturmia scutellata* (Robineau-Dosvoidy) see *Blepharipa pratensis* (Meigen)  
tachinid (in cocoon of *Hyalophora cecropia*): *Monodontomerus minor*  
*Townsendiellomyia nidicola* (Townsend): *Monodontomerus aereus*  
*Zenillia libatrix* (Panzer): *Monodontomerus minor*

### Tephritidae:

- Acanthophilus helianthi* Rossi: *Torymoides kiesewetteri*  
*Chetostoma completum* Kapoor, Malla, and Ghosh: *Torymoides kiesewetteri*  
*Myopites blotii* de Brebisson see *Myopites inulaedyssentericae* Blot  
*Myopites frauenfeldi* (Schiner) see *Myopites longirostis* (Loew)

*Myopites inulaedysentericae* Blot: *Torymoides kiesenwetteri*  
*Myopites longirostis* (Loew): *Torymoides kiesenwetteri*  
*Myopites stylatus* (Fabricius): *Torymoides kiesenwetteri*  
*Neotephritis finalis* (Loew): *Zaglyptonotus mississippiensis*  
*Procecidochares utilis* Stone: *Torymoides kiesenwetteri*, *Torymoides vibidia*  
*Urophora affinis* Frauenfeld: *Microdontomerus anthonomi*  
 flower head of *Vernonia*: *Zaglyptonotus schwarzi*

## HETEROPTERA

### Coreidae:

*Physomerus* sp. (eggs): *Chrysochalcissa physomeri*  
 coreid eggs: *Chrysochalcissa afra*, *Chrysochalcissa oviceps*

### Pentatomidae:

*Apodiphus amygdalis* (Germar): *Oopristus turkestanica*  
*Sarju eremica* (Hoberlandt): *Oopristus turkestanica*  
 pentatomid eggs: *Microdontomerus* sp.

### Unspecified family:

“bug eggs”: *Chrysochalcissa olivacea*, *Rhynchotocida ovivora*

## HYMENOPTERA

### “Aculeate Hymenoptera”:

in burrows in dead wood: *Ecdamua macrotelus*

### Anthophoridae:

*Allodapula* sp. see *Braunsapis*  
*Ancyloscelis apiformis* (Fabricius): *Monodontomerus mexicanus*  
*Ancyloscelis armataus* Smith see *Ancyloscelis apiformis* (Fabricius)  
*Anthophora abrupta* Say: *Monodontomerus mandibularis*  
*Anthophora bomboides bomboides* Kirby: *Monodontomerus mandibularis*  
*Anthophora bomboides neomexicana* Cockerell: *Monodontomerus montivagus*  
*Anthophora linsleyi* Timberlake: *Monodontomerus montivagus*  
 ?*Anthophora occidentalis* Cresson: *Monodontomerus montivagus*  
*Anthophora retusa* (L.): *Monodontomerus aeneus*  
 ?*Anthophora vallorum* (Cockerell): *Monodontomerus montivagus*  
*Braunsapis rolini* (Vachal): *Echthrodape africana*  
*Braunsapis rufipes* (Friese): *Echthrodape africana*  
*Braunsapis simplicipes* Michener: *Echthrodape africana*  
*Braunsapis* sp.: *Echthrodape africana*  
*Ceratina dupla* Say: *Diomorus zabriskiei*  
*Ceratina callosa* (Fabricius): *Monodontomerus aeneus*  
*Ceratina japonica* Cockerell in *Rubus* twigs: *Diomorus armatus*  
 ?*Melissoides* sp.: *Monodontomerus montivagus*  
*Melitoma taurea* (Say): *Monodontomerus mandibularis*  
*Xylocopa fenestrata* Fabricius: *Monodontomerus obscurus*  
*Xylocopa tabaniformis orpifex* Smith: *Monodontomerus montivagus*

### Apidae:

*Bombus morrisoni* Cresson: *Monodontomerus montivagus*  
*Eufriesea nigresens* (Friese): *Monodontomerus argentinus*

*Euplusia longipennis* (Friese) see *Eufriesea nigresens* (Friese)

### Braconidae:

*Aleiodes* sp.: Monodontomerus minor

*Apanteles glomeratus* (L.) see *Cotesia glomerata* (L.)

*Apanteles lacteicolor* Viereck see *Dolichogenidea lacteicolor* (Viereck)

*Apanteles liparidis* (Bouche) see *Glyptapanteles liparidis* (Bouche)

*Apanteles melanoscelus* (Ratzeburg) see *Cotesia melanoscelus* (Ratzeburg)

*Bracon mellitor* Say: Microdontomerus anthonomi

*Bracon* sp.: Pseudotorymus africanus

*Cotesia glomerata* (L.): Monodontomerus minor

*Cotesia melanoscelus* (Ratzeburg): Monodontomerus aereus

*Dolichogenidea lacteicolor* (Viereck): Monodontomerus aereus

*Glyptapanteles liparidis* (Bouche): Monodontomerus minor

*Meteorus* sp.: Pradontomerus hyper

*Meteorus versicolor* (Wesmael): Monodontomerus aereus

*Rogas* sp. see *Aleiodes* sp.

*Rogas unicolor* (Wesmael) see *Aleiodes pallidator* (Thunberg)

### Chalcididae:

*Brachymeria intermedia* Nees: Monodontomerus aereus

### Chrysididae:

?*Omalus auratus* Dahlbom: Diomorus calcaratus

### Cimbicidae:

*Trichiosoma betuleti* (Klug) see *Trichiosoma lucorum* (L.)

*Trichiosoma lucorum* (L.): Monodontomerus vicicellae, Monodontomerus minor

*Trichiosoma nanae* Vikberg and Viitasaari: Monodontomerus vicicellae

*Trichiosoma tibiale* Stephens: Monodontomerus minor

### Cynipidae:

*Adleria quercustozae* (Bosc) (gall with ?crabronine wasp): Diomorus calcaratus

*Andricus kollari* (Hartig) (galls with *Omalus auratus* Dahlbom): Diomorus calcaratus

*Andricus kollari* (Hartig): Adontomerus crassipes

*Antistrophus lygodesmiaepisum* Walsh: Microdontomerus bicoloripes

*Asiocynips caulina* D'Iakonchuk: Pseuderimerus luteolus

*Asiocynips cousinia* D'Iakonchuk: Pseuderimerus luteolus

*Aulacidea nigriceps* Barbotin (in *Papaver* seed capsules): Chalcimerus borceai

*Aulacidea parvula* D'Iakonchuk: Pseuderimerus luteolus

*Aulacidea scorzonerae* (Giraud): Idiomacromerus mayri

*Aulacidea sicolor* D'Iakonchuk: Pseuderimerus luteolus

*Aulacidea subterminalis* Niblett: Glyphomerus tibialis

*Aulacidea tragopogonis* (Thomson): Adontomerus impolitus

*Aylax rhoeadis* Hartig see *Aylax papaveris* (Perris)

*Aylax minor* Hartig: Idiomacromerus papaveris

*Aylax oraniensis* Barbotin: Chalcimerus borceai, Idiomacromerus papaveris

*Aylax papaveris* (Perris): Idiomacromerus papaveris, Pseudotorymus papaveris

*Cynips argentea* Hartig see *Adleria quercustozae* (Bosc)

*Cynips guatemalensis* Cameron: Diomorus mayri

*Cynips kollari* Hartig see *Andricus kollari* (Hartig)

*Diastrophus mayri* Reinhard: Glyphomerus tibialis  
*Diplolepis centrifoliae* (Hartig): Glyphomerus stigma  
*Diplolepis eglantheriae* (Hartig): Glyphomerus stigma  
*Diplolepis fructuum* Kieffer: Pseudotorymus rosarum  
*Diplolepis fukudae* (Shinji): Glyphomerus stigma  
*Diplolepis mayri* (Schlechtendal): Glyphomerus stigma  
*Diplolepis polita* (Ashmead): Glyphomerus stigma  
*Diplolepis rosae* (L.): Glyphomerus stigma  
*Diplolepis spinosissime* (Giraud): Glyphomerus signifer  
*Isocolus tavaresi* Nieves: Adontomerus crassipes  
*Neuroterus* sp. (galls): Lissotorymus laevigatus  
*Phanacis centaureae* Forster: Idiomacromerus centaureae  
*Phanacis compactus* D'Iakonchuk: Pseuderimerus luteolus  
*Phanacis cousiniae* D'Iakonchuk: Pseuderimerus luteolus  
*Phanacis hypochoeridis* Kieffer: Thaumatorymus notanisoides  
*Xestophanes potentillae* (Retzius): Glyphomerus stigma  
*Xestophanes szepligetii* Balas: Idiomacromerus papaveris  
galls on *Hypochaeris*: Thaumatorymus notanisoides

#### Diprionidae:

*Diprion abieticolor* Dalla Torre see *Gilpinia abieticola* (Dalla Torre)  
*Diprion nipponica* Rohwer: Monodontomerus japonicus  
*Diprion pini* (L.): Monodontomerus aereus, Monodontomerus strobili,  
Monodontomerus vicicellae  
*Diprion polytomus* Hartig see *Gilpinia polytoma* (Hartig)  
*Diprion similis* (Hartig): Monodontomerus dentipes  
*Gilpinia abieticola* (Dalla Torre): Monodontomerus dentipes  
*Gilpinia frutetorum* (Fabricius): Monodontomerus dentipes  
*Gilpinia hercyniae* (Hartig): Monodontomerus dentipes  
*Gilpinia polytoma* (Hartig): Monodontomerus dentipes, Monodontomerus noyesi  
*Heterarthrus nemoratus* (Fallen): Monodontomerus indiscretus  
*Neodiprion abietis* (Harris): Monodontomerus dentipes  
*Neodiprion excitans* Rohwer: Monodontomerus dentipes  
*Neodiprion lecontei* (Fitch): Monodontomerus dentipes  
*Neodiprion pinetum* (Norton): Monodontomerus dentipes  
*Neodiprion sertifer* (Geoffroy): Monodontomerus laricis, Monodontomerus  
dentipes  
*Neodiprion swainei* Middleton: Monodontomerus dentipes  
*Phyllotoma nemoratus* Fallen see *Heterarthrus nemoratus* (Fallen)

#### Eurytomidae:

*Aiolomorpha rhopaloides* Walker: Diomorpha aiolomorpha  
*Bruchophagus funebris* Howard see *Bruchophagus gibbus* (Boheman)  
*Bruchophagus gibbus* (Boheman): Idiomacromerus insuetus, Idiomacromerus  
longfellowi  
*Bruchophagus kolobovae* Fedoseeva see *Bruchophagus platypterus* (Walker)  
*Bruchophagus platypterus* (Walker): Idiomacromerus perplexus  
*Bruchophagus roddi* (Gussakovsky): Idiomacromerus insuetus, I. lysander, I.  
pannonicus, I. perplexus



- Bruchophagus* sp.: *Idiomacromerus lysander*  
*Eurytoma amygdali* Enderlein: *Adontomerus amygdali*  
*Eurytoma onobrychidis* Nikol'skaya: *Idiomacromerus perplexus*  
*Eurytoma parva* Phillips: *Ditropinotus aureoviridis*  
*Eurytoma seminis* Bugbee: *Idiomacromerus bimaculipennis*  
*Eurytoma* sp.: *Pseudotorymus africanus*  
*Risbecoma capensis* (Walker): *Pseudotorymus leguminosae*  
*Tetramesa aciculata* Schlechtendal: *Eridontomerus isosomatis*  
*Tetramesa albomaculata* (Ashmead): *Eridontomerus isosomatis*, *Pseudotorymus lazulellus*  
*Tetramesa elymicola* (Phillips and Emery): *Ditropinotus aureoviridis*  
*Tetramesa festucae* (Phillips and Emery): *Eridontomerus isosomatis*  
*Tetramesa grandis* (Riley): *Cryptopristus harrisii*, *Ditropinotus aureoviridis*, *Eridontomerus isosomatis*  
*Tetramesa hordei* Harris: *Cryptopristus harrisii*, *Eridontomerus isosomatis*  
*Tetramesa linearis* (Walker): *Ditropinotus aureoviridis*, *Eridontomerus isosomatis*  
*Tetramesa longula* (Dalman): *Eridontomerus isosomatis*  
*Tetramesa maculata* (Howard): *Eridontomerus isosomatis*  
*Tetramesa russoi* Viggiani: *Idiomacromerus regillus*  
*Tetramesa scheppigi* Schlechtendal: *Eridontomerus arrabonicus*  
*Tetramesa secale* (Fitch): *Ditropinotus aureoviridis*, *Eridontomerus isosomatis*  
*Tetramesa* sp. in *Agropyron* stems: *Eridontomerus biroi*  
*Tetramesa* sp. in *Ampelodesmos* stems: *Idiomacromerus regillus*  
*Tetramesa* sp. in *Calamagrostis* stems: *Eridontomerus isosomatis*  
*Tetramesa* sp. in *Cynodon* stems: *Eridontomerus isosomatis*  
*Tetramesa* sp. in *Elymus* stems: *Eridontomerus syrphi*  
*Tetramesa* sp. in *Elytrigia* stems: *Eridontomerus laticornis*  
*Tetramesa* sp. in *Stipa* stems: *Eridontomerus arrabonicus*  
*Tetramesa* sp.: *Idarnotorymus pulcher*, *Idiomacromerus regillus*, *Pseuderimerus flavus*  
? *Tetramesa* sp.: *Erimerus wickhami*, *Eridontomerus bouceki*  
*Tetramesa stipae* Desteffano: *Eridontomerus isosomatis*  
*Tetramesa tritici* (Fitch): *Cryptopristus harrisii*, *Ditropinotus aureoviridis*, *Eridontomerus isosomatis*  
*Tetramesa vaginicola* (Doane): *Cryptopristus harrisii*, *Ditropinotus aureoviridis*, *Eridontomerus isosomatis*  
*Tetramesa websteri* (Howard): *Eridontomerus isosomatis*

### **Ichneumonidae:**

- Agrothereutes adustus* (Gravenhorst): *Monodontomerus vicicellae*  
*Agrothereutes migrator* (Fabricius): *Monodontomerus minor*  
*Casinaria cavigena* Walley: *Perissocentrus striatulus*  
*Coccygomimus* sp.: *Monodontomerus aereus*  
*Coelichneumon garugawensis* Uchida see *Ichneumon garugawensis* (Uchida)  
*Cryptus subquadratus* Thomson: *Monodontomerus minor*  
*Cryptus xylocopae* Rondani: *Monodontomerus vicicellae*  
*Ephialtes bazani* (Blanchard): *Perissocentrus phormio*

- Ephialtes compunctor* (L.): Monodontomerus minor  
*Gambrus canadensis* (Provancher): Monodontomerus viridiscapus  
*Gambrus extrematis* (Cresson): Monodontomerus minor  
*Gelis* sp.: Pradontomerus hyper  
*Hyposoter takagii* (Matsumura): Monodontomerus minor  
*Ichneumon garugawensis* (Uchida): Monodontomerus minor  
 ichneumonid: Monodontomerus laricis  
 ichneumonid "cocoon": Monodontomerus laricis  
 ?ichneumonid larva: *Zdenekia smithi*  
*Iseropus coelebs* (Walsh): Monodontomerus aereus  
*Itopectis conquisitor* (Say): Monodontomerus minor  
*Parapechthis bazani* Blanchard see *Ephialtes bazani* (Blanchard)  
*Phobocampe uncinata* (Gravenhorst): Monodontomerus aereus  
*Phytodietus fumiferanae* Rohwer: Monodontomerus viridiscapus  
*Pimpla* sp. see *Coccygomimus* spp.  
*Pimpla varicornis* (Fabricius) see *Ephialtes compunctor* (L.)  
*Rhythmonotus takagii* Matsumura see *Hyposoter takagii* (Matsumura)  
*Scambus hispae* (Harris): Monodontomerus viridiscapus  
*Spilocryptus extrematis* Cresson see *Gambrus extrematis* (Cresson)  
*Spilocryptus migrator* Fabricius see *Agrothereutes migrator* (Fabricius)  
*Theronia atalantae gestator* (Thunberg): Monodontomerus minor

### Megachilidae:

- Anthidium consimile* Ashmead see *Dianthidium pudicum consimile*  
*Anthidium emarginatum* (Say): Monodontomerus montivagus  
*Anthidium florentinum* Fabricius: Monodontomerus aeneus, Monodontomerus  
 laticornis  
*Anthidium lituratum* Panzer see *Paraanthidiellum lituratum* (Panzer)  
*Anthidium sticticum* Friese see *Rhodanthidium sticticum* (Friese)  
*Ashmediella californica* (Ashmead): Monodontomerus montivagus  
*Chalicodoma muraria* (Fabricius): Monodontomerus aeneus  
*Chalicodoma parietina* (Geoffrey): Monodontomerus aeneus  
*Chalicodoma sicula* (Rossi): Monodontomerus aeneus  
*Chalicodoma* sp.: Monodontomerus obscurus  
*Dianthidium curvatum sayi* Cockerell: Monodontomerus montivagus  
*Dianthidium heterulkei* Schwarz: Monodontomerus clementi  
*Dianthidium pudicum consimile* (Ashmead): Microdontomerus anthidii,  
 Monodontomerus montivagus  
*Dianthidium pudicum pudicum* (Cresson): Monodontomerus montivagus  
*Dianthidium* sp.: Monodontomerus dianthidii  
*Hoplitis adunca* (Panzer): Monodontomerus aeneus, Monodontomerus obscurus  
*Hoplitis anthocopoides* (Schenck): Monodontomerus montivagus  
 "leaf-cutting bee": *Pseudotorymus indicus*  
*Megachile apicalis* Spinola: Monodontomerus aeneus  
*Megachile centuncularis* (L.): Monodontomerus laticornis, Monodontomerus  
 montivagus  
*Megachile peruviana* Smith: Monodontomerus mexicanus  
*Megachile pugnata* Say: Monodontomerus bakeri

- Megachile ramulorum* Rondani: Monodontomerus vicicellae  
*Megachile relativa* Cresson: Monodontomerus bakeri, Monodontomerus montivagus  
*Megachile rotundata* (Fabricius): Monodontomerus aeneus, Monodontomerus clementi, Monodontomerus laticornis, Monodontomerus montivagus, Monodontomerus obscurus  
*Megachile willughbiella* (Kirby): Monodontomerus obscurus  
*Metallinella brevicornis* (Fabricius): Monodontomerus aeneus  
*Osmia adunca* Panzer see *Hoplitis adunca* (Panzer)  
*Osmia coerulescens* (Linnaeus): Monodontomerus aeneus  
*Osmia coloradensis* Cresson: Monodontomerus bakeri  
*Osmia cordata* Robertson: Monodontomerus mandibularis, Monodontomerus montivagus, Monodontomerus obscurus  
*Osmia cornifrons* Radoszkowski: Monodontomerus osmiae  
*Osmia cornuta* (Latreille): Monodontomerus aeneus  
*Osmia emarginata* Lepeletier: Monodontomerus aeneus  
*Osmia excavata* Alfken: Monodontomerus osmiae  
*Osmia fulviventris* (Panzer): Monodontomerus aeneus  
*Osmia kincaidii* Cockerell: Monodontomerus montivagus  
*Osmia latreillei* (Spinola): Monodontomerus aeneus  
*Osmia lignaria* Say: Monodontomerus montivagus, Monodontomerus obscurus  
*Osmia ribifloris* Cockerell: Monodontomerus montivagus  
*Osmia rufa* (L.): Monodontomerus obscurus  
*Osmia rufa cornigera* (Rossi): Monodontomerus aeneus  
*Osmia sanrafaelae* Parker: Monodontomerus montivagus  
*Osmia* sp. (cocoon in *Trypargilum politum* nest): Monodontomerus montivagus  
*Osmia* sp.: Diomorus cupreus  
*Osmia submicans* Morawitz: Monodontomerus aeneus  
*Osmia taurus* Smith: Monodontomerus osmiae  
*Osmia texana* Cresson: Monodontomerus montivagus, Monodontomerus bakeri  
*Osmia tricornis* Latreille: Monodontomerus aeneus  
*Paraanthidiellum lituratum* (Panzer): Adontomerus gregalis, Adontomerus nesterovi  
*Rhodanthidium stricticum* (Friese): Monodontomerus anthidiorum  
*Stelis nasuta* Latreille: Monodontomerus aeneus

**Mutillidae:**

- Photopsis auraria* Blake see *Sphaerophthalma unicolor* (Cresson)  
*Sphaerophthalma unicolor* (Cresson): Monodontomerus montivagus

**Pteromalidae:**

- Catolaccus* sp.: Pseudotorymus africanus

**Sphecidae:**

- Cenomus unicolor* Panzer see *Pemphredon rufiger* Dahlbom  
*Crabro clavipes* L. see *Rhopalum clavipes* (L.)  
*Crabro rubicola* Dufour and Perris see *Ectemnius rubicola* (Dufour and Perris)  
*Crabro stirpicola* Packard see *Ectemnius stirpicola* (Packard)  
*Crabro* sp.: Diomorus cupreus  
 crabronine larva: Zdenekius smithi

- Crossocerus capitosus* (Shuckard): *Diomorus armatus*  
*Crossocerus fergusonii* Pate: *Diomorus zabriskiei*  
*Crossocerus insolens* (W. Fox): *Diomorus zabriskiei*  
*Ectemnius lapidarius* (Panzer): *Diomorus zabriskiei*  
*Ectemnius paucimaculatus* (Packard): *Diomorus zabriskiei*  
*Ectemnius rubicola* (Dufour and Perris) in stems of *Rubus*: *Diomorus calcaratus*,  
*Diomorus cupreus*  
*Ectemnius spiniferus* (W. Fox): *Diomorus zabriskiei*  
*Ectemnius stirpicola* (Packard): *Diomorus zabriskiei*  
*Euphilis arapaho* Pate see *Rhopalum pedicellatum* Packard  
*Euphilis rufigaster* Packard see *Rhopalum rufigaster* (Packard)  
*Oryttus mirandus* (W. Fox): *Monodontomerus montivagus*  
*Passaloeus pusillus* (Saussure) see *Polemistus pusillus* Saussure  
? *Pemphredon rufiger* Dahlbom: *Diomorus calcaratus*  
*Pemphredon* sp.: *Diomorus calcaratus*  
*Polemistus luzonensis* (Rohwer): *Ecdamua* sp.  
*Polemistus pusillus* Saussure: *Monodontomerus mexicanus*  
*Rhopalum clavipes* (L.) cocoons: *Diomorus armatus*  
*Rhopalum pedicellatum* Packard: *Diomorus zabriskiei*  
*Rhopalum rufigaster* (Packard): *Diomorus zabriskiei*  
*Sceliphron caementarium* (Drury): *Monodontomerus montivagus*  
*Sceliphron distillatorium* Illiger: *Monodontomerus obscurus*  
*Solenius rubicola* Dufour and Perris see *Ectemnius rubicola* (Dufour and Perris)  
sphecid larva: *Diomorus orientalis*  
*Stigmus pendulus* Panzer (in *Rubus* stems): *Diomorus calcaratus*  
*Stigmus solskyi* A. Morawitz: *Diomorus calcaratus*  
? *Stigmus* pupa in *Sambucus* twigs: *Diomorus armatus*  
*Trypargilum politum* (Say) see *Trypoxylon politum* Say  
*Trypargilum tridentatum* (Packard) see *Trypoxylon tridentatum* Packard  
*Trypoxylon mexicanum* Saussure: *Monodontomerus mexicanus*  
*Trypoxylon monteverdeae* Coville: *Monodontomerus mexicanus*  
*Trypoxylon politum* Say (nest): *Monodontomerus montivagus*  
*Trypoxylon* sp. near *albitarse* Fabricius: *Monodontomerus montivagus*  
*Trypoxylon* sp. near *palliditarsus* Saussure see *Trypoxylon* sp. near *albitarse*  
Fabricius  
*Trypoxylon tridentatum* Packard: *Monodontomerus montivagus*

**Tenthredinidae:**

- Nematus vallisnerii* Hartig see *Pontania proxima* (Lepeletier)  
*Pontania capreae* L. see *Pontania proxima* (Lepeletier)  
*Pontania proxima* (Lepeletier): *Pseudotorymus salicis*  
*Trichiocampus ulmi* (L.): *Monodontomerus aereus*

**Torymidae:**

- Megastigmus* sp.: *Torymoides piceae*

**Vespididae:**

- Ancistrocerus parietum* (L.): *Monodontomerus aeneus*  
*Ancistrocerus tuberculocephalus* (Saussure): *Monodontomerus montivagus*  
*Eumenes pomiformis* (Fabricius): *Monodontomerus obscurus*, *Monodontomerus aeneus*

- Eumenes* sp.: *Monodontomerus schrottkyi*  
*Euodynerus* sp.: *Monodontomerus montivagus*  
*Microdynerus bakerianus* (Cameron): *Monodontomerus montivagus*  
*Mischocyttarus flavitarsis* (Saussure): *Monodontomerus* sp.  
*Odynerus parietum* (L.) see *Ancistrocerus parietum* (L.)  
*Parancistrocerus vagus* (Saussure): *Monodontomerus dianthidii*  
*Polistes gallicus* L. see *Polistes niminulus* L.  
*Polistes niminulus* L.: *Monodontomerus aeneus*  
*Ropalidia plebeiana* Richards (nest): *Amoturoides breviscapus*  
*Symmorphus canadensis* (Saussure): *Zdenekius smithi*  
*Symmorphus debilis* (Saussure) see *Symmorphus canadensis* (Saussure)

### LEPIDOPTERA

#### Arctiidae:

- Hyphantria cunea* (Drury): *Monodontomerus aereus*, *Monodontomerus minor*  
 chrysalid: *Perissocentrus argentinae*

#### Cecidosidae:

- Cecidoses eremita* Curtis: *Rhynchodontomerus inclusus*  
*Clistoses artifex* Kieffer and Jorgensen see *Cecidoses eremita* Curtis

#### Coleophoridae:

- Coleophora malivorella* Riley: *Microdontomerus anthonomi*

#### Cossidae:

- Indarbela tetraonis* Moore: *Podagrimonella indarbelae*

#### Dioptidae:

- Cyanotricha necyria* Felder: *Perissocentrus striatulus*  
*Phryganidia californica* Packard: *Monodontomerus minor*

#### Gelechiidae:

- Isophrictis similiella* (Chambers): *Zaglyptonotus schwarzi*  
*Oecocercis guyonella* Guenee: *Microdontomerus albipes*  
*Scrobipalpa* sp.: *Pseudotorymus africanus*

#### Geometridae:

- Leuculopsis pulverulenta* Dognin: *Perissocentrus striatulus*

#### Lasiocampidae:

- Dendrolimus pini* L.: *Monodontomerus aereus*  
*Dendrolimus spectabilis* Butler: *Monodontomerus minor*, *Monodontomerus laricis*, *Monodontomerus dentipes*  
*Dendrolimus superans* Butler: *Monodontomerus minor*  
*Eriogaster henckei* Staudinger (cocoons): *Adontomerus eriogasteris*  
*Eutachyptera psidii* (Salle): *Monodontomerus* sp.  
*Leucoma salicis* (L.): *Monodontomerus aereus*  
*Malacosoma americanum* (Fabricius): *Monodontomerus minor*,  
*Monodontomerus aereus*  
*Malacosoma californicum fragile* (Stretch): *Microdontomerus fumipennis*  
*Malacosoma disstria* (Hubner): *Monodontomerus viridiscapus*  
*Malacosoma franconica* Esper: *Monodontomerus aereus*  
*Malacosoma neustria* L.: *Monodontomerus aereus*, *Monodontomerus minor*

**Limacodidae:**

*Leucophobeton argentiflua* (Geyer): *Monodontomerus cubensis*

**Lymantriidae:**

*Dasychira fortunata* Rogenhofer: *Monodontomerus canariensis*

*Euproctis argentiflua* Hubner [sic] see *Leucophobeton argentiflua* (Geyer)  
(Limacodidae)

*Euproctis chrysorrhoea* (L.): *Monodontomerus aereus*, *Monodontomerus minor*

*Euproctis similis* (Fuessly): *Monodontomerus minor*

*Hemerocampa pseudotsugata* McDunnough see *Orgyia pseudotsugata*  
(McDunnough)

*Lymantria concolor* Walker: *Monodontomerus lymantriae*

*Lymantria dispar* (L.): *Monodontomerus minor*, *Monodontomerus aereus*

*Lymantria monacha* (L.): *Monodontomerus aereus*

*Lymantria obfuscata* (L.): *Monodontomerus aereus*

*Lymantria* sp.: *Monodontomerus aereus*, *Monodontomerus lymantriae*

*Orgyia antiqua* (L.): *Monodontomerus minor*, *Monodontomerus vicicellae*,  
*Perissocentrus phormio*

*Orgyia leucostigma* (J.E. Smith): *Monodontomerus aereus*

*Orgyia pseudotsugata* (McDunnough): *Monodontomerus dentipes*,  
*Monodontomerus viridiscapus*

*Porthetria* sp. see *Lymantria* sp.

**Noctuidae:**

*Alabama argillacea* Hubner: *Perissocentrus phormio*

*Ariola pulchra* Butler: *Monodontomerus laricis*

*Chloephora bicolorana* Fuessl see *Chloephora prasinana* (L.)

*Chloephora prasinana* (L.): *Monodontomerus minor*

*Cirphis* sp. see *Leucania* sp.

*Leucania* sp.: *Perissocentrus phormio*

*Melipotis* sp.: *Perissocentrus phormio*

**Papilionidae:**

*Battus polydamas* (L.): *Perissocentrus argentinae*, *Perissocentrus caridei*

**Pieridae:**

*Aporia crataegi* L.: *Monodontomerus aereus*

*Eucheira socialis* Westwood: *Monodontomerus viridiscapus*

*Pieris brassicae* (L.): *Monodontomerus minor*

*Pieris rapae* (L.): *Monodontomerus minor*, *Monodontomerus aereus*

**Psychidae:**

*Acanthopsyche atra* L.: *Monodontomerus vicicellae*

*Cryptothelea formosicola* Strand: *Monodontomerus minor*

*Eumeta japonica* Heylaerts: *Monodontomerus minor*

*Eumeta minuscula* Butler: *Monodontomerus minor*

*Lumacra kunkeli* (Heylaerts): ?*Perissocentrus phormio*

*Megalophanes constancella* (Bruand): *Monodontomerus vicicellae*

*Megalophanes viciella* (Schiffermuller): *Monodontomerus vicicellae*

*Oiketicus geyeri* Berg: *Perissocentrus caridei*

*Oiketicus* ?*geyeri* Berg: *Perissocentrus argentinae*

*Oiketicus platensis* Berg: *Perissocentrus argentinae*, *Perissocentrus caridei*,  
*Perissocentrus phormio*

- Oiketicus* sp.: Perissocentrus phormio  
*Pachythelia villosella* Ochseneheimer: Monodontomerus vicicellae  
*Psyche constancella* Bruand see *Megalophanes constancella* (Bruand)  
*Psyche kunckeli* Heylaerts see *Lumacra kunckeli* (Heylaerts)  
*Psyche viciella* Schiffermuller see *Megalophanes viciella* (Schiffermuller)  
*Thanatopsyche chilensis* (Philippi): Perissocentrus chilensis, Perissocentrus tumidulus  
*Thyridopteryx ephemeraeformis* (Haworth): Monodontomerus minor

**Pyralidae:**

- Hypsipyla robusta* Moore: Diomorus orientalis  
*Pyrausta sanguinalis* L.: Pseudotorymus sanguinalis

**Saturniidae:**

- Agapema galbina anona* (Ottolengui): Microdontomerus fumipennis  
*Cercophana frauenfeldii* Felder: Perissocentrus chilensis  
*Cercophana* sp.: Perissocentrus tumidulus  
*Hemileuca oliviae* Cockerell: Microdontomerus sp.  
*Hyalophora cecropia* (L.): Monodontomerus minor  
*Ormiscodes cinnamomea* (Guerin-Meneville): Perissocentrus chilensis  
*Ormiscodes crinita* Blanchard see *Ormiscodes cinnamomea* (Guerin-Meneville)  
*Ormiscodes* sp.: Perissocentrus phormio  
 saturniid cocoon : Monodontomerus viridiscapus

**Sphingidae:**

- Dilina tiliae* L. see *Mimas tiliae* (L.)  
*Mimas tiliae* (L.): Monodontomerus minor

**Thaumetopoeidae**

- Thaumetopoea processionea* L.: Monodontomerus minor

**Tortricidae:**

- Archips argyrospila* (Walker): Monodontomerus aereus, Monodontomerus minor  
*Ancylis comptana* (Froelich): Microdontomerus anthonomi  
*Choristoneura fumiferana* (Clemens): Monodontomerus minor  
*Choristoneura rosaceana* (Harris): Microdontomerus fumipennis,  
 Monodontomerus aereus  
*Grapholitha molestae* (Busck): Monodontomerus minor  
*Olethreutes sororiana* (Herrich-Schaffer): Microdontomerus annulata  
*Ptycholomoides aeriferana* Herrich-Schaffer: Monodontomerus laricis  
*Rhyacionia buoliana* (Denis and Schiffermuller): Monodontomerus minor,  
 Monodontomerus vicicellae (as hyperparasite)  
*Rhyacionia zozana* (Kearfott): Microdontomerus fumipennis  
*Tortrix viridana* (L.): Monodontomerus aereus  
 "Tortrix" sp.: Monodontomerus laricis

**Yponomeutidae:**

- Yponomeuta evonymella* L.: Monodontomerus minor  
*Yponomeuta malinellus* Zeller: Monodontomerus aereus  
*Yponomeuta rorella* Hubner: Monodontomerus aereus

**Zygaenidae:**

- Zygaena carniolica* Scopoli: Monodontomerus vicicellae  
*Zygaena filipendulae* L.: Monodontomerus vicicellae

- Zygaena occitanica* deVillers: Monodontomerus vicicellae  
*Zygaena onobrychis* Denis and Schiffermuller: Monodontomerus vicicellae  
*Zygaena sarpedon* Hubner: Monodontomerus vicicellae  
*Zygaena transalpina* Esper: Monodontomerus vicicellae

## MANTODEA

## Mantidae:

- Blepharodes sudanensis* Werner see *Phlaebarodes sudanensis* (Werner)  
*Blepharopsis mendica* Fabricius: Podagrionella korsakowi  
*Coptopteryx argentina* (Burmeister): Podagrion macrurum  
*Empusa guttula* (Thunberg): Podagrionella empusae  
*Gonatista reticulata* (Thunberg): Podagrion texanus (nomen nudum)  
*Gonygaster guttula* Thunberg see *Empusa guttula* (Thunberg)  
*Hierodula patellifera* (Serville): Podagrion philippense philippense, Podagrion sinensis  
*Hoplocorypha galeata* (Gerstecker) see *Hoplocorypha saussurii* Giglio-Tos  
*Hoplocorypha saussurii* Giglio-Tos: Podagrion galeata  
*Hoplocorypha* sp.: Podagrion diospiri  
*Iris oratoria* (L.): Podagrionella lichtensteini  
“mantid egg case” (these records apply only to parasite species for which a host genus or species name was not given): Mantiphagum apperti, Palachia mangalae, Podagrion abbreviatum, Podagrion ahlonei, Podagrion batesi, Podagrion beneficium, Podagrion brasiliense, Podagrion coeruleoviride, Podagrion koebelei, Podagrion mantidiphagum, Podagrion mantisiphagum, Podagrion nigriclava, Podagrion ophthalmicum, Podagrion pax, Podagrion risbeci, Podagrionella lamborni  
“*Mantidis brasiliae*” (this name cannot be verified): Podagrion melleum  
*Mantis pustulata* Stoll see *Polyspilota aeruginosa* (Goeze)  
*Mantis religiosa* L.: Podagrion pachymerum, Podagrion splendens gibba  
*Orthodera* sp.: Podagrion metatarsum  
*Paratenodera aridifolia* Stoll see *Tenodera aridifolia* (Stoll)  
*Paratenodera sinensis* Saussure see *Tenodera aridifolia sinensis* (Saussure)  
*Phlaebarodes sudanensis* (Werner): Mantiphaga gongylusae, Podagrionella korsakowi  
*Polyspilota aeruginosa* (Goeze): Micropodagrion pauliani, Palmon polyspilotae, Podagrion fraternum  
*Polyspilota variegata* (Olivier) see *Polyspilota aeruginosa* (Goeze)  
*Pseudocreobotra ocellata* (Palisot de Beauvois): Mantiphaga gongylusae  
*Pseudocreobotra* sp.: Mantiphaga pseudocreobotrae  
*Solygia sulcatifrons* (Serville): Podagrion diospiri  
*Sphodromantis lineola* (Burmeister): Podagrion enei  
*Sphodromantis* sp.: Micropodagrion pauliani, Palmon sphodromantidis sphodromantidis  
*Sphodromantis viridis* Forskal: Podagrion meridionale  
*Stagmomantis carolina* (Johansson): Podagrion mantis, Podagrion oon  
*Stagmomantis limbata* (Hahn): Podagrion crassiclava, Podagrion mantis  
*Tarachodes saussurei* Giglio-Tos: Microdontomerus senegalensis, Podagrionella senegalensis



- Tenodera angustipennis* Saussure: Podagrion mantis, Podagrion nipponicum  
*Tenodera aridifolia aridifolia* (Stoll): Podagrion nipponicum, Podagrion shirakii  
*Tenodera aridifolia sinensis* (Saussure): Podagrion sinensis  
*Tenodera australasiae* (Leach): Podagrion pavo

#### ORTHOPTERA

##### Tettigoniidae:

tettigoniid eggs: Amoturoides pachymerus

#### STREPSIPTERA

##### Mengenillidae:

*Mengenilla quaesita* Silvestri: Idiomacromerus gregarius

#### PLANT HOSTS

##### (animal host unknown)

When a torymid is known *only* from a plant host, it is listed here. In most cases the plants listed below undoubtedly act as the host for some gall-former or seed-feeding insect upon which the parasite is actually feeding. Because there are some strictly phytophagous torymids and some that can feed on both the gall-former and the plant tissue which surrounds it, the following hosts are listed merely as "indications" of potential biological relationship. The information may act as a source of further research and for possible aid in identification of some species for which we have no other biological information. I have not listed here *all* of the plants for those hosts cited above in the main host list. Above we know with some degree of certainty that the torymids are associated with insect hosts. Below we are not certain what the host is. Nomenclature for this list is from Gunn *et al.* (1992).

#### AIZOACEAE

*Mesembryanthemum* (bud gall): Pseudotorymus mesembryanthemumi

#### APIACEAE

*Eryngium campestre* (galls): Pseudotorymus sapphyrinus sapphyrinus

#### ASTERACEAE

*Brachylaena ramiflora*: Pseudotorymus gallephila

*Centaurea aspera* (seed heads): Liodotomerus carayoni

*Centaurea* sp. (galls): Eridontomerus fulviventris, Exopristus trigonomerus  
 "Hazotokana" see *Brachylaena ramiflora*

*Rudbeckia* (gall): Pseudotorymus lazulellus

#### CHENOPODIACEAE

*Salsola laricina*: Torymoides bouceki

#### COMBRETACEAE

*Guiera senegalensis* (galls): Pseudotorymus gallephila

**FABACEAE**

- Acacia arabica* (pods): Pseudotorymus leguminosae  
*Acacia seyal*: Pseudotorymus leguminosae  
*Acacia* sp. (leaf galls): Torymoides acaciae  
*Cajanus indicus* (pods): Pseudotorymus harithavarnus  
*Dalbergia sissoo* (flower bud galls): Pseudotorymus indicus  
*Dalbergia* sp. (leaf gall): Pseudotorymus gallephila  
*Poinciana pulcherima* (larva in stem): Diomorus indicus  
*Vicia cracca* (pods): Pseudotorymus medicaginis  
*Vicia tenuifolia* (root galls): Pseudotorymus medicaginis  
*Vigna sinensis*: Pseudotorymus leguminosae  
wattle (galls): Torymoides atricornis

**LAMIACEAE**

- Stachys sylvatica* (galls): Pseudotorymus stachidis

**MORACEAE**

- Ficus altissima*: Physothorax bidentulus  
*Ficus aurea*: ?Physothorax bidentulus, Physothorax pallidus, Physothorax russelli  
*Ficus citrifolia*: Physothorax bidentulus, Physothorax pallidus  
*Ficus doliaria* see *Ficus gomelleira*  
*Ficus gomelleira*: Physothorax annuliger, Physothorax bicolor, Physothorax disciger, Physothorax serratus  
*Ficus laevigata* see *Ficus citrifolia*  
*Ficus lapathifolia*: Physothorax percaudatus, Physothorax serratus  
*Ficus pedunculata* see *Ficus citrifolia*  
fig fruits: Physothorax annuliger, Physothorax biarticulatus, Physothorax disciger

**MYRTACEAE**

- Eucalyptus haemastoma* (leaf galls): Torymoides aligherini  
*Eucalyptus* sp. (soft galls): Torymoides eucalypti

**ORCHIDACEAE**

- orchids (gall in racines): Idiomacromerus gallicola

**PAPAVERACEAE**

- Papaver* sp.: Exopristus trigonomerus

**PINACEAE**

- Picea glehnii*: Torymoides piceae  
*Picea jezoensis*: Torymoides piceae  
*Picea polita*: Torymoides piceae

**POACEAE**

- Agropyron fragile* (stems): Eridontomerus bouceki

*Carex humilis*: *Idiomacromerus splendidus*

*Elytrigia repens* (stems): *Eridontomerus bouceki*

*Festuca rupicola rupicola*: *Liodontmerus splendidus*, *Idiomacromerus variegatus*

*Hilaria* (galls): *Erimerus wickhami*

*Stipa ioannis* (stems): *Eridontomerus arrabonicus*

*Trachypogon polymorphum* (stem galls): *Idiomacromerus trachypogonis*

### ROSACEAE

*Rosa eglanteriae* (galls): *Pseudotorymus sapphyrinus sapphyrinus*

### RUBIACEAE

*Mantania* sp. (leaf gall): *Pseudotorymus gallephila*

"*Mantalia (terminalis)*" see *Mantania* sp.

### SCROPHULARIACEAE

*Verbascum* (galls): *Exopristus trigonomerus*

### UNVERIFIABLE PLANT HOSTS

"*Caricetum humilis*" see *Carex humilis* (Poaceae)

"*Festucetum sulcatae*" see *Festuca rupicola rupicola* (Poaceae)

## INDEX TO HOSTS

In the following list, any species name without an author is a plant. All host names given in the literature are presented here whether correct or not. When the incorrect name is found in the host list, the reader is then referred to the correct name.

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## APPENDICES

## APPENDIX I: GENERA REMOVED FROM TORYMIDAE

At the beginning of my study the taxa included in this section were treated as Torymidae. During the course of my work most of these were transferred to other families by Bouček (1988) while one (*Austroamotura*) was transferred into Torymidae. I consider all of the taxa mentioned below as non-torymids and explain my reasons for some taxa which remain problematic.

*Austroamotura* Girault

*Austroamotura* Girault 1934/443:3 (unpaged).

Type-species: *Austroamotura punctatiscutum* Girault (monotypic, QM, examined).

Girault (1934/443) placed this genus in Pteromalidae. Bouček (1988) transferred it to Torymidae with the comment that "all ... characters [other than the ovipositor] clearly place it ... in Torymidae, Monodontomerinae." I do not agree with this placement, and return the genus to its original position in the Pteromalidae.

I have seen only the type specimen of the only known species, and the structure of metasomal terga 8 and 9 is typical of Pteromalidae, not Torymidae. It is this structure alone, so far as I have been able to determine, that defines the monophyly of Torymidae. In Torymidae Mt8 and Mt9 are separated from each other, the cercus is situated on a transparent posterolateral edge of Mt8, and in the majority of taxa Mt8 (Figs. 27-28) is partially divided longitudinally. The structure of Mt8 + 9 in *Austroamotura* is unquestionable pteromalid-like in having the two fused with the cercus placed medially upon its surface (as in Fig. 23). Although other characters have a superficial resemblance to torymids, especially the wing venation and the toothed hind femur, these are homoplasious throughout the Chalcidoidea and do not define higher-level taxa.

*Amonodontomerus* Girault

*Amonodontomerus* Girault 1913/175:99.

Type-species: *Amonodontomerus viridis* Girault (monotypic, SAM, examined).

Bouček (1988) transferred this genus to Pteromalidae as a synonym of *Chromeurytoma*. I have seen 5 of the 8 female types housed in the SAM. These are all placed upon 2 cards pinned on the same pin (3 bodies are missing, but wings and glue still on card). I am somewhat perplexed by the placement of *Chromeurytoma* and discussed it in some detail on p. 19. I agree with Bouček (1988) that the type species (at least) of *Amonodontomerus* is a pteromalid. I have no knowledge of other species assigned to either *Chromeurytoma* or *Amonodontomerus*.

*Diplesiostigma* Girault

*Diplesiostigma* Girault 1920/352:40.

Type-species: *Diplesiostigma particolor* Girault (orig. desig., QM, examined).

I examined a single type (?syntype) of this species (body on tag with head and two legs on slide with *Miscogasteromorpha* and *Eupelmiformis*) and agree with Bouček (1988) that it is not a torymid. He places the genus as Tetracampidae and I defer to his judgment. Dahms (1986) discussed the rather confused state of the type material.

***Ditropinotella* Girault**

*Ditropinotella* Girault 1915/243:281.

Type-species: *Ditropinotella compressiventris* Girault (orig. desig. and monotypic, NMV, examined).

I examined the 5 female syntypes on a single point (with parts on 2 slides) and agree with Bouček (1988) that these should be placed as Pteromalidae.

***Proplesiostigma* Girault**

*Proplesiostigma* Girault 1915/243:280.

Type-species: *Proplesiostigma un fasciatum* Girault (orig. desig., QM, examined).

The type material of *P. un fasciatum* poses some problems in interpretation because one must deal with a head, antennae, and leg on a slide, but the headless body is on a point and is missing most of its legs. I demonstrate below that the type slide material represents the valid type material, which is a pteromalid, whereas the body represents a torymid of no validity in the problem. Bouček (1988) credits me with informing him of this problem and in his decision to recognize the species as a synonym of *Gastrancistus* in the Pteromalidae. In his short discussion (1988:476) some words were mixed up, and I take this opportunity to correct them.

The tentative type material exists as a head, antennae, and hind leg on a slide and a body on a point. That the two do not go together is evidenced by the following information. The head is scarcely 0.3 mm in diameter, whereas the width of the pronotum of the body is 0.6 mm. Thus, the head is one-half the width of the pronotum. In most chalcidoids the head is at least as wide as the pronotum, and usually wider. Secondly, the hind leg on the slide has the shortest basitarsus length equal to the width of the tibial apex, whereas the hind leg on the point has the shortest basitarsus length at least 1.5 to 1.75 times the tibial apex. Thus, the two legs would not appear to be from the same specimen. Thirdly, the slide material (head/legs) agrees with the original description of *un fasciatum* in details of the mandibles, color of hind leg, and position of toruli, whereas the pointed material (body) does not agree with the description in respect to overall length, hind femur shape, color of leg, wing vein proportions, ovipositor length, or abdominal color.

My conclusions are that the slide material is different from the pointed material. The slide material is certainly what Girault described in his paper. The pointed material has nothing in common with the original description or the slide and therefore is misassociated. The description (except see note on antenna below) and the slide readily fits the concept of Pireninae of the Pteromalidae because the funicle is 5-segmented without anelli, the toruli are placed near the clypeal margin, and the wing venation has the postmarginal and stigmal veins short compared to the marginal vein (about 1/5 to 1/6 length). The pointed material represents a torymid, most likely *Torymoides*, based upon the hind femur (slightly angulate), size, color and ovipositor length.

The problem of the disagreement between number of antennal segments and the number found on the slide-mounted antennae needs to be discussed, but it does not alter my conclusions above. All torymids have 13-segmented antennae, whereas some pteromalids have 12 or less. When Girault described the species he stated that the antennae were "12-jointed" and he listed scape, pedicel, 2 anelli, and 3-segmented club. This leaves 5 funicular segments. The two antennae on the slide have only 10

segments, thus leaving 2 unaccounted for. In both cases, the antennae are separated by a gap between segments 4 and 5 (i.e., after scape + pedicel + anellus 1 (or flagellomere 1) + anellus 2 (or flagellomere 2). Then there are 3 segments plus the club. A total of 10 segments. I suggest that Girault interpreted the gap between segments as evidence of missing segments. Why he extrapolated only 2 missing segments (instead of 3) is beyond me, but Girault is not above suspicion when it comes to random inconsistencies.

## APPENDIX II: SUMMARY OF PROPOSED NOMENCLATRURAL CHANGES

**New genus:**

*Gummilumpus* Grissell

**New synonymy:****Genera**

*Ameromicrus* now = *Torymoides*  
*Exopristoides* now = *Exopristus*  
*Iridophagoides* now = *Podagrionella*  
*Liodontomerus* now = *Idiomacromerus*  
*Lochitimorpha* now = *Pseuderimerus*  
*Mellitotorymus* now = *Adontomerus*  
*Pachytomoides* now = *Palmon*  
*Pondorymus* now = *Torymoides*  
*Senegalella* now = *Pseudotorymus*  
*Tarachodiphaga* now = *Podagrionella*  
*Thiesia* now = *Pseudotorymus*

**Species**

*Callimome caburus* Walker now = *Torymoides sulcius* (Walker)  
*Megastigmus cecidomyiae* Walker now = *Torymoides sulcius* (Walker)  
*Monodontomerus emarginatus* Gahan now = *Monodontomerus bakeri* Gahan  
*Monodontomerus calcaratus* Kamijo now = *Monodontomerus laricis* Mayr  
*Monodontomerus kashmiricus* Narendran now = *Monodontomerus aereus*  
Walker  
*Monodontomerus saltuosus* Grissell now = *Monodontomerus viridiscapus* Gahan  
*Propachytomoides semialbiclavus* Girault now = *Propachytomoides*  
*fasciatipennis* Girault  
*Thiesia gallephila madagascariensis* Risbec now = *Pseudotorymus gallephila*  
Risbec  
*Torymus japonicus* Ashmead now = *Torymoides gifuensis* Ashmead  
*Torymus ventralis* Howard now = *Torymoides sulcius* (Walker)

**New status:**

*Monodontomerus virens laricis* Mayr now = *Monodontomerus laricis* Mayr

**Changes in Nomina nuda**

*Eridontomeroidella* see *Pseudotorymus*  
*Eridontomeroidella gibboni* Girault see *Pseudotorymus leguminosae* (Risbec)  
*Perissocentroides* see *Zaglyptonotus*  
*Torymus marchali* Ashmead see *Torymus ulmariae* Ruschka

**New combinations:** In the following list where two or more generic names are listed in parentheses, the last generic name is the genus from which the species was transferred, and the other names are genera in which the species have been cited in the literature.

*Adontomerus amygdali* (Bouček) (from *Plastotorymus/Paraholapsis/Microdontomerus*)

- Adontomerus crassipes* (Bouček) (from *Microdontomerus*)  
*Adontomerus gregalis* (Steffan) (from *Mellitotorymus*)  
*Adontomerus impolitus* (Askew and Nieves) (from *Microdontomerus*)  
*Adontomerus robustus* (Bouček) (from *Paraholaspis/Microdontomerus*)  
*Exopristus dentatus* (Bouček) (from *Exopristoides*)  
*Gummilumpus bouceki* (Grissell) (from *Neopalachia*)  
*Idiomacromerus africanus* (Erdös) (from *Liodontomerus*)  
*Idiomacromerus arcus* (Bouček) (from *Liodontomerus*)  
*Idiomacromerus augustini* (Erdös) (from *Liodontomerus*)  
*Idiomacromerus balasi* (Szelenyi) (from *Liodontomerus*)  
*Idiomacromerus budensis* (Erdös) (from *Liodontomerus*)  
*Idiomacromerus carayoni* (Steffan) (from *Liodontomerus*)  
*Idiomacromerus centaureae* (Askew and Nieves) (from *Liodontomerus*)  
*Idiomacromerus curticaudatus* (Szelenyi) (from *Liodontomerus*)  
*Idiomacromerus gallicola* (Risbec) (from *Epicopterus/Liodontomerus*)  
*Idiomacromerus gregarius* (Steffan) (from *Lochites/Liodontomerus*)  
*Idiomacromerus insuetus* (Gahan) (from *Liodontomerus*)  
*Idiomacromerus kaszabi* (Szelenyi) (from *Liodontomerus*)  
*Idiomacromerus lysander* (Szelenyi) (from *Liodontomerus*)  
*Idiomacromerus mayri* (Wachtl) (from *Lochites/Liodontomerus*)  
*Idiomacromerus nitens* (Bouček) (from *Liodontomerus*)  
*Idiomacromerus obscuripennis* (Szelenyi) (from *Liodontomerus*)  
*Idiomacromerus pannonicus* (Ruschka) (from *Lochites/Liodontomerus*)  
*Idiomacromerus papaveris* (Förster) (from *Lochites/Liodontomerus*)  
*Idiomacromerus perplexus* (Gahan) (from *Liodontomerus*)  
*Idiomacromerus regillus* (Steffan) (from *Liotorymus*)  
*Idiomacromerus splendidus* Förster (from *Liodontomerus*)  
*Idiomacromerus terebrator* (Masi) (from *Lochites/Liodontomerus*)  
*Idiomacromerus trachypogonis* (Risbec) (from *Lochistical/Liodontomerus*)  
*Idiomacromerus variegatus* (Szelenyi) (from *Liodontomerus*)  
*Microdontomerus senegalensis* (Risbec) (from *Lioterphus/Antistrophoplex*)  
*Palmon ashmeadi* (Crawford) (from *Podagrion/Pachytomoides*)  
*Palmon bellator* Dalman (from *Podagrion*)  
*Palmon bicinctus* (Girault) (from *Pachytomoides*)  
*Palmon frater* (Girault) (from *Pachytomoides*)  
*Palmon ghesquierei* (Ferrière) (from *Pachytomoides*)  
*Palmon greeni* (Crawford) (from *Podagrion/Pachytomoides*)  
*Palmon insolens* (De Santis) (from *Podagrion/Pachytomoides*)  
*Palmon kivuensis* (Ferrière) (from *Pachytomoides*)  
*Palmon megarhopalus* (Masi) (from *Pachytomoides*)  
*Palmon megistus* (De Santis) (from *Podagrion/Pachytomoides*)  
*Palmon mirus* (Girault) (from *Pachytomoides*)  
*Palmon orchesticus* (Masi) (from *Pachytomoides*)  
*Palmon polyspilota* (Ferrière) (from *Pachytomoides*)  
*Palmon queenslandica* (Girault) (from *Pachytomoides*)  
*Palmon seyrigi* (Ferrière) (from *Pachytomoides*)  
*Palmon sphodromantidis madagascariensis* (Risbec) (from *Podagrion/Pachytomoides*)



- Palmon sphodromantidis sphodromantidis* (Risbec) (from *Podagrion/ Pachytomoides*)  
*Palmon turneri* (Ferrière) (from *Pachytomoides*)  
*Palmon zygas* (Grissell and Goodpasture) (from *Pachytomoides*)  
*Pseuderimerus indicus* (Subba Rao and Bhatia) (from *Liodontomerus*)  
*Pseuderimerus semiaenea* (Szelenyi) (from *Lochitimorpha*)  
*Pseudotorymus acythopeusi* (Risbec) (from *Senegalella/Antistrophoplex/ Microdontomerus*)  
*Pseudotorymus africanus* (Crosby) (from *Hemitorymus/ Antistrophoplex*)  
*Pseudotorymus australis* (Risbec) (from *Senegalella*)  
*Pseudotorymus gallephila* (Risbec) (from *Thiesial/Lochites*)  
*Pseudotorymus leguminosae* (Risbec) (from *Senegalella/Antistrophoplex/ Microdontomerus*)  
*Pseudotorymus mesembryanthemumi* (Cameron) (from *Torymus/ Antistrophoplex/Microdontomerus*)  
*Pseudotorymus metallica* (Risbec) (from *Senegalella*)  
*Pseudotorymus rosarum* (Zerova and Seregina) (from *Adontomerus*)  
*Torymoides akdenizeus* (Doganlar) (from *Ameromicrus*)  
*Torymoides anamalaianus* (Mani and Kaul) (from *Holaspis/ Pseudotorymus*)  
*Torymoides asphondyliarum* (Kieffer and Jorgensen) (from *Lochites/ Liodontomerus*)  
*Torymoides bipunctatus* (Szelenyi) (from *Liodontomerus/ Ameromicrus*)  
*Torymoides bouceki* (Zerova and Seregina) (from *Ameromicrus*)  
*Torymoides confluens* (Bouček) (from *Ameromicrus*)  
*Torymoides eltonicus* (Zerova and Seregina) (from *Ameromicrus*)  
*Torymoides erythromma* (Kieffer and Jorgensen) (from *Lochites/ Liodontomerus*)  
*Torymoides festiva* (Kieffer and Jorgensen) (from *Lochites/ Liodontomerus*)  
*Torymoides gifuensis* (Ashmead) (from *Torymus*)  
*Torymoides hyalipennis* (Szelenyi) (from *Liodontomerus/ Ameromicrus*)  
*Torymoides latus* (Bouček) (from *Pondorymus*)  
*Torymoides maculiventris* (Szelenyi) (from *Liodontomerus/ Ameromicrus*)  
*Torymoides nikolskayae* (Zerova and Seregina) (from *Ameromicrus*)  
*Torymoides piceae* (Kamijo) (from *Ameromicrus*)  
*Torymoides sulcius* (Walker) (from *Callimome/Dimeromicrus*)  
*Torymoides swaedicola* (Kieffer and Jorgensen) (from *Lochites/ Liodontomerus*)  
*Torymoides testacea* (Kieffer and Jorgensen) (from *Lochites/ Liodontomerus*)  
*Torymoides transrugosus* (Szelenyi) (from *Ameromicrus*)  
*Torymoides violaceus* (Nikol'skaya) (from *Ameromicrus*)  
*Torymoides yumurtalikiensis* (Doganlar) (from *Ameromicrus*)

**Lectotypes selected:**

- Antistrophoplex bicoloripes* Crawford (= *Microdontomerus*)  
*Didactyliocerus dispar* Masi (= *Torymoides*)  
*Ditropinotus aureoviridis* Crawford  
*Ditropintous flavicoxus* Gahan (= *Ditropinotus aureoviridis* Crawford)  
*Eridontomerus primus* Crawford (= *Eridontomerus isosomatis* Riley)

- Cryptopristus trigonomerus* Masi (= *Exopristus*)  
*Idiomacromerus longfellowi* Girault  
*Liodontomerus insuetus* Gahan (= *Idiomacromerus*)  
*Liodontomerus perplexus* Gahan (= *Idiomacromerus*)  
*Liodontomerus secundus* Gahan (= *Idiomacromerus longfellowi* Girault)  
*Lochites smithi* Schread (= *Torymoides*)  
*Megastigma cecidomyiae* Ashmead (= *Torymoides sulcius*)  
*Microdontomerus fumipennis* Crawford  
*Monodontomerus schrottkyi* Brethes  
*Paraholaspis cothurnata* Masi (= *Microdontomerus annulata* (Spinola))  
*Podagrion echthrus* Crawford  
*Podagrion macrurum* Schrottky  
*Senegalella acythopeusi* Risbec (= *Pseudotorymus*)  
*Stictonotus isosomatis* Riley (= *Eridontomerus*)  
*Torymus anthidii* Ashmead (= *Microdontomerus*)  
*Torymus anthonomi* Crawford (= *Microdontomerus*)  
*Torymus gifuensis* Ashmead (= *Torymoides*)  
*Torymus wickhami* Ashmead (= *Erimerus*)  
*Websterellus tritici* Ashmead (= *Cryptopristus harrisii* Fitch)  
*Zaglyptonotus schwarzi* Crawford

**APPENDIX III: CHARACTER MATRIX FOR WORKING HYPOTHESIS**

(Fig. 37, and discussion p. 31-54)

This data matrix was used to produce the cladogram in Fig. 37. This was the first finalized working matrix and is based upon stabilized transformation series and agreement between Wagner and Successive Weighter trees for 44 PHYSIS analyses (see p. 29 for discussion). This is the data from which nomenclatural decisions were derived in conjunction with the cladogram. Although anelli character states and the taxon *Torymus* were read into most of the analyses, they were not used to produce the final working tree (see p. 36 for discussion). The character statements below follow the format used by PHYSIS and are reproduced exactly as entered for analyses, except that the names of characters have been spelled out [in brackets]. The data matrix below is the output of the analysis. Taxa are arranged in more or less random (i.e., non-phylogenetic) order.

OCCIPCAR [OCCIPITAL CARINA]: NO-WEAK,YES-SIDE,ABOVE.

ANELLI: 2-[1-4],3,5.

ANTCLUB [ANTENNAL CLUB]: 3SEG-3SEG\*,1SEG.

GENA/EYE [MALE EYE]: NORM-REDUCED.

DORHEAD [DORSAL SHAPE OF HEAD]: TRANS-SQUARE\*,SQUARE.

CLYAPEX [CLYPEAL APEX]: BILOBED-STRAIGHT-[CONVEX-RECESSED,  
EMARG], TOOTHED, ENLARGED,CONCAVE.

MALKEEL [MALAR KEEL]: NO-YES.

WINGVEIN [WING VENATION]: PTERO-MEGA,MONO-TORY.

HINDFEM [HINDFEMUR]: SIMPLE-SERRATE,ANGLE-TOOTH-[LOBED-  
2ROWS-2ROWS\*], [BIGTEETH-TOOTHOUT-SWOLLEN-NEO-2TEETH].

HINDTIB [HINDTIBIA]: STRAIGHT-CURVED,CURVED\*.

SPURLENG [HINDTIBIAL SPUR LENGTH]: NORM-LONG,THICK.

SPURINS [HINDTIBIAL SPUR INSERTION]: APEX-PREAPEX.

SPURNO [HINDTIBIAL SPUR NUMBER]: TWO-ONE.

FRENLINE [FRENAL LINE]: YES-NO.

NOTAULI: YES-FAINT.

PROPOD [PROPODEUM]: ONE-NOCARIN-MODIFIED,ZOPHO,MULTI,TWO,  
CHALCI,PROPAL.

CX3SETA [HINDCOXAL SETAE]: YES-NO,YES\*.

TIB3APEX [HINDTIBIAL APEX]: TRUN-DIAGONAL,[SUBPOINT-POINTED].

SCUT/AX [RELATIONSHIP OF NOTAULI TO SCUTOSCUTELLAR SUTURE]:  
NO-MEET.METASTER [METASTERNUM]: CRYPTO-,MONO,[NEOPAL-PALACHIA],  
[CHALCI-PODAG, MICROPOD].TERGMAR3 [METASOMAL TERGAL EMARGINATIONS, THIRD INTERPRE-  
TATION]: 0-1,[2-2A],[3-3A],4 PALACH.

META [METAPLEURAL MARGIN]: STRAIGHT-SINUATE.

CERCUS [EXSERTED CERCI METASOMAL TERGUM 8]: NO-YES.

MT9 [ARTICULATED METASOMAL TERGUM 9 (EPIPYGIUM)]: NO-YES.

The following list of alphabetical abbreviations gives the complete generic names for taxa which are abbreviated by convention in the data matrix which follows:

ADONTO = <i>Adontomerus</i>	PONDO = <i>Pondorymus</i>
ALOOMBA = <i>Aloomba</i>	PRADONT = <i>Pradontomerus</i>
AMOTUR = <i>Amoturoides</i>	PROPACHY = <i>Propachytomoides</i>
ANNECK = <i>Anneckeida</i>	PROPAL = <i>Propalachia</i>
CHALCI = <i>Chalcimerus</i>	PSEUDO = <i>Pseudotorymus</i>
CHRYSO = <i>Chrysochalcissa</i>	PSEUDER = <i>Pseuderimerus</i>
CRYPTO = <i>Cryptopristus</i>	PTEROMAL = <i>Pteromalus</i>
DIMERO = <i>Dimeromicrus</i>	RHYNCHOD = <i>Rhynchodontomerus</i>
DITROP = <i>Ditropinotus</i>	RHYNCHOT = <i>Rhynchotocida</i>
ERID/A = ? <i>Eridontomerus</i> sp.	SENEGAL = <i>Senegalella</i>
ERIDONT = <i>Eridontomerus</i>	STENO = <i>Stenotorymus</i>
ERIM/A = ? <i>Erimerus</i> sp.	TARACHOD = <i>Tarachodiphaga</i>
ERIMERUS = <i>Erimerus</i>	TORYMUS = <i>Torymus</i>
EXOIDES = <i>Exopristoides</i>	TORYMOID = <i>Torymoides</i>
EXOPRIS = <i>Exopristus</i>	ZAGLYPTO = <i>Zaglyptonotus</i>
GENUSA = ?New genus	ZDENEK = <i>Zdenekius</i>
GLYPHOM = <i>Glyphomerus</i>	ZOPHO = <i>Zophodetus</i>
HEMADAS = <i>Hemadas</i>	
IDARNO = <i>Idarnotorymus</i>	
IDIOMAC = <i>Idiomacromerus</i>	
IRIDO = <i>Iridophaga</i>	
JANSON = <i>Jansoniella</i>	
LAMPROT = <i>Lamprotatus</i>	
LIO/INDI = <i>Liodontomerus indicus</i>	
LIODONT = <i>Liodontomerus</i>	
LIOTO = <i>Liotorymus</i>	
LOCHIMER = <i>Lochimerus</i>	
LOCHITES = <i>Lochites papaveris</i>	
LOCHITI = <i>Lochitimorpha</i>	
MANTI = <i>Mantiphaga</i>	
MEGASTIG = <i>Megastigmus</i>	
MELLITO = <i>Mellitotorymus</i>	
MICRO = <i>Microdontomerus</i>	
MICROA = <i>Microdontomerus crassipes</i>	
MICRO/SP = ? <i>Microdontomerus</i> sp.	
MICROPOD = <i>Micropodagrion</i>	
MONODONT = <i>Monodontomerus</i>	
NEOPAL = <i>Neopalachia</i>	
OOPRIS = <i>Oopristus</i>	
PACHYTOM = <i>Pachytomoides</i>	
PALACHIA = <i>Palachia</i>	
PARAHOL = <i>Paraholaspis</i>	
PERISSO = <i>Perissocentrus</i>	
PLATY/A = ? <i>Platykula</i> sp.	
PLATYKUL = <i>Platykula</i>	
PODAGRI = <i>Podagrion</i>	
PODELLA = <i>Podagrionella</i>	

	MONODONT 1	IDIOMAC 2	PLATYKUL 3	ZAGLYPTO 4	GLYPHOM 5
OCCIPCAR	YES	YES	YES	YES	YES
ANELLI	1	2	2	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	TORY	MONO	PTERO
HINDFEM	TOOTH	SIMPLE	SIMPLE	?	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	LONG	LONG	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	YES	NO	NO	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	MODIFIED	NOCARIN	ONE	ONE	NOCARIN
CX3SETA	YES	YES	NO	YES	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	MONO	CRYPTO	CRYPTO	MONO	CRYPTO
TERGMAR3	0	0	2	1	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES
	ERIDONT 6	PSEUDO 7	CRYPTO 8	DITROP 9	MICRO 10
OCCIPCAR	WEAK	YES	YES	NO	NO
ANELLI	3	1	1	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	TORY	PTERO	MONO	MONO
HINDFEM	SERRATE	TOOTH	TOOTH	SERRATE	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	NO	NO	NO	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	TWO	NOCARIN	NOCARIN	TWO	NOCARIN
CX3SETA	YES	YES	YES	YES*	NO
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	CRYPTO	CRYPTO	CRYPTO	CRYPTO
TERGMAR3	2	4	2A	2	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES

	MICROA 11	LIODONT 12	LOCHITES 13	ERIMERUS 14	PSEUDER 15
OCCIPCAR	YES	NO	YES	NO	NO
ANELLI	1	2	2	1	4
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	REDUCED	REDUCED
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	MONO	MONO	MONO
HINDFEM	SWOLLEN	SIMPLE	SIMPLE	SIMPLE	SIMPLE
HINDTIB	CURVED*	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	ONE	ONE
FRENLINE	NO	NO	NO	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	NOCARIN	NOCARIN	NOCARIN	NOCARIN	NOCARIN
CX3SETA	YES*	YES	YES	YES	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	CRYPTO	CRYPTO	CRYPTO	CRYPTO
TERGMAR3	1	2	2	0	1
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES

	PERISSO 16	RHYNCHOD 17	IDARNO 18	LOCHIMER 19	MELLITO 20
OCCIPCAR	YES	SIDE	NO	NO	ABOVE
ANELLI	1	1	2	5	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	?	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	ENLARGED	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	MONO	MONO	MONO
HINDFEM	TOOTH	TOOTH	SERRATE	SIMPLE	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	LONG	NORM	NORM	NORM	NORM
SPURINS	PREAPEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	YES	YES	NO	NO	NO
NOTAULI	YES	YES	FAINT	YES	YES
PROPOD	MODIFIED	MODIFIED	NOCARIN	NOCARIN	NOCARIN
CX3SETA	YES	NO	YES	YES*	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	MONO	CRYPTO	CRYPTO	?	CRYPTO
TERGMAR3	0	0	2A	2	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES

	ALOOMBA 21	AMOTUR 22	ANNECK 23	STENO 24	SENEGAL 25
OCCIPCAR	YES	YES	YES	NO	YES
ANELLI	3	1	?	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	?	NORM	NORM	?	NORM
DORHEAD	TRANS	TRANS	TRANS	SQUARE	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	CONVEX	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	YES	NO	NO
WINGVEIN	MONO	MONO	MONO	MONO	TORY
HINDFEM	ANGLE	TOOTH	2ROWS	TOOTH	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	CURVED	STRAIGHT	STRAIGHT
SPURLENG	LONG	NORM	NORM	NORM	NORM
SPURINS	PREAPEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	NO	NO	YES	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	MODIFIED	MODIFIED	MODIFIED	NOCARIN	NOCARIN
CX3SETA	NO	YES	YES	NO	NO
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	?	MONO	MONO	?	CRYPTO
TERGMAR3	1	0	0	0	4
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES

	PRADONT 26	LOCHITI 27	DIMERO 28	GENUSA 29	TORYMOID 30
OCCIPCAR	YES	NO	YES	YES	YES
ANELLI	1	2	2	5	2
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	?	NORM	NORM	?
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	TORY	TORY	TORY
HINDFEM	LOBED	SIMPLE	SIMPLE	SIMPLE	ANGLE
HINDTIB	CURVED	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	YES	NO	NO	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	MODIFIED	NOCARIN	NOCARIN	NOCARIN	NOCARIN
CX3SETA	YES	YES	NO	NO	NO
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	MONO	?	CRYPTO	CRYPTO	CRYPTO
TERGMAR3	0	0	4	2	4
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES

	EXOIDES 31	RHYNCHOT 32	PONDO 33	EXOPRIS 34	ADONTO 35
OCCIPCAR	YES	YES	YES	YES	ABOVE
ANELLI	1	1	3	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	CONVEX	CONVEX	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	YES	NO	NO	NO
WINGVEIN	PTERO	MONO	MONO	PTERO	MONO
HINDFEM	TOOTHOUT	2ROWS*	SIMPLE	TOOTHOUT	SIMPLE
HINDTIB	CURVED*	CURVED	STRAIGHT	CURVED*	STRAIGHT
SPURLENG	NORM	THICK	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	YES	?	NO	NO	NO
NOTAULI	YES	YES	FAINT	YES	FAINT
PROPOD	NOCARIN	MODIFIED	NOCARIN	NOCARIN	NOCARIN
CX3SETA	YES	YES	NO	YES	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	?	NO	NO	NO	NO
METASTER	?	MONO	?	CRYPTO	?
TERGMAR3	0	0	?	2	2
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES
	PARAHOL 36	LIOTO 37	PODAGRI 38	IRIDO 39	MANTI 40
OCCIPCAR	NO	YES	YES	YES	YES
ANELLI	1	2	1	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	TORY	TORY	TORY
HINDFEM	SIMPLE	SIMPLE	BIGTEETH	BIGTEETH	BIGTEETH
HINDTIB	STRAIGHT	STRAIGHT	CURVED	CURVED	CURVED
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	ONE	ONE	ONE
FRENLINE	NO	NO	?	NO	NO
NOTAULI	YES	YES	FAINT	YES	YES
PROPOD	NOCARIN	NOCARIN	MULTI	MULTI	MULTI
CX3SETA	NO	YES	YES	NO	YES
TIB3APEX	TRUN	TRUN	SUBPOINT	POINTED	SUBPOINT
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	?	PODAG	PODAG	PODAG
TERGMAR3	4	?	3A	3	3
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES



	MICROPOD 41	PACHYTOM 42	TARACHOD 43	PROPACHY 44	CHALCI 45
OCCIPCAR	YES	YES	SIDE	YES	YES
ANELLI	1	1	1	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	?	NORM	NORM
DORHEAD	TRANS	SQUARE*	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	TORY	TORY	TORY	TORY	PTERO
HINDFEM	BIGTEETH	BIGTEETH	BIGTEETH	BIGTEETH	BIGTEETH
HINDTIB	CURVED	CURVED	CURVED	CURVED	CURVED
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	ONE	ONE	ONE	ONE	ONE
FRENLINE	NO	NO	YES	YES	YES
NOTAULI	FAINT	FAINT	YES	YES	YES
PROPOD	MULTI	MULTI	MULTI	MULTI	CHALCI
CX3SETA	YES	YES	YES*	NO	YES
TIB3APEX	SUBPOINT	SUBPOINT	POINTED	SUBPOINT	SUBPOINT
SCUT/AX	NO	NO	NO	NO	NO
METASTER	MICROPOD	PODAG	PODAG	PODAG	CHALCI
TERGMAR3	3	3A	3	3	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES
	OOPRIS 46	CHRYSO 47	NEOPAL 48	PROPAL 49	PALACHIA 50
OCCIPCAR	NO	YES	YES	YES	YES
ANELLI	1	2	1	1	1
ANTCLUB	3SEG	3SEG	3SEG*	1SEG	1SEG
GENA/EYE	NORM	NORM	?	NORM	NORM
DORHEAD	TRANS	TRANS	SQUARE*	SQUARE*	SQUARE*
CLYAPEX	RECESSED	EMARG	STRAIGHT	STRAIGHT	TOOTHED
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	MONO	MONO	TORY
HINDFEM	2ROWS	2ROWS	NEO	2TEETH	2TEETH
HINDTIB	CURVED	CURVED	CURVED	CURVED*	CURVED*
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	NO	NO	NO	NO	?
NOTAULI	YES	FAINT	FAINT	FAINT	YES
PROPOD	NOCARIN	NOCARIN	PROPAL	PROPAL	?
CX3SETA	NO	NO	NO	NO	NO
TIB3APEX	TRUN	SUBPOINT	DIAGONAL	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	MEET
METASTER	MONO	?	NEOPAL	NEOPAL	PALACHIA
TERGMAR3	0	0	?	0	PALACH
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES	YES
MT9	YES	YES	YES	YES	YES

	HEMADAS 51	LAMPROT 52	JANSON 53	ZOPHO 54	PODELLA 55
OCCIPCAR	YES	NO	NO	YES	NO
ANELLI	2	2	2	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	1SEG
GENA/EYE	NORM	NORM	NORM	?	?
DORHEAD	TRANS	TRANS	TRANS	TRANS	?
CLYAPEX	STRAIGHT	BILOBED	STRAIGHT	CONCAVE	?
MALKEEL	NO	NO	NO	NO	?
WINGVEIN	PTERO	PTERO	PTERO	MONO	TORY
HINDFEM	SIMPLE	SIMPLE	SIMPLE	SIMPLE	BIGTEETH
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	CURVED
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	?
FRENLINE	NO	YES	YES	?	YES
NOTAULI	FAINT	YES	YES	YES	YES
PROPOD	ONE	ONE	ONE	ZOPHO	MULTI
CX3SETA	NO	YES	YES	NO	NO
TIB3APEX	TRUN	TRUN	TRUN	TRUN	POINTED
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	CRYPTO	CRYPTO	?	PODAG
TERGMAR3	0	0	0	4	?
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	NO	NO	NO	YES	YES
MT9	NO	NO	NO	YES	YES

	PTEROMAL 56	MEGASTIG 57	TORYMUS 58	ERID/A 59	PLATY/A 60
OCCIPCAR	?	YES	YES	WEAK	YES
ANELLI	?	1	?	3	2
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	?	?	?	TRANS	TRANS
CLYAPEX	?	BILOBED	?	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	PTERO	MEGA	TORY	MONO	TORY
HINDFEM	SIMPLE	SIMPLE	?	SIMPLE	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM	NORM	LONG
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	?	TWO	TWO	TWO	TWO
FRENLINE	?	?	?	NO	NO
NOTAULI	?	YES	?	YES	YES
PROPOD	?	NOCARIN	?	NOCARIN	NOCARIN
CX3SETA	?	?	?	YES	NO
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	?	?	NO	NO	NO
METASTER	?	?	CRYPTO	CRYPTO	CRYPTO
TERGMAR3	?	?	?	1	2
META	STRAIGHT	STRAIGHT	SINUATE	STRAIGHT	STRAIGHT
CERCUS	NO	YES	YES	YES	YES
MT9	NO	YES	YES	YES	YES

	LIO/INDI 61	ERIM/A 62	MICRO/SP 63	ZDENEK 64
OCCIPCAR	NO	NO	NO	YES
ANELLI	5	1	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG
GENA/EYE	REDUCED	REDUCED	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO
WINGVEIN	MONO	MONO	MONO	MONO
HINDFEM	SIMPLE	SIMPLE	SIMPLE	TOOTH
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX
SPURNO	ONE	ONE	TWO	TWO
FRENLINE	NO	NO	NO	YES
NOTAULI	YES	YES	YES	YES
PROPOD	NOCARIN	NOCARIN	NOCARIN	MODIFIED
CX3SETA	YES*	YES	YES*	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO
METASTER	CRYPTO	CRYPTO	CRYPTO	CRYPTO
TERGMAR3	2	1	2	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
CERCUS	YES	YES	YES	YES
MT9	YES	YES	YES	YES

**Appendix IV: Character Matrix for Ending Hypothesis**

(Fig. 38, and discussion p. 31-54)

This data matrix was used to produce the cladogram in Fig.38. This was the final working matrix from which the ending PHYSYS analyses were made. These analyses did not include *Ophiopinotus* which was omitted for reasons stated on page 97. *Torymini* was not included in the calculation of the ending hypothesis but was placed as discussed on p. 99.

CCPCAR [OCCIPITAL CARINA]: 1-NO,2,4,3A,3  
 ANELLI: 2-1,2\*,4  
 ANTCLUB [ANTENNAL CLUB]: 3SEG-3SEG\*,1SEG  
 GENA/EYE [MALE EYE]: NORM-REDUCED  
 DORHEAD [DORSAL SHAPE OF HEAD]: TRANS-SQUARE\*,SQUARE  
 CLYAPEX [CLYPEAL APEX]: BILOBED-STRAIGHT-[CONVEX-RECESSED,  
 EMARG],TOOTHED, ENLARGED,CONCAVE  
 MALKEEL [MALAR KEEL]: NO-YES  
 WINGVEIN [WING VENATION]: MEGA-PTERO-[MONO-THAUMAT]-TORY-  
 NEOPAL  
 HINDFEM [HINDFEMUR]: SIMPLE-SERRATE,TOOTH-  
 LOBED,TOOTHOUT,[2ROWS-2ROWS\*], [BIGTEETH-2TEETH-NEO]  
 HINDTIB [HINDTIBIA]: STRAIGHT-CURVED,CURVED\*  
 SPURLENG [HINDTIBIAL SPUR LENGTH]: NORM-LONG,SPINE,THICK,  
 WIDE  
 SPURINS [HINDTIBIAL SPUR INSERTION]: APEX-PREAPEX  
 SPURNO [HINDTIBIAL SPUR NUMBER]: ONE-TWO  
 FRENLINE [FRENAL LINE]: YES-NO  
 NOTAULI: YES-FAINT  
 PROPOD [PROPODEUM]: NOCARIN-ONE\*,STENO,MODIFIED,ZOPHO,  
 MULTI,TWO,CHALCI,PROPAL,PALACH,TORY  
 CX3SETA [HINDCOXAL SETAE]: YES-NO,YES\*  
 TIB3APEX [HINDTIBIAL APEX]: TRUN-DIAGONAL,[SUBPOINT-POINTED]  
 SCUT/AX [RELATIONSHIP NOTAULI TO SCUTOScutellar SUTURE]:  
 NO-MEET  
 METASTER [METASTERNUM]: CRYPTO-MONO,[NEOPAL-PALACHIA],  
 [CHALCI-PODAG-MICROPOD]  
 TERGMAR3 [METASOMAL TERGAL EMARGINATIONS]: 0-[1/2-2A,1/4,4],3A,  
 PALACH  
 META [METAPLEURAL MARGIN]: STRAIGHT-INTERMED,SINUATE  
 CERCUS [EXSERTED CERCI METASOMAL TERGUM 8]: NO-YES  
 MT9 [ARTICULATED METASOMAL TERGUM 9 (EPIPYGIUM)]: NO-YES

Complete generic names for the taxa abbreviated below were given under Appendix III (page 325), but the following are new for this section:

GUMMI = *Gummilumpus*  
 THAUMAT = *Thaumatorymus*  
 TORYDEL = *Torymoidellus*

	MONODONT 1	PLATYKUL 2	ZAGLYPTO 3	GLYPHOM 4	ERIDONT 5
OCCIPCAR	4	1	1	1	NO
ANELLI	1	2	1	1	2*
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	TORY	?	PTERO	MONO
HINDFEM	TOOTH	SIMPLE	SIMPLE	SIMPLE	SERRATE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	SPINE	LONG	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	YES	NO	NO	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	MODIFIED	ONE*	ONE*	NOCARIN	TWO
CX3SETA	YES	NO	YES	YES	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	MONO	CRYPTO	?	CRYPTO	CRYPTO
TERGMAR3	0	1/2	1/2	0	1/2
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	PSEUDO 6	CRYPTO 7	DITROP 8	MICRO 9	IDIOMAC 10
OCCIPCAR	1	1	NO	NO	NO
ANELLI	1	1	1	1	2*
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	TORY	PTERO	MONO	MONO	MONO
HINDFEM	SIMPLE	TOOTH	SERRATE	SIMPLE	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	NO	NO	NO	NO	NO
NOTAULI	YES	YES	YES	YES	YES
PROPOD	NOCARIN	NOCARIN	TWO	ONE*	NOCARIN
CX3SETA	YES	YES	YES*	YES*	YES*
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	CRYPTO	CRYPTO	CRYPTO	CRYPTO
TERGMAR3	4	2A	1/2	1/4	1/2
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	ERIMERUS 11	PSEUDER 12	PERISSO 13	RHYNCHOD 14	IDARNO 15
OCCIPCAR	NO	NO	4	4	NO
ANELLI	1	4	1	1	2
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	REDUCED	REDUCED	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	ENLARGED	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	MONO	MONO	MONO	MONO
HINDFEM	SIMPLE	SIMPLE	TOOTH	TOOTH	SERRATE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	LONG	NORM	NORM
SPURINS	APEX	APEX	PREAPEX	APEX	APEX
SPURNO	ONE	ONE	TWO	TWO	TWO
FRENLINE	NO	NO	YES	YES	NO
NOTAULI	YES	YES	YES	YES	FAINT
PROPOD	NOCARIN	NOCARIN	MODIFIED	?	NOCARIN
CX3SETA	YES	YES*	YES	NO	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	CRYPTO	MONO	CRYPTO	CRYPTO
TERGMAR3	1/2	1/2	0	0	2A
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	ALOOMBA 16	AMOTUR 17	ANNECK 18	STENO 19	PRADONT 20
OCCIPCAR	1	4	4	NO	4
ANELLI	2	1	?	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG
GENA/EYE	?	NORM	NORM	?	NORM
DORHEAD	TRANS	TRANS	TRANS	SQUARE	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	CONVEX	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	YES	NO	NO
WINGVEIN	TORY	MONO	MONO	MONO	MONO
HINDFEM	SIMPLE	TOOTH	2ROWS	TOOTH	LOBED
HINDTIB	STRAIGHT	STRAIGHT	CURVED	STRAIGHT	CURVED
SPURLENG	LONG	NORM	NORM	NORM	NORM
SPURINS	PREAPEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	NO	NO	YES	NO	YES
NOTAULI	YES	YES	YES	YES	YES
PROPOD	MODIFIED	MODIFIED	MODIFIED	STENO	MODIFIED
CX3SETA	NO	YES	YES	NO	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	NO
METASTER	?	MONO	MONO	?	MONO
TERGMAR3	1/2	0	0	0	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	TORYMOID 21	RHYNCHOT 22	EXOPRIS 23	ADONTO 24	PODAGRI 25
OCCIPCAR	1	4	1	NO	3
ANELLI	2*	1	1	1	1
ANTCLUB	3SEG	3SEG	3SEG	3SEG	3SEG*
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	CONVEX	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	YES	NO	NO	NO
WINGVEIN	TORY	MONO	PTERO	MONO	TORY
HINDFEM	SIMPLE	2ROWS*	TOOTHOUT	SIMPLE	BIGTEETH
HINDTIB	STRAIGHT	CURVED	CURVED*	STRAIGHT	CURVED
SPURLENG	NORM	THICK	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	ONE
FRENLINE	NO	?	NO	NO	?
NOTAULI	YES	YES	YES	YES	FAINT
PROPOD	NOCARIN	MODIFIED	NOCARIN	NOCARIN	MULTI
CX3SETA	NO	YES	YES	YES	YES
TIB3APEX	TRUN	TRUN	TRUN	TRUN	SUBPOINT
SCUT/AX	NO	NO	NO	NO	NO
METASTER	CRYPTO	MONO	CRYPTO	?	PODAG
TERGMAR3	4	0	1/2	1/2	3A
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	MANTI 26	MICROPOD 27	PACHYTOM 28	PROPACHY 29	CHALCI 30
OCCIPCAR	3	3	3	3	1
ANELLI	1	1	1	1	1
ANTCLUB	3SEG	3SEG*	3SEG*	3SEG*	3SEG
GENA/EYE	NORM	NORM	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	SQUARE*	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	TORY	TORY	TORY	TORY	PTERO
HINDFEM	BIGTEETH	BIGTEETH	BIGTEETH	BIGTEETH	BIGTEETH
HINDTIB	CURVED	CURVED	CURVED	CURVED	CURVED
SPURLENG	NORM	NORM	NORM	NORM	WIDE
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	ONE	ONE	ONE	ONE	ONE
FRENLINE	NO	NO	NO	YES	YES
NOTAULI	YES	FAINT	FAINT	YES	YES
PROPOD	MULTI	MULTI	MULTI	MULTI	CHALCI
CX3SETA	YES	YES	YES	NO	YES
TIB3APEX	SUBPOINT	SUBPOINT	SUBPOINT	SUBPOINT	SUBPOINT
SCUT/AX	NO	NO	NO	NO	NO
METASTER	PODAG	MICROPOD	PODAG	PODAG	CHALCI
TERGMAR3	3A	3A	3A	3A	0
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	OOPRIS 31	CHRYSO 32	NEOPAL 33	PROPAL 34	PALACHIA 35
OCCIPCAR	NO	4	3A	3A	3A
ANELLI	1	2	1	1	1
ANTCLUB	3SEG	3SEG	3SEG*	1SEG	1SEG
GENA/EYE	NORM	NORM	?	NORM	NORM
DORHEAD	TRANS	TRANS	SQUARE*	SQUARE*	SQUARE*
CLYAPEX	RECESSED	EMARG	STRAIGHT	STRAIGHT	TOOTHED
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	TORY	NEOPAL	NEOPAL	TORY
HINDFEM	2ROWS	2ROWS	NEO	2TEETH	2TEETH
HINDTIB	CURVED	CURVED	CURVED	CURVED*	CURVED*
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO	TWO	TWO
FRENLINE	NO	NO	NO	NO	?
NOTAULI	YES	FAINT	FAINT	FAINT	YES
PROPOD	?	NOCARIN	PROPAL	PROPAL	PALACH
CX3SETA	NO	NO	NO	NO	NO
TIB3APEX	TRUN	SUBPOINT	DIAGONAL	TRUN	TRUN
SCUT/AX	NO	NO	NO	NO	MEET
METASTER	MONO	?	NEOPAL	NEOPAL	PALACHIA
TERGMAR3	1/2	0	1/2	0	PALACH
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT

	ZOPHO 36	PODELLA 37	MEGASTIG 38	ZDENEK 39	GUMMI 40
OCCIPCAR	?	3	1	4	?
ANELLI	1	1	1	1	1
ANTCLUB	3SEG	3SEG*	3SEG	3SEG	3SEG
GENA/EYE	?	NORM	NORM	NORM	?
DORHEAD	TRANS	TRANS	SQUARE*	TRANS	SQUARE*
CLYAPEX	CONCAVE	STRAIGHT	BILOBED	STRAIGHT	?
MALKEEL	NO	NO	NO	NO	NO
WINGVEIN	MONO	TORY	MEGA	MONO	?
HINDFEM	SIMPLE	BIGTEETH	SIMPLE	TOOTH	2TEETH
HINDTIB	STRAIGHT	CURVED	STRAIGHT	STRAIGHT	CURVED*
SPURLENG	NORM	NORM	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX	APEX	APEX
SPURNO	TWO	ONE	TWO	TWO	TWO
FRENLINE	?	YES	?	YES	YES
NOTAULI	YES	YES	YES	YES	YES
PROPOD	ZOPHO	MULTI	NOCARIN	MODIFIED	?
CX3SETA	?	YES*	YES	YES	NO
TIB3APEX	TRUN	POINTED	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	?	NO	NO
METASTER	?	PODAG	?	CRYPTO	?
TERGMAR3	4	3A	1/2	0	?
META	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT	STRAIGHT



	THAUMAT 41	TORYDEL 42	TORYMINI 43
OCCIPCAR	1	1	2
ANELLI	1	2	1
ANTCLUB	3SEG	3SEG	3SEG
GENA/EYE	NORM	NORM	NORM
DORHEAD	TRANS	TRANS	TRANS
CLYAPEX	STRAIGHT	STRAIGHT	STRAIGHT
MALKEEL	NO	NO	NO
WINGVEIN	THAUMAT	TORY	TORY
HINDFEM	TOOTH	SIMPLE	SIMPLE
HINDTIB	STRAIGHT	STRAIGHT	STRAIGHT
SPURLENG	NORM	NORM	NORM
SPURINS	APEX	APEX	APEX
SPURNO	TWO	TWO	TWO
FRENLINE	NO	NO	?
NOTAULI	YES	YES	?
PROPOD	NOCARIN	TORY	NOCARIN
CX3SETA	YES	NO	?
TIB3APEX	TRUN	TRUN	TRUN
SCUT/AX	NO	NO	NO
METASTER	?	?	CRYPTO
TERGMAR3	0	1/2	?
META	INTERMED	STRAIGHT	SINUATE

## APPENDIX V: TABLES

**TABLE 1A**  
**TORYMIDAE: NUMBER of WORLD TAXA**  
**by SUBFAMILY and TRIBE**

	<u>VALID</u>		<u>NOMINAL</u>	
	<u>GENERA</u>	<u>SPECIES</u>	<u>GENERA</u>	<u>SPECIES</u>
MEGASTIGMINAE <sup>1</sup>	11	125	22	142
TORYMINAE <sup>2</sup>				
CHALCIMERINI	1	1	1	1
MICRODONTOMERINI	10	67	23	72
MONODONTOMERINI	10	59	11	88
PALACHIINI	4	16	4	16
PODAGRIONINI	6	135	21	146
TORYMINI	11	355	23	532
TORYMOIDINI	5	94	13	106
INCERTAE SEDIS	7	16	10	19
Total Toryminae	54	743	106	980

<sup>1</sup> Megastigminae figures approximate, compiled from Milliron (1949) and Bouček (1988).

<sup>2</sup> Toryminae figures from this work.

**TABLE 1B**  
**TORYMINAE: NUMBER OF WORLD TAXA BY GENUS**

Figures do not include names cited as *nomen nuda*, misidentifications, misspellings, or subspecies other than the nominal name

Genus	Valid	Synonyms	
	Species	Species	Genera
1 <i>Adontomerus</i>	7		1
2 <i>Allotorymus</i>	1		
3 <i>Aloomba</i>	1		
4 <i>Amoturoides</i>	2		
5 <i>Anneckeida</i>	5		

6 <i>Austorymus</i>	1		
7 <i>Chalcimerus</i>	1		
8 <i>Chrysochalcissa</i>	5		
9 <i>Cryptopristus</i>	2	2	1
10 <i>Diomorus</i>	14	6	

11 <i>Ditropinotus</i>	2	1	
12 <i>Ecdamua</i>	5	3	1
13 <i>Echthrodape</i>	2		
14 <i>Eridontomerus</i>	12	1	1
15 <i>Eriemerus</i>	1		

16 <i>Exopristus</i>	2		1
17 <i>Glyphomerus</i>	5	1	1
18 <i>Gummilumpus</i>	1		
19 <i>Idarnotorymus</i>	1	1	1
20 <i>Idiomacromerus</i>	26	1	6

21 <i>Lissotorymus</i>	1		
22 <i>Mantiphaga</i>	6		
23 <i>Mesodiomorus</i>	1		
24 <i>Microdontomerus</i>	8	1	3
25 <i>Micropodagrion</i>	1		
26 <i>Monodontomerus</i>	32	26	1
27 <i>Neopalachia</i>	1		

Genus	Valid	Synonyms	
	Species	Species	Genera
28 <i>Odopoia</i>	4	1	3
29 <i>Oopristus</i>	1	1	
30 <i>Ophiopinotus</i>	1		
31 <i>Ovidia</i>	1		
32 <i>Palachia</i>	11		

33 <i>Palmon</i>	18	3	1
34 <i>Perissocentrus</i>	6	2	
35 <i>Physothorax</i>	9	1	1
36 <i>Platykula</i>	1	1	
37 <i>Plesiostigmodes</i>	1		

38 <i>Podagrion</i>	97	6	10
39 <i>Podagrionella</i>	10	1	3
40 <i>Pradontomerus</i>	1		
41 <i>Propachytomoides</i>	3	1	1
42 <i>Propalachia</i>	3		

43 <i>Pseuderimerus</i>	8		1
44 <i>Pseudotorymus</i>	43	2	3
45 <i>Rhynchodontomerus</i>	1		
46 <i>Rhynchotocida</i>	5		
47 <i>Stenotorymus</i>	1		

48 <i>Thaumatorymus</i>	1		
49 <i>Torymoidellus</i>	1		
50 <i>Torymoides</i>	48	9	5
51 <i>Torymus</i>	317	166	7
52 <i>Zaglyptonotus</i>	3		
53 <i>Zdenekius</i>	1		
54 <i>Zophodetus</i>	1		
TOTALS	743	237	52

**TABLE 2**  
**MEGASTIGMINAE: WORLD HOST SUMMARY<sup>1</sup>**

PLANT HOST (of phytophagous species)	INSECT HOST	
	Host Plant <sup>2</sup>	Host Insect
GYMNOSPERMAE Pinaceae Taxodiaceae Cupressaceae		
ANGIOSPERMAE		
Casuarinaceae		
	Fagaceae	Hymenoptera: Cynipidae
	Moraceae	"gall"
	Proteaceae	"gall"
Rosaceae		
	Leguminosae	Hymenoptera: Pteromalidae (in fruit, pods)
	Rutaceae	Hymenoptera: Eurytomidae
Anacardiaceae ( <i>Pistacia</i> , <i>Schinus</i> , <i>Rhus</i> )	Anacardiaceae ( <i>Mangifera</i> )	Diptera: Cecidomyiidae
Aquifoliaceae		
	Sterculiaceae	"gall"
	Myrtaceae	"gall"
	Solanaceae	Diptera: Cecidomyiidae
	Compositae	Diptera: ?
	?	Homoptera: Coccidae galls

<sup>1</sup> Compiled from Milliron 1949, Bouček 1988, and unpublished data. A record for Megastigminae associated with "figs" (Bouček 1988) is not included above because of its ambiguous nature.

<sup>2</sup> Host plants of insects (center column) arranged in phylogenetic order relative to host plants of phytophagous megastigmines (left column). See text pages 57-58 for additional explanation.

**TABLE 3: TORYMINAE: WORLD HOST SUMMARY**  
(based upon all known species except *Torymus*<sup>1</sup>)

Host <sup>3</sup>	NUMBER OF SPECIES PER TRIBE WITH KNOWN HOSTS <sup>2</sup>						TOTAL <sup>4</sup>
	Chalcimerini	Microdontomerini	Monodontomerini	Palaehiini	Podagrionini	Torymini <sup>1</sup> ( <i>Torymus</i> )	
Egg (endoparasitoid)							
Coleoptera	1						1
Hemiptera			6				1
Egg (ectoparasitoid)							6
Mantidae	1			1	39		41
Tetrigoniidae			1				1
Cicadidae						(1)	
Larva or pupa							
Coleoptera		1					
Hymenoptera	1	21	27			1	2
Lepidoptera		4	15		1	(64)	7
Diptera		11	3			(1)	2
Strepsiptera		1				(94)	19
Nymph							
Homoptera						(3)	
Phytophagous						(5)	
							1
							188
Host Unknown	0	30	15	15	99	26	55
						(25)	8
Total Number of Valid Species in Tribe (from Table 1A)	1	67	59	16	135	38	94
						(194)	16

(continued next page)

(continued from previous page)

TABLE 3: TORYMINAE: WORLD HOST SUMMARY

	Chalcimerini	Monodontomerini	Palachiini	Podagrionini	Torymini <sup>1</sup>	Torymoidini	<i>Incertae Sedis</i>		
	Microdontomerini				( <i>Torymus</i> )				
Percent of Species per Tribe with Hosts Unknown (from this Table)	0	45	25	93	73	68	(13)	61	50
Percent of Species per Tribe with Hosts Known <sup>5</sup>	100	55	75	7	27	32	(87)	39	50

<sup>1</sup> *Torymus* treated separately from remainder of Torymini with host data based upon a survey of 194 Holarctic *Torymus* species (of 317 valid species) as reported in Nikol'skaya and Zerova (1978) and Grissell (1979). Host numbers are presented for relative comparative purposes to other taxa.

<sup>2</sup> Some species attack more than one host group (left column) and are listed once for each of those groups.

<sup>3</sup> Host associations only, exact host not always known, therefore not necessarily true biological relationship.

<sup>4</sup> Excluding *Torymus* (for which data is incomplete).

<sup>5</sup> Percent of species with hosts known is calculated indirectly, because species may have more than one host and may be reported multiple times in different host categories. The percent of species with hosts unknown is calculated based on total number of species per tribe and then is subtracted from 100 percent to derive the actual percent of species with hosts known.

**TABLE 4**  
**BIOLOGICAL ASSOCIATIONS OF SOME *MICRODONTOMERUS***

SPECIES	HOST	HABITAT	DISTRIBUTION
<i>anthidii</i>	Megachilidae	resin or twig nests	NEARCTIC
<i>anthonomi</i>	Bruchidae Curculionidae Coleophoridae Olethreutidae Tephritidae Braconidae	larvae in buds, stems, and flower heads	NEARCTIC
<i>bicoloripes</i>	Cynipidae	bud galls	NEARCTIC
<i>fumipennis</i>	Lasiocampidae Tortricidae Saturniidae	plant stems and tied leaves	NEARCTIC
n. sp.	Saturniidae	egg	NEARCTIC/ NEOTROPICAL
<i>ovivorus</i>	Buprestidae	egg	PALEARCTIC

**TABLE 5**  
**TABULAR COMPARISON OF TAXA PLACED IN *PODAGRIONELLA***  
 (see text, p. 151, for explanation)

Taxon	Club	Genal sulcus	Wing spot	Inner basal tooth on hind femur	Frenal area	Propodeum	Petiole (Mt1)
<i>Iridophaga lichtensteini</i> **	3 Seg <sup>†</sup>	Yes	No	Yes	Polished Setose No groove	Lateral arched carinae	No
<i>Iridophagoides petiolata</i> **	3 Seg <sup>†</sup>	No	Yes	No	Polished Asetose Groove	No carinae	Yes
<i>Iridophagoides tatianae</i>	3 Seg <sup>†</sup>	No	Yes	?	Polished Asetose Groove	No carinae	No
<i>Podagrionella bella</i> **	3 Seg*	Yes	No	No	Polished Asetose Groove	Median transverse carina	No
<i>Podagrionella indarbelae</i>	3 Seg*	Yes	No	No	Polished Asetose No groove	Apical transverse carina	No
<i>Tarachodiphaga senegalensis</i> **	3 Seg <sup>†</sup>	Yes	No	Yes	Sculptured Setose Groove	Lateral arched carinae	No
Mozambique species	3 Seg <sup>†</sup>	Yes	No	Yes	Polished Asetose No groove	No carina	No
Botswana species	3 Seg <sup>†</sup>	Yes	Yes	No	Polished Asetose No groove	Median transverse carina	No
Somalia species	3 Seg*	Yes	No	Yes	Polished Setose No groove	Apical transverse carina	No

3 Seg<sup>†</sup> = dorsum clearly divided by sutures

3 Seg\* = dorsum with indistinct sutures, club may appear 1-segmented

\*\*Type-species of genus



APPENDIX VI: FOSSIL TORYMIDAE AND *PALAEOTORYMUS*

Below is a summary list of fossil Torymidae. All species are treated under their respective genera in the main part of this volume except the genus *Palaeotorymus* which was not treated in this study. I discuss this genus and its species below.

*Gummilumpus* Grissell 1995

TAXONOMY. - *Gummilumpus*, described earlier in this work, is based upon a single species, *G. bouceki* (Grissell), from Dominican amber. For additional information see pages 135-137 and 194.

*Monodontomerus* Westwood 1833

TAXONOMY. - Based upon 31 extant species, this genus has a single known fossil species, *M. primaveus* Brues [not seen], from Baltic amber. For additional information see page 221.

*Palaeotorymus* Brues 1910

*Palaeotorymus* Brues 1910:18. Type-species: *Palaeotorymus typicus* Brues (orig. desig.).

TAXONOMY. - This genus is based upon 4 species from Florissant shale (all housed in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts): *aciculatus* Brues 1910 [examined], *laevis* Brues 1910 [examined], *striatus* Brues 1910 [examined], *typicus* Brues 1910 [examined]. According to Brues (1910), the Florissant (Miocene) flora of Colorado showed a "tropical element" based upon the presence of fossil fig leaves and the presence of at least one fig wasp (Agaoninae, *sensu* Bouček 1988) as well as the "abundance of Ophioninae and Pimplinae" (Ichneumonidae) which "appear to be expressions of Neotropical tendencies." The type-species of the genus, *typicus*, was described from 14 "specimens" (but Brues listed 15, and an additional reverse of one of these, as well) of which I have seen all but one (#5511). Based upon these specimens, at least 6 are so poorly represented as to be of questionable placement to family (#'s 2073, 2075, 2080, 2082, 2195, 2198), 3 appear not to be the same taxon as the type (#'s 2196, 2074, 2081), and 3 might be the same based upon the antenna (#'s 2079, 2197) and abdomen (#2077 and its reverse #2078). My discussion of this genus, therefore, is based largely upon the holotype specimen (#2072). The genus *Palaeotorymus* was distinguished entirely by the "immensely elongated postmarginal vein which extends nearly to the apex of the wing." After careful examination of the holotype specimen I can find no evidence that any such elongation is present. The marginal vein appears to be slightly longer than 3 times the postmarginal vein and nearly 4 times the length of the stigmal vein. Brues figured and numbered the type specimen, and I have examined the exact same fossil piece. The wing venation is nearly like that found in extant *Monodontomerini*, or uncommonly in some members of Torymini such as *Diomorus*. The presence of a strong frenal line and slightly toothed hind femur indicates possible comparison with *Monodontomerus* or *Diomorus* as well. In *Palaeotorymus laevis* the wing venation appears as found in *typicus*, but it may be that the postmarginal vein is shortened by virtue of a

fracture in the rock surface. In both *Palaeotorymus aciculatus* and *striatus* the postmarginal vein is definitely longer than the marginal vein, and thus fits the definition of the genus as given by Brues (but not supported by the type-species *typicus*). In my opinion, however, neither *aciculatus* nor *striatus* can definitely be placed even to family. They could as easily be considered Pteromalidæ based upon the wing venation. In *aciculatus* there is evidence of an exerted ovipositor which is broken off close to its base, and in *striatus* it is possible that the very base of the ovipositor is visible. In neither case, however, is there any other evidence for placement in Torymidæ. With many of the shale fossils I do not believe it is possible to draw detailed conclusions based upon what can be seen on imperfect specimens; it is difficult enough to interpret extant species. In my opinion, the genus *Palaeotorymus* is not readily definable based upon the holotype or even other specimens in the type series, which may or may not even represent the same family. The other species of *Palaeotorymus* may not belong to the same family either. At this point I would not place much emphasis on the identities of these fossils, much less use them to support theories of phylogeny.

***Palmon* Dalman 1825**

TAXONOMY. - There is a single fossil species known in this genus of 17 extant species: *P. bellator* Dalman 1825 [examined]. This genus was removed from synonymy with *Podagrion* where it had been placed for many years. It is discussed further on page 227.

***Podagrion* Spinola 1811**

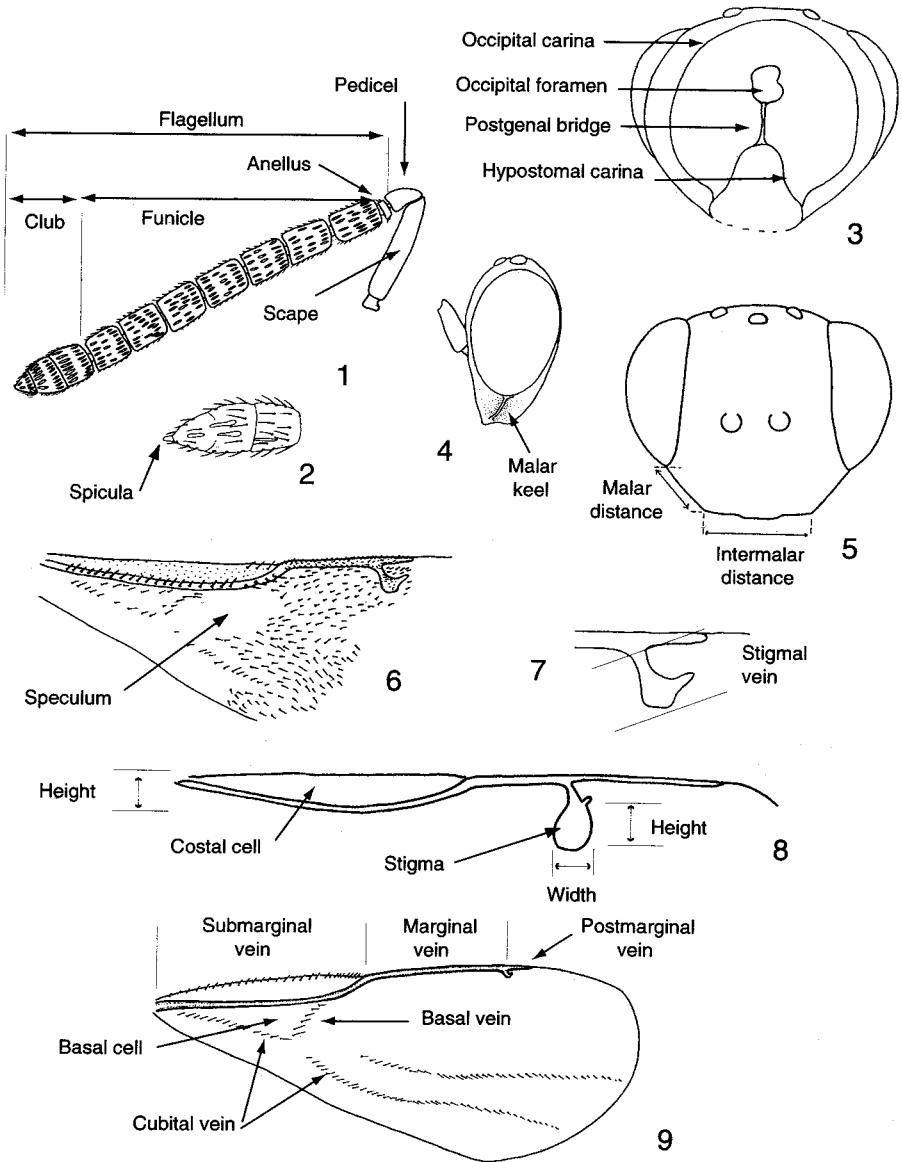
TAXONOMY. - There are now 2 copal fossil species (of unknown origin) attributed to this genus: *capitellatum* Dalman 1825 [not seen] and *clavellatum* 1825 [examined]. Earlier in this work I removed *Palmon bellator* from *Podagrion* where it had been placed in synonymy. I can confirm that *clavellatum* is a true *Podagrion* based upon examination, but I cannot confirm the placement of *capitellatum* based upon personal examination of the type. Currently 95 extant species are recognized in the genus (page 234).

***Torymus* Dalman 1820**

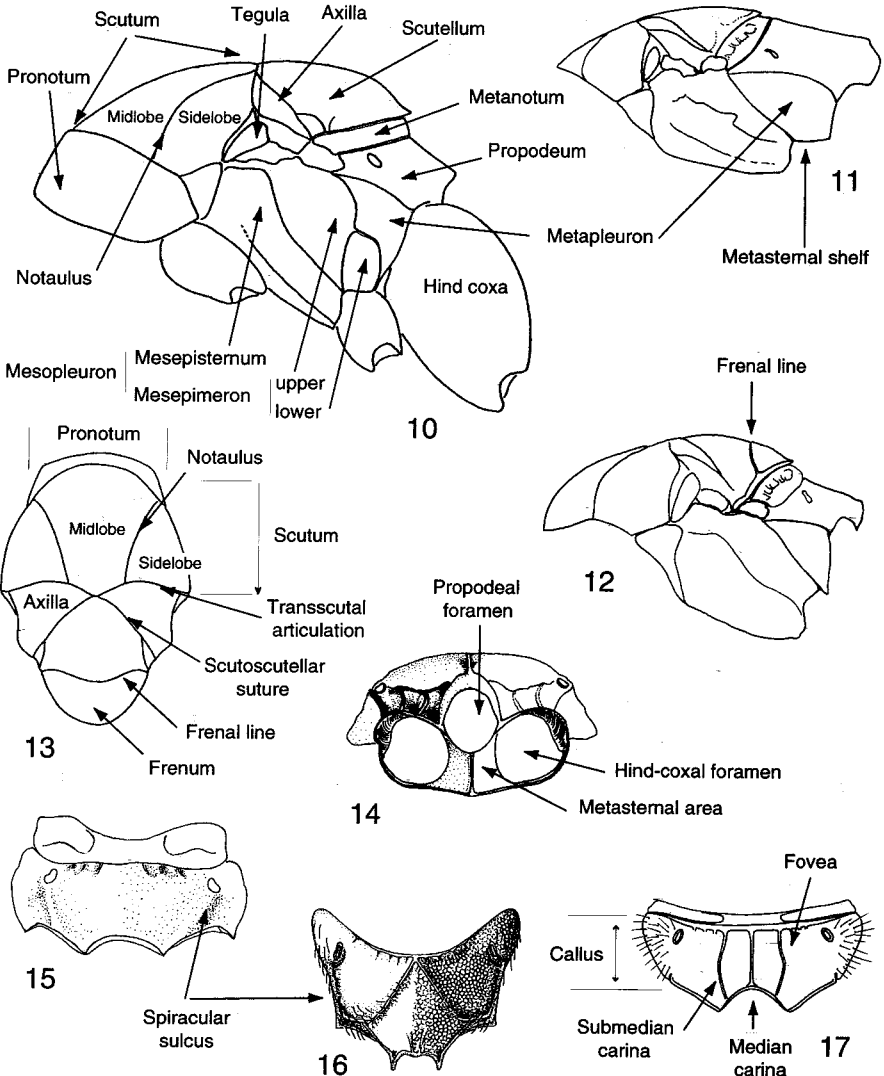
TAXONOMY. - This genus has 2 fossil species attributed to it: *T. pertinax* Förster [not seen] and *T. bruesi* Huber [examined]. There are another 315 extant species. Previously I illustrated *bruesi* and discussed its placement (Grissell 1976:89-90). It is listed in the catalog on page 277.

***Zophodetus* Grissell 1980**

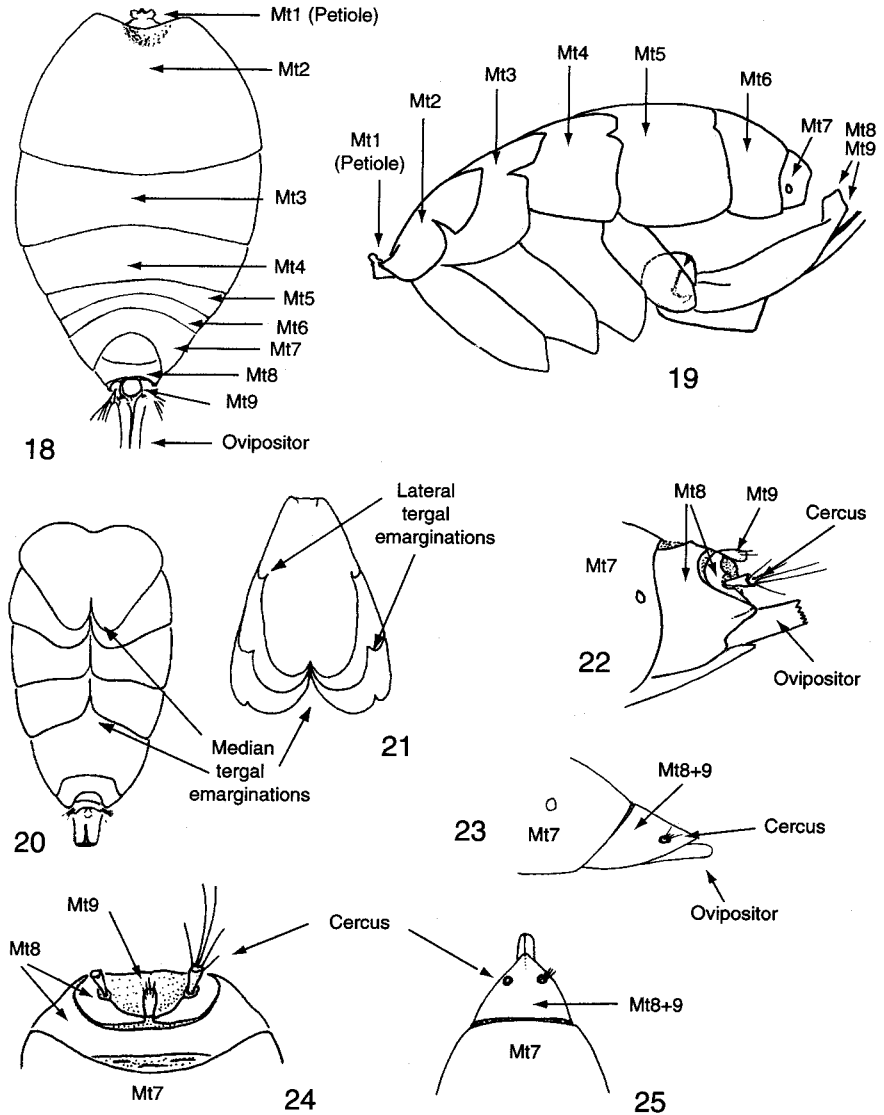
TAXONOMY. - This genus is based upon a single species, *Z. woodruffi* Grissell, from Dominican amber. For additional information see pages 75-76 and 291.



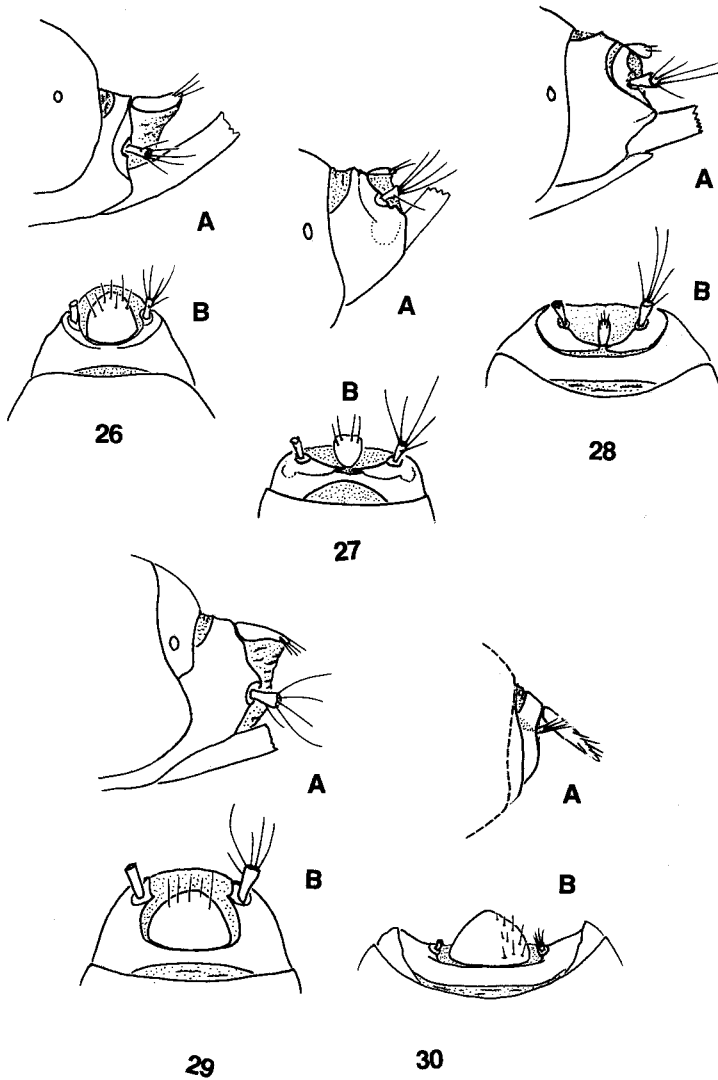
**Figs. 1-9.** Terminology, Torymidae. 1. Antenna (*Torymus*). 2. Antennal club (*Pseuderimerus*). 3-5. Head: 3, posterior view (*Podagrion*); 4, side view (*Rhynchotocida*); 5, anterior view (*Torymus*). 6. Forewing, basal view (*Zdenekius*). 7. Wing vein, apex (lines show stigmal vein length) (*Zdenekius*). 8-9. Forewing: 8, anterior view (*Megastigmus*); 9, overview (*Torymus*).



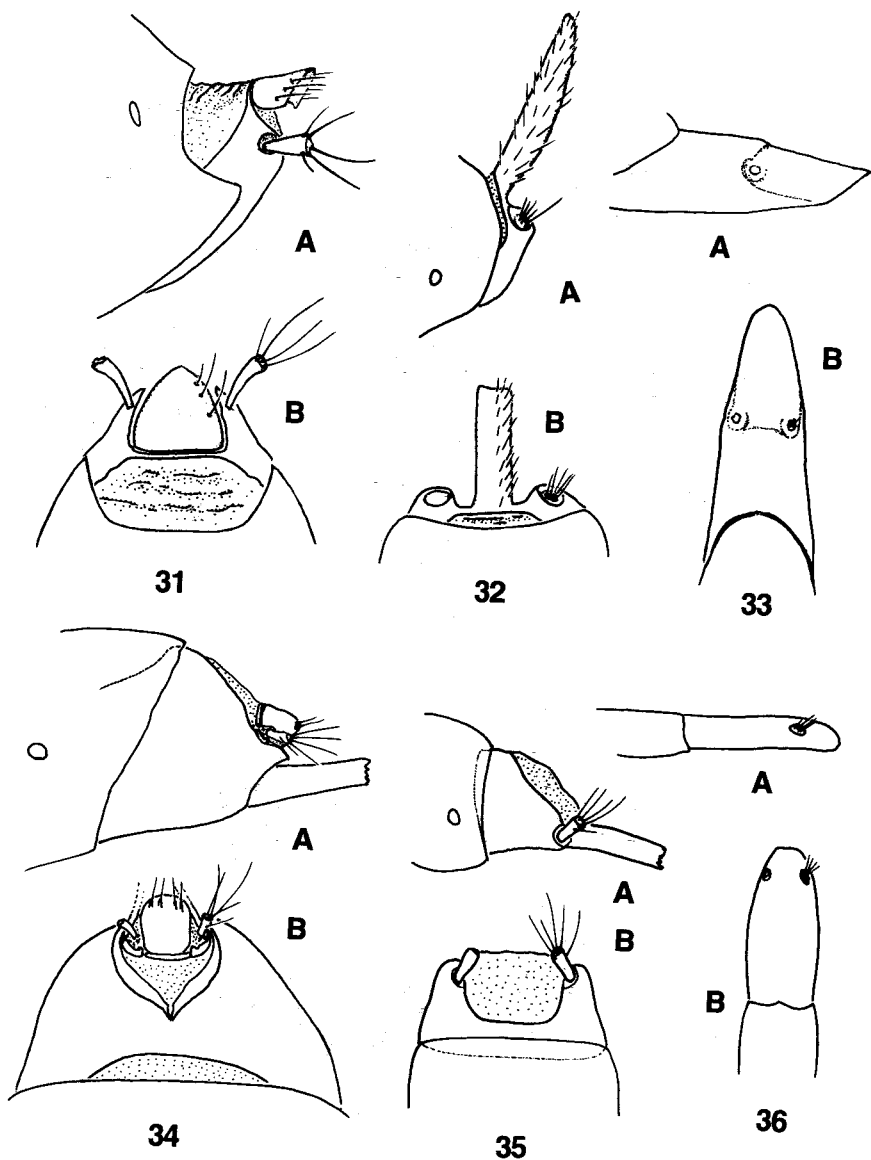
**Figs. 10-17.** Terminology, Teromyidae. 10-12. Mesosoma, lateral view (10, *Torymus*; 11, *Podagrion*; 12, *Monodontomerus*). 13. Mesosoma, dorsal view (*Torymus*). 14. Metasternum, ventral view (*Zdenekius*). 15-17. Propodeum, dorsal view (16, *Podagrion*; 17, *Torymus*).



**Figs. 18-25.** Terminology, Torymidae (except 23, 25, Pteromalidae), metasoma. 18. Dorsal view (*Glyphomerus*, Mt, Metasomal tergum). 19. Lateral view (*Podagrion*). 20-21: Dorsal view (20, *Torymus*; 21, *Podagrion*). 22-23: Apex, lateral view (22, *Torymus*; 23, *Pteromalus*). 24-25: Apex, dorsal view (24, *Torymus*; 25, *Pteromalus*).



**Figs. 26-30.** Torymidae, metasomal terga 8 and 9 (A, lateral view, ovipositor sheaths partially indicated; B, dorsal view, ovipositor sheaths not shown; stipple, membranous area). 26. *Megastigmus aculeatus*. 27. *Monodontomerus aereus*. 28. *Torymus* sp. (USA). 29. *Podagrion mantis*. 30. *Echthrodape africana*.



**Figs. 31-36.** Pteromalidae, Agaonidae, metasomal terga 8 and 9 (A, lateral view, ovipositor sheaths partially indicated; B, dorsal view, ovipositor sheaths not shown; stipple, membranous area). 31-33. Pteromalidae, 31. *Chromeurytoma nobilis*. 32. *Ditropinotella compressiventris*. 33. *Epistenia* sp. (USA). 34-36. Agaonidae, 34. *Idarnes* sp. (Peru). 35. *Blastophaga* sp. (Costa Rica). 36. *Philotrypesis caricae*.





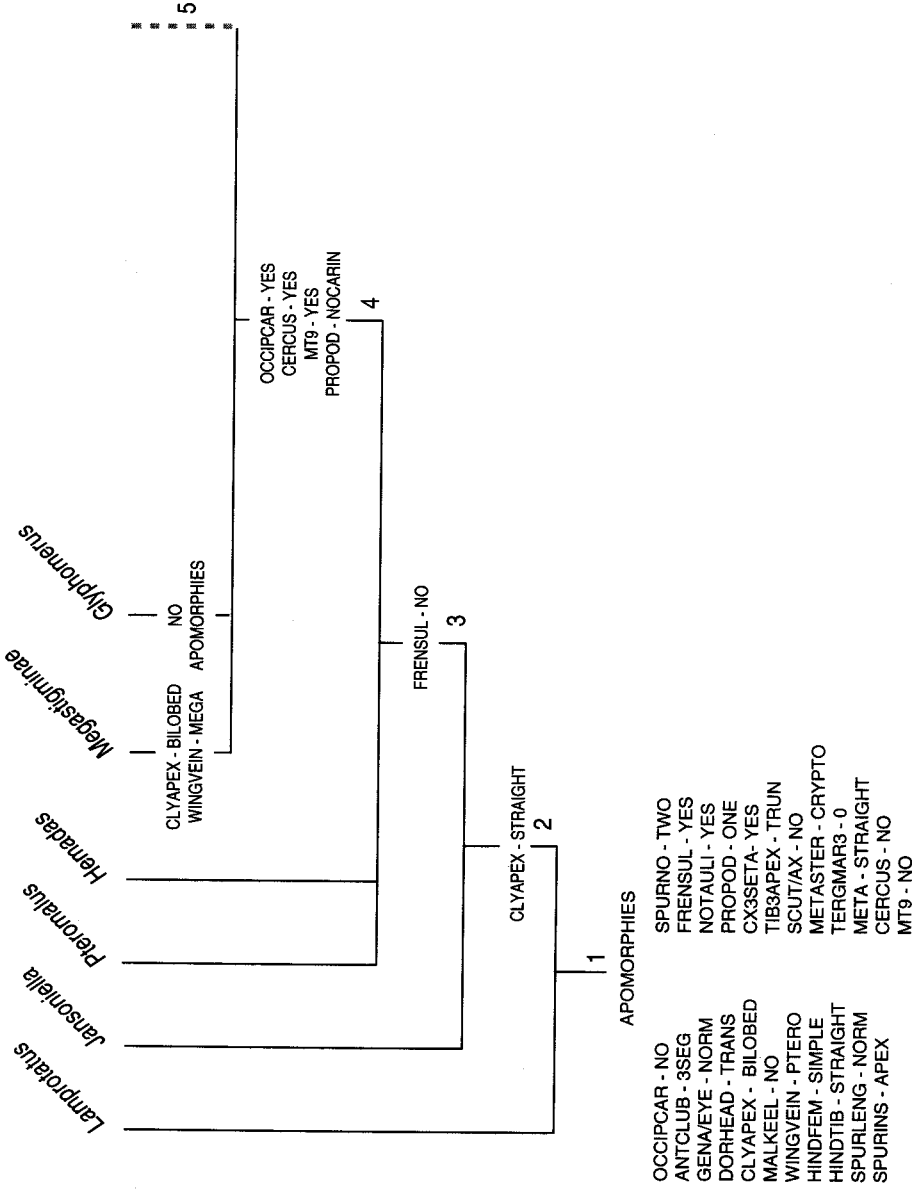


Fig. 37A. Fig. 37 cont'd. Node 1 enlarged, apomorphies and character state changes.

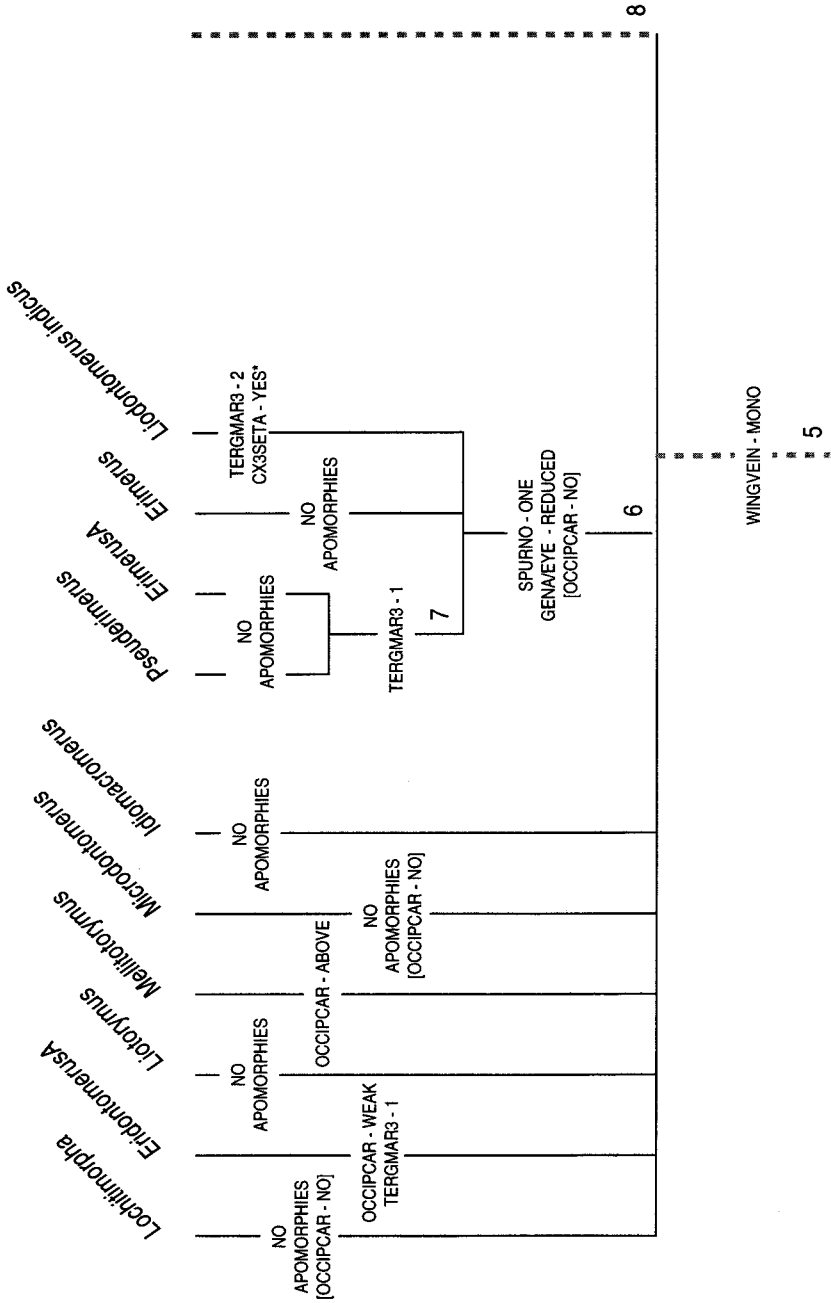


Fig. 37B. Fig. 37 cont'd, character state changes. Node 5 enlarged.

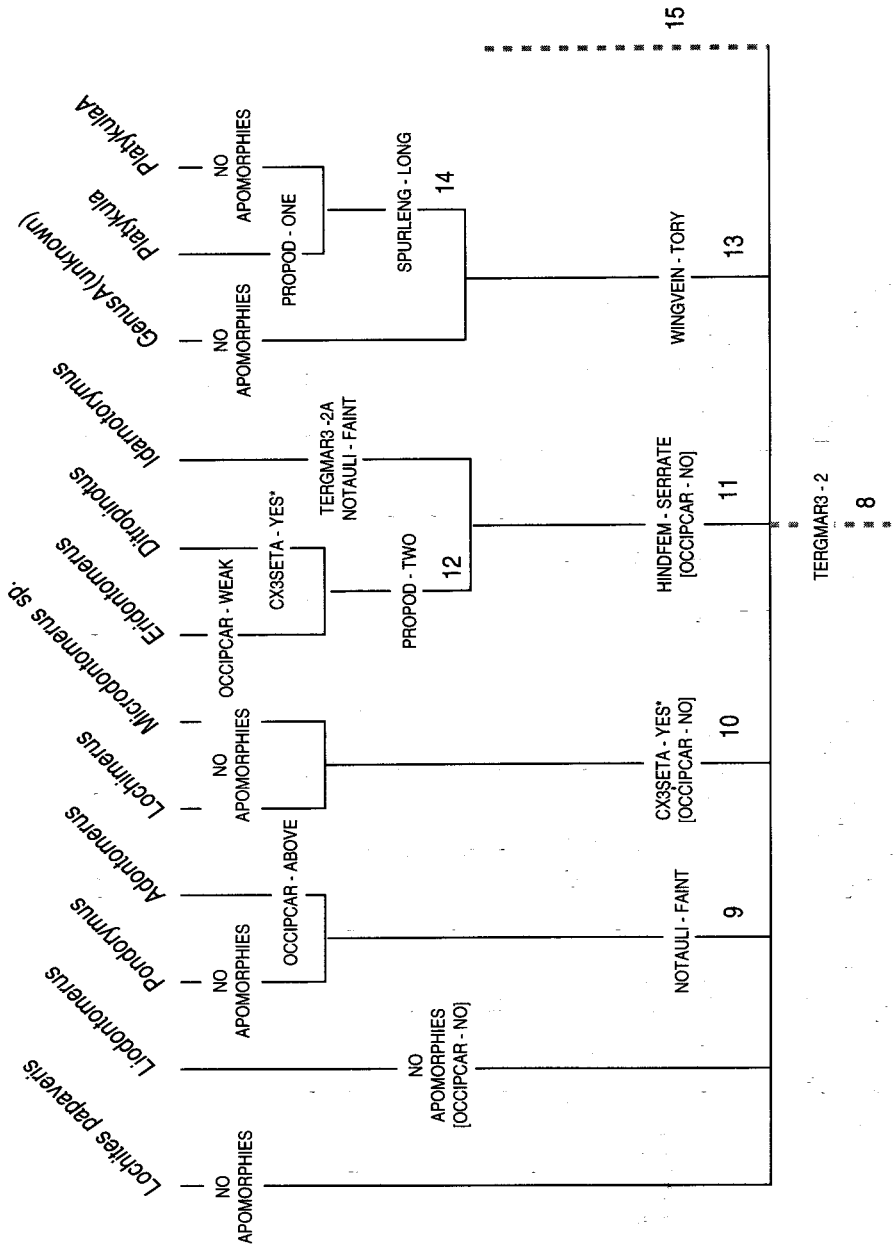


Fig. 37C. Fig. 37 cont'd, character state changes. Node 8 enlarged.

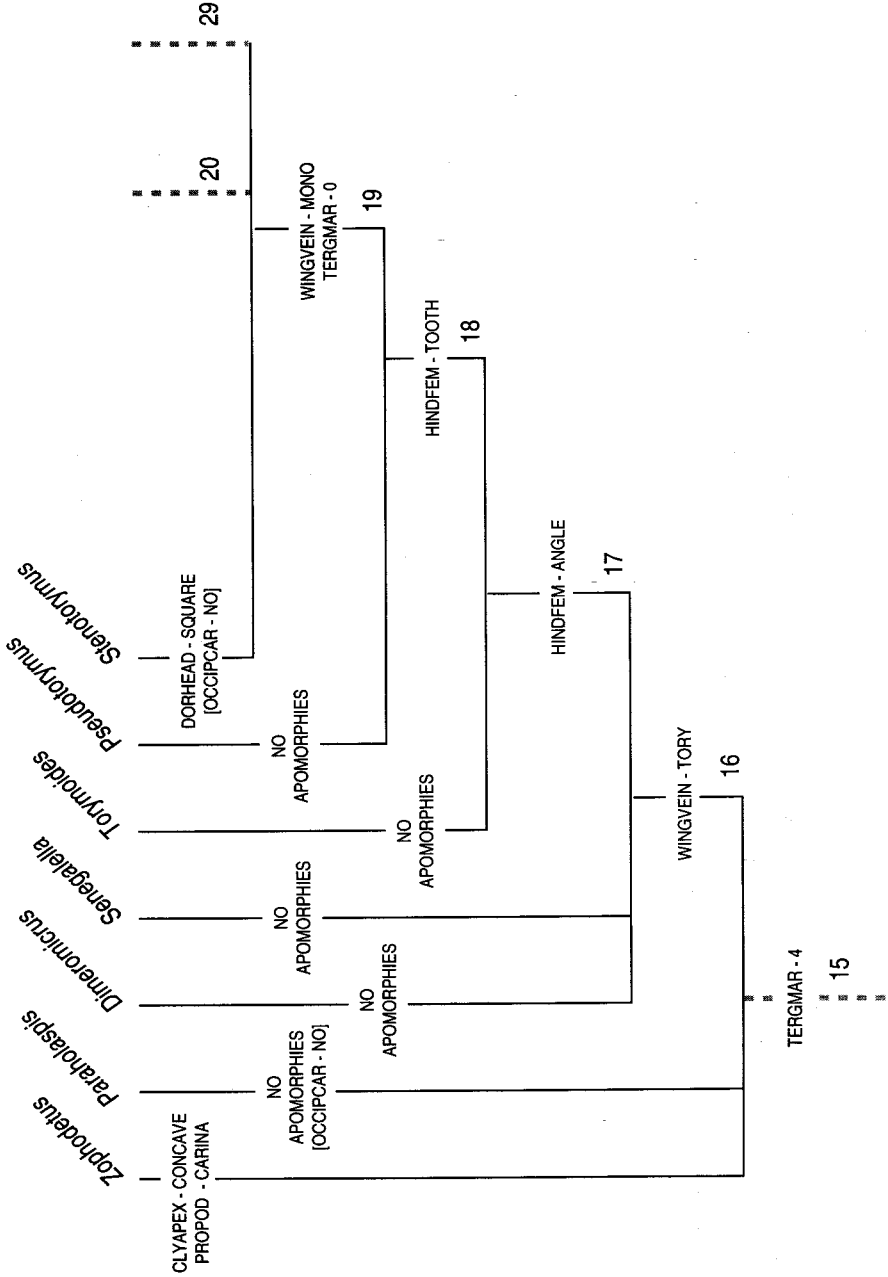


Fig. 37D. Fig. 37 cont'd, character state changes. Node 15 enlarged.

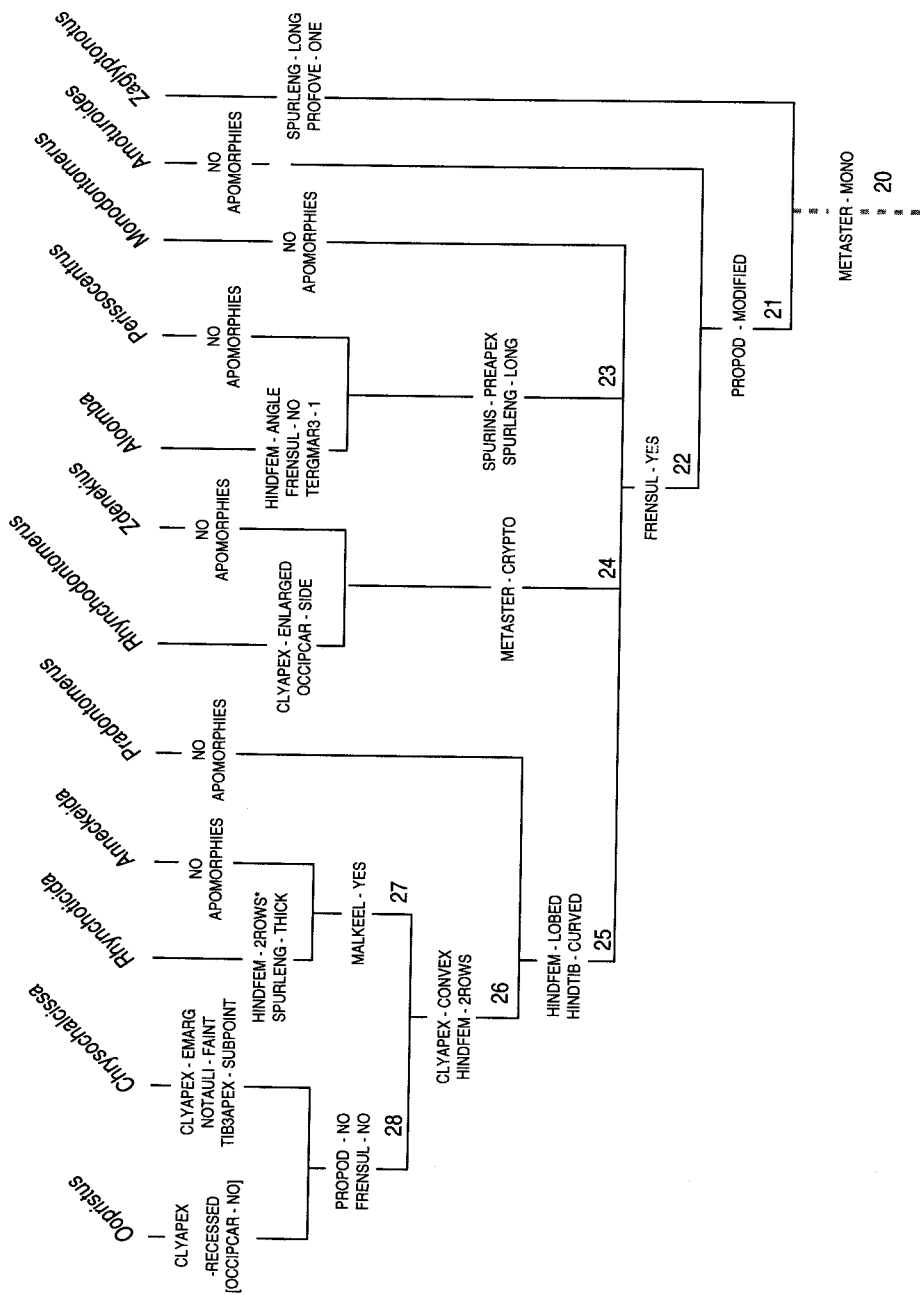


Fig. 37E. Fig. 37 cont'd, character state changes. Node 20 enlarged.

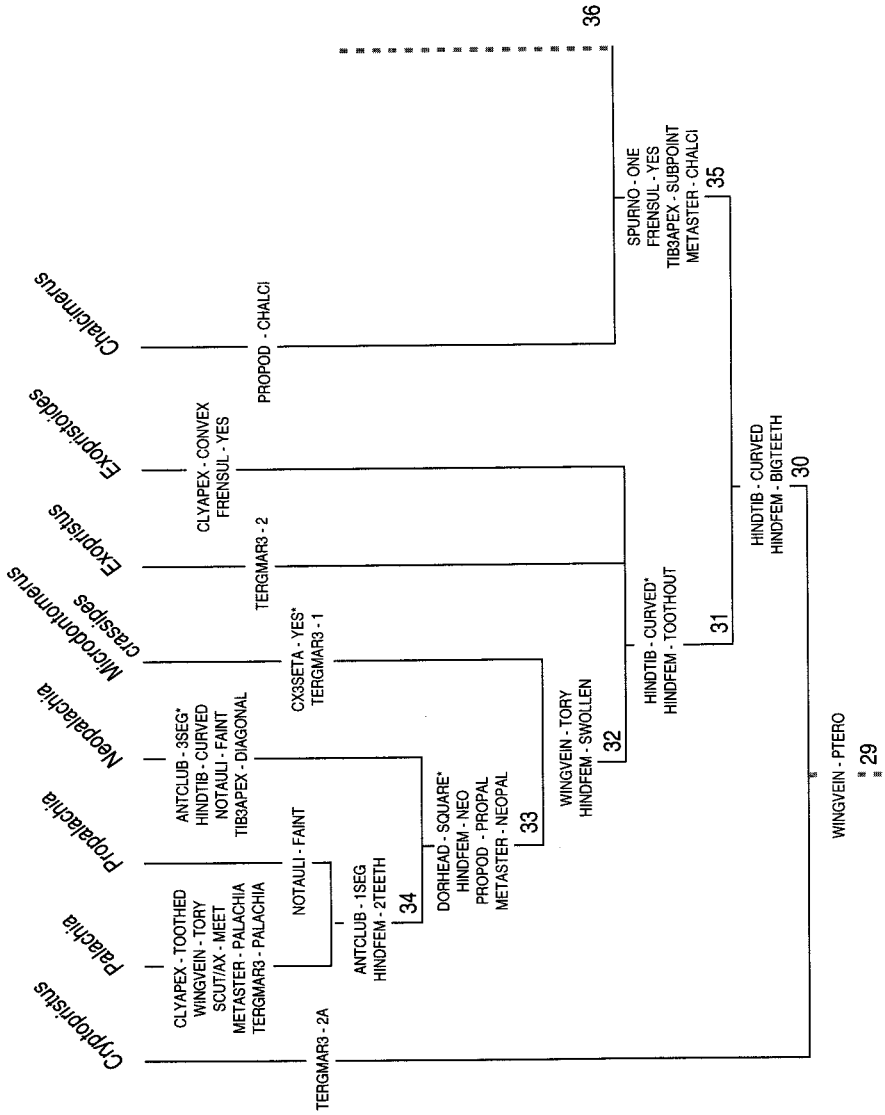


Fig. 37F. Fig. 37 cont'd, character state changes. Node 29 enlarged.

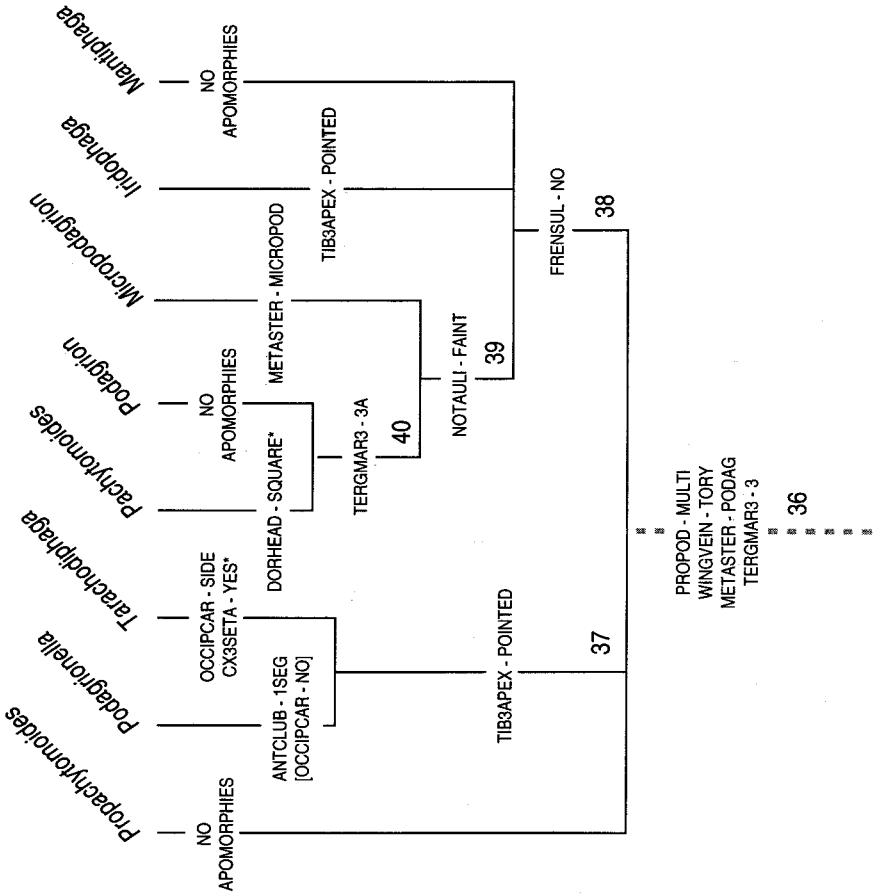


Fig. 37G. Fig. 37 cont'd, character state changes. Node 36 enlarged.

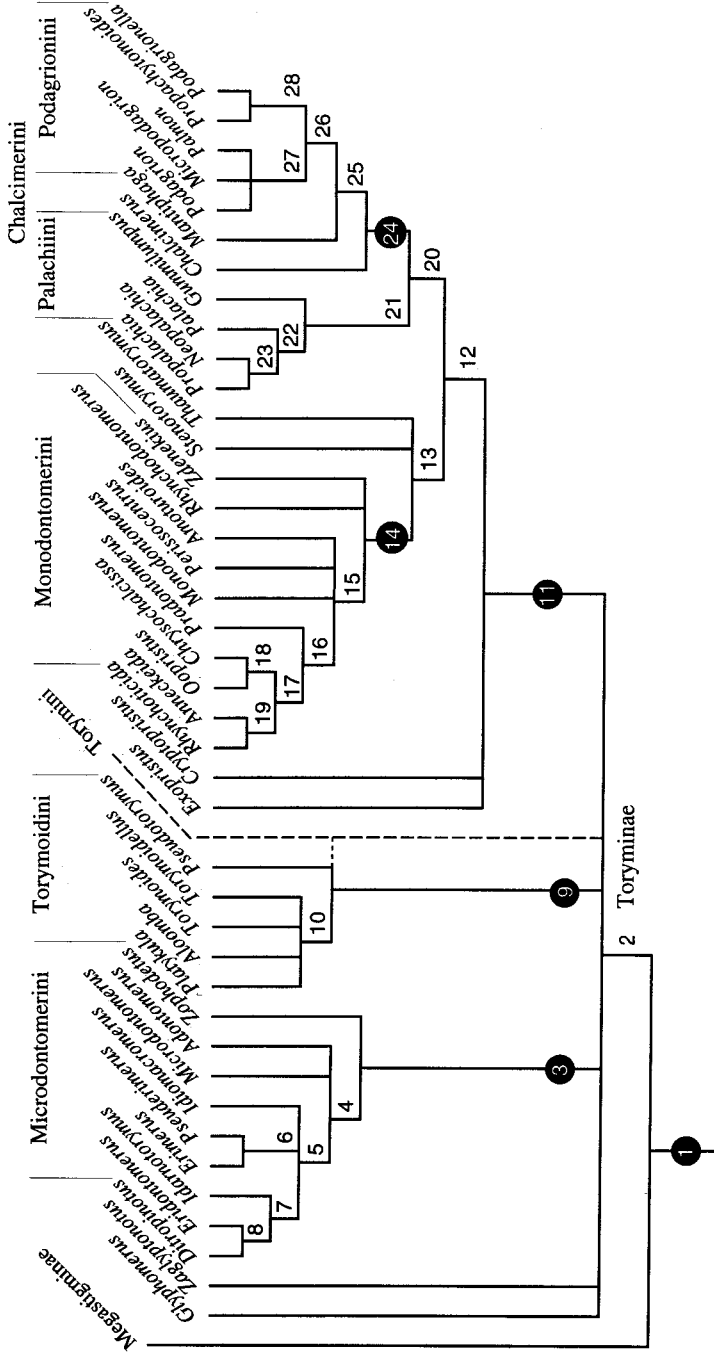


Fig. 38. Ending Hypothesis (based on data matrix, Appendix IV, p. 333). Overview cladogram of Torymidae genera. Character state changes detailed on following pages are keyed to nodes in black circle (characters and states discussed under Phylogenetic Analyses p. 31). Position of Torymini tentative (see p. 99 for explanation).



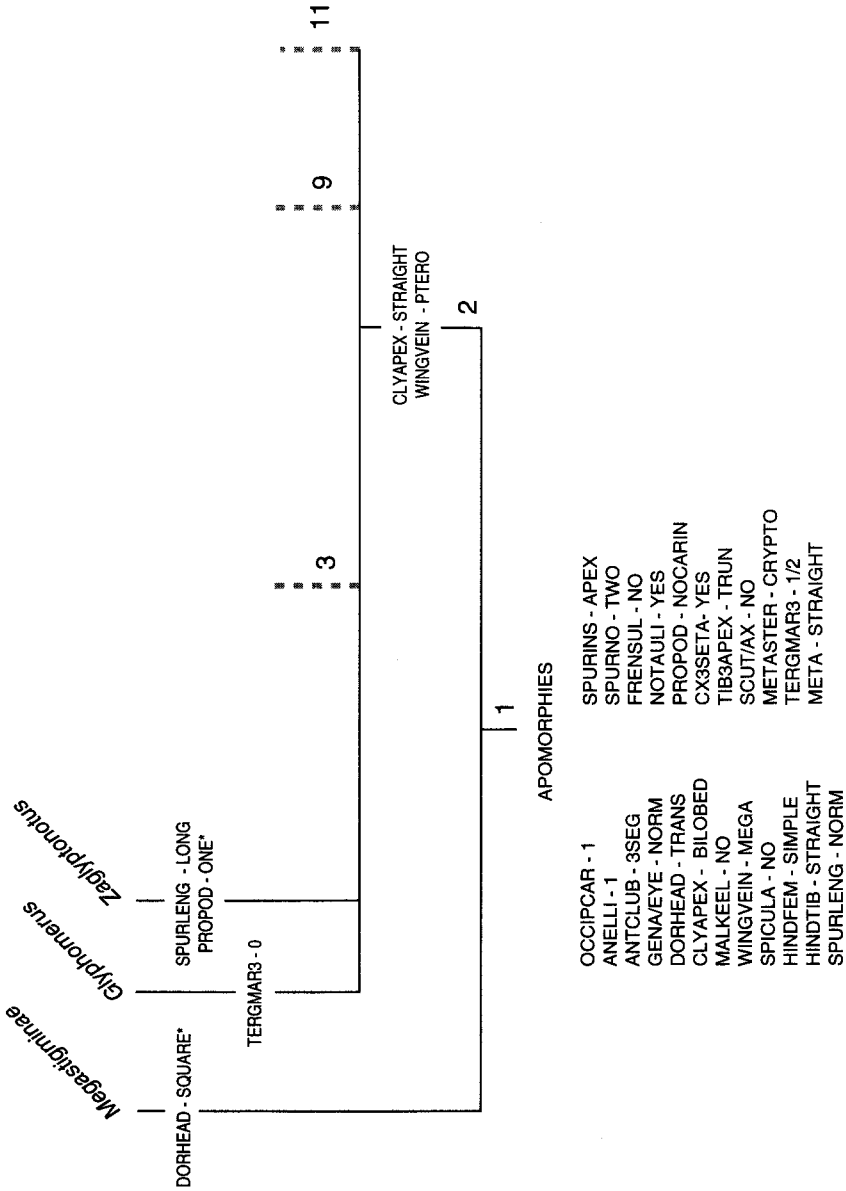


Fig. 38A. Fig. 38 cont'd, character state changes. Node 1 enlarged, apomorphies.

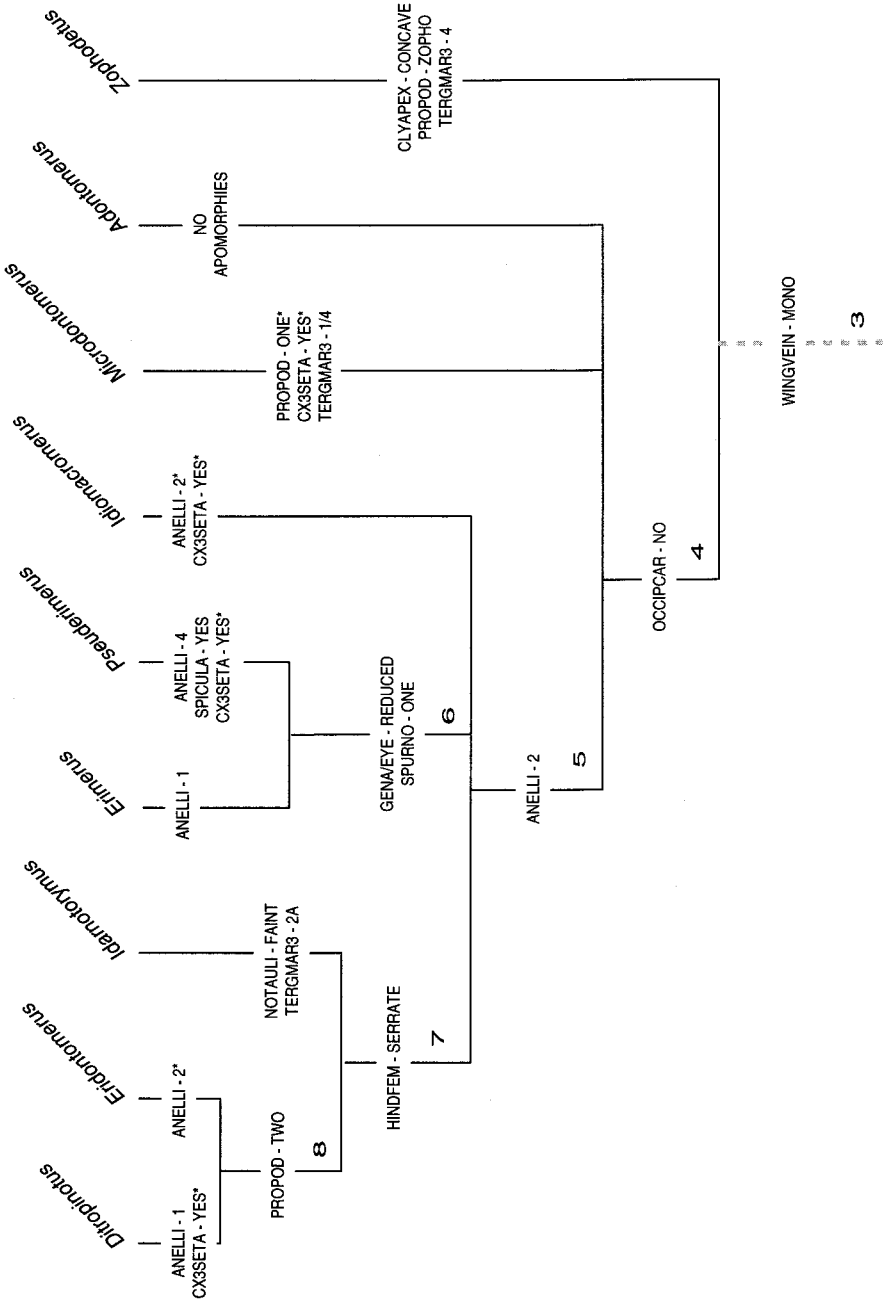


Fig. 38B. Fig. 38 cont'd, character state changes. Node 3 enlarged.

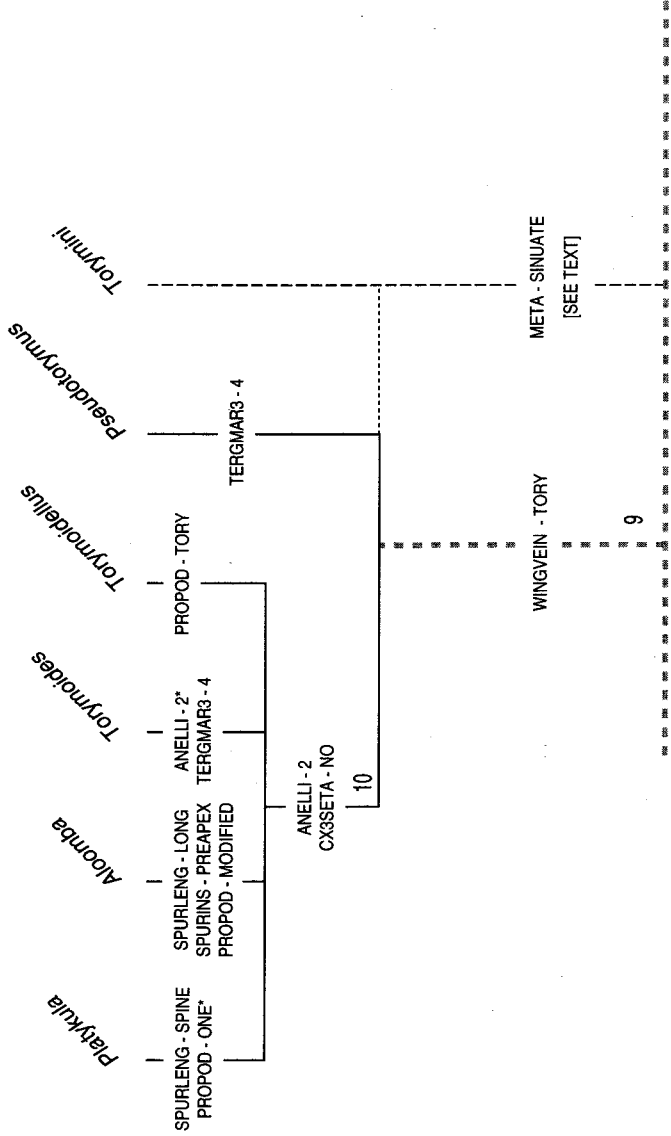


Fig. 38C. Fig. 38 cont'd, character state changes. Node 9 enlarged.

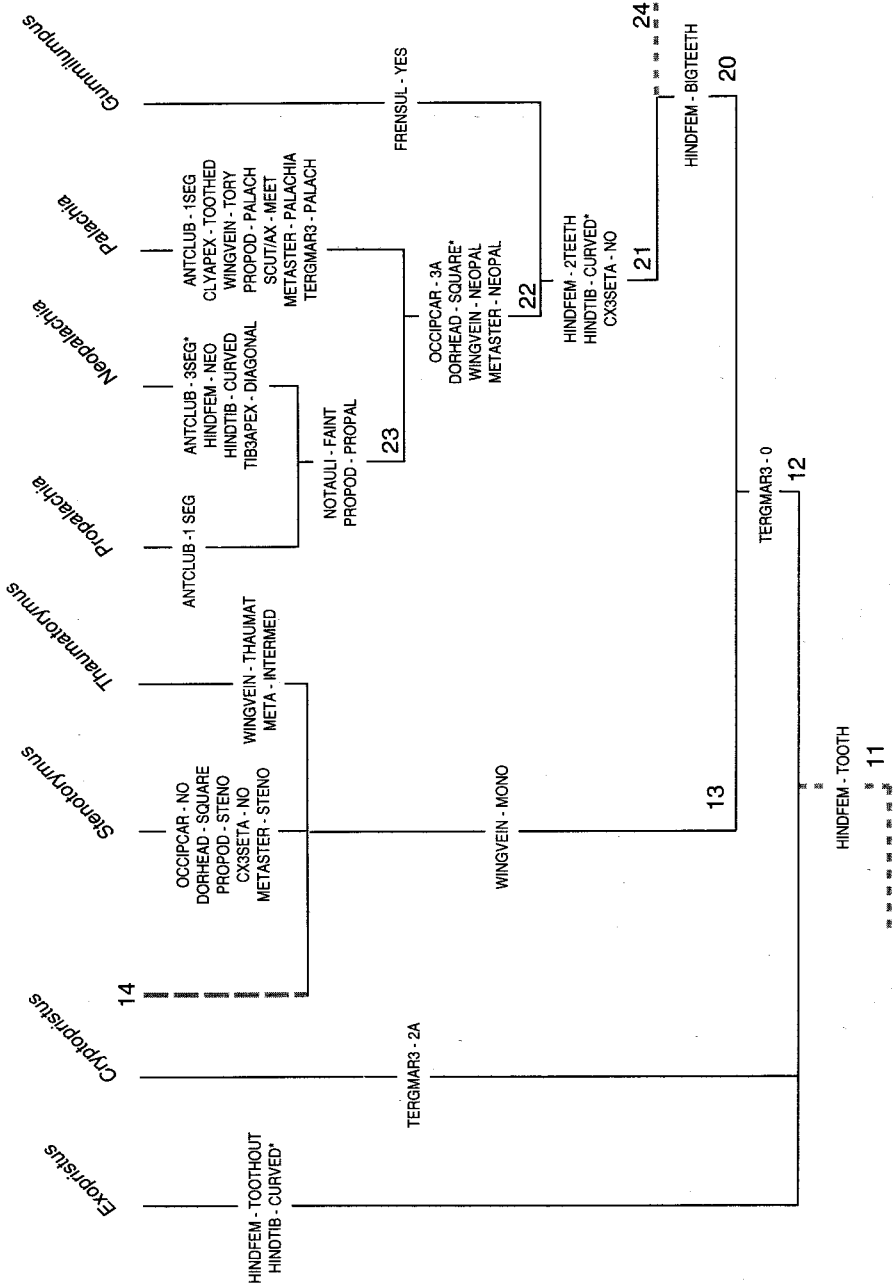


Fig. 38D. Fig. 38 cont'd, character state changes. Node 11 enlarged.

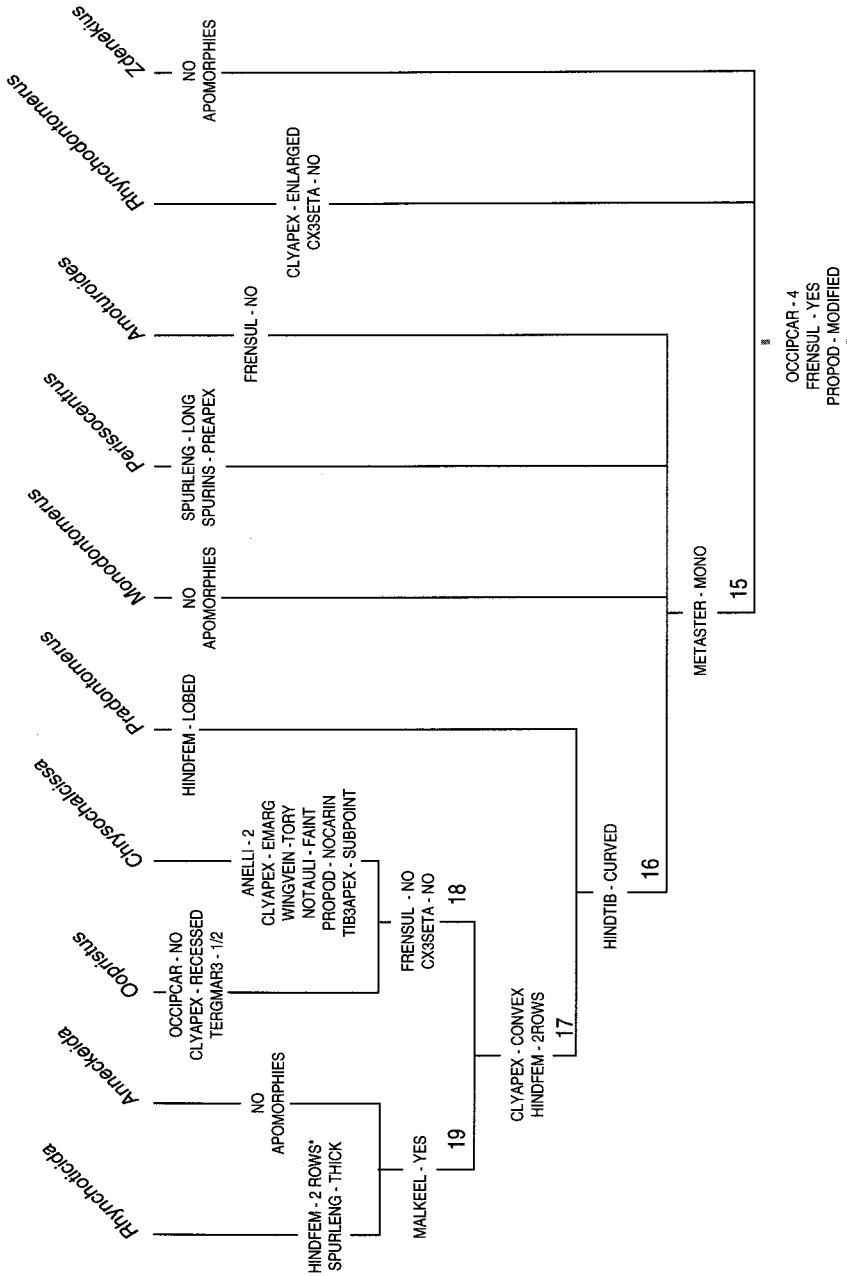


Fig. 38E. Fig. 38 cont'd, character state changes. Node 14 enlarged.

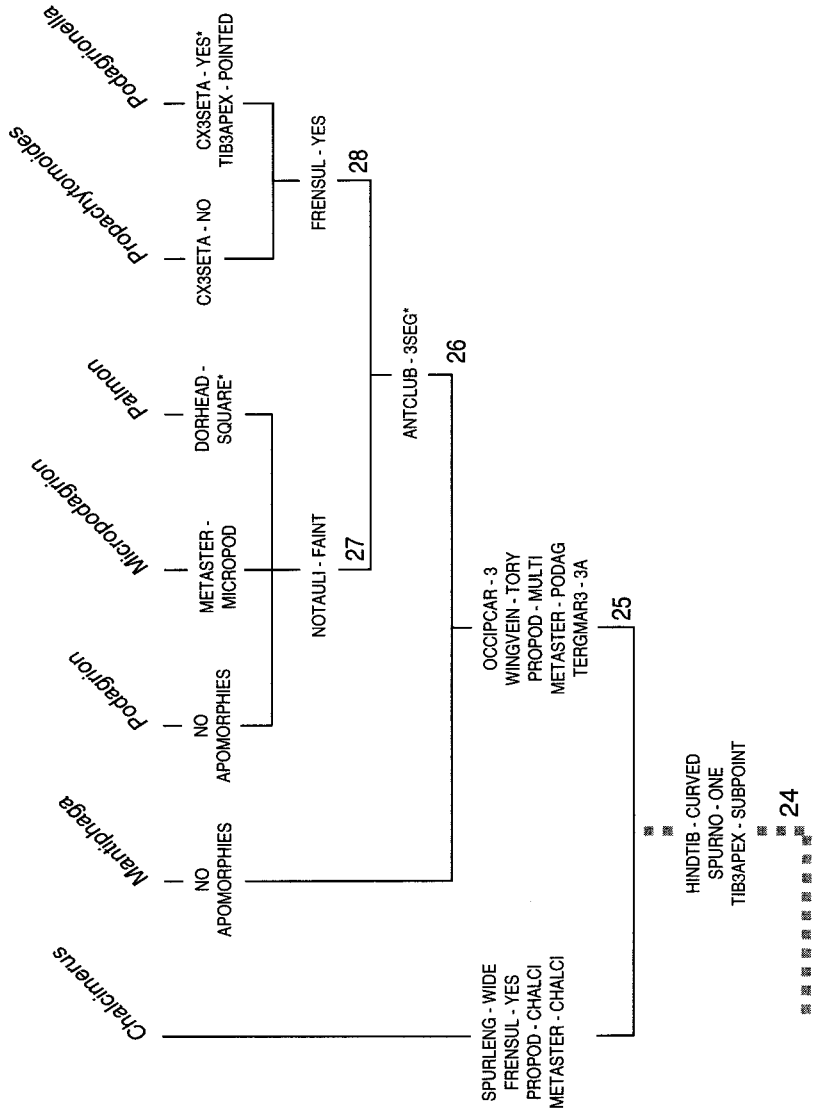
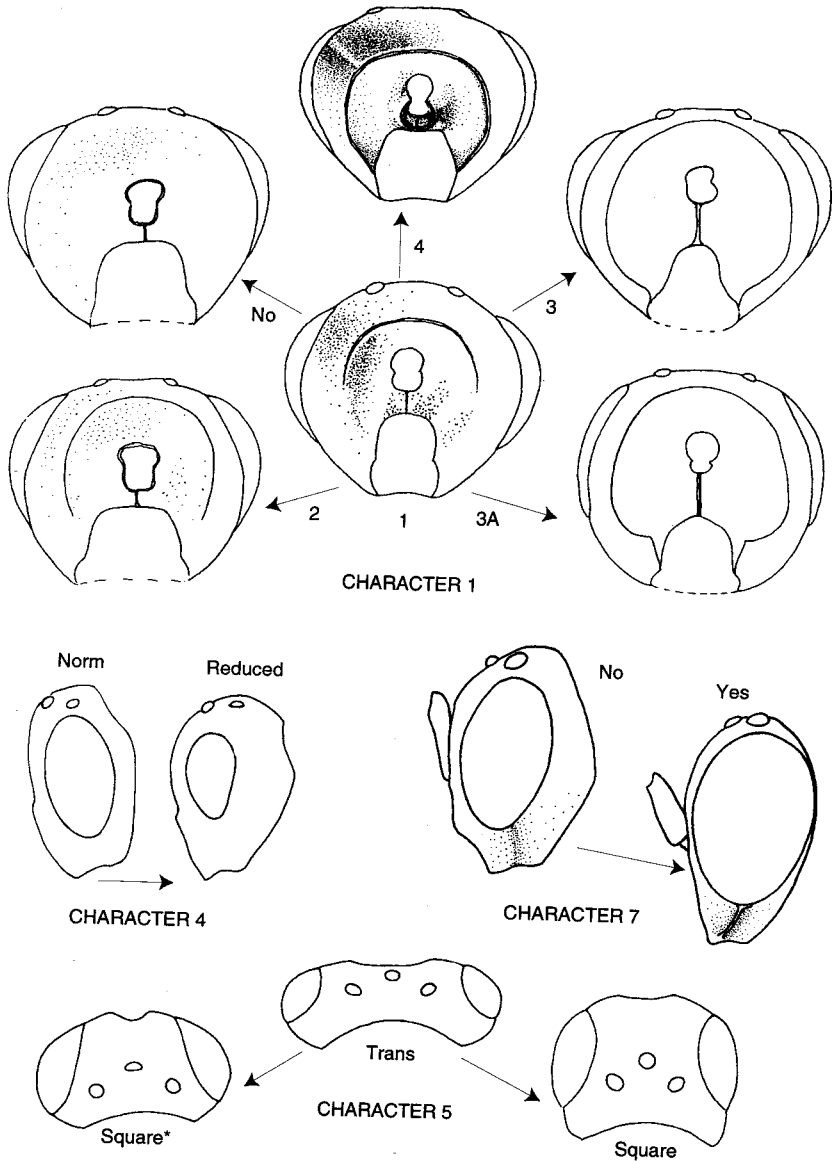
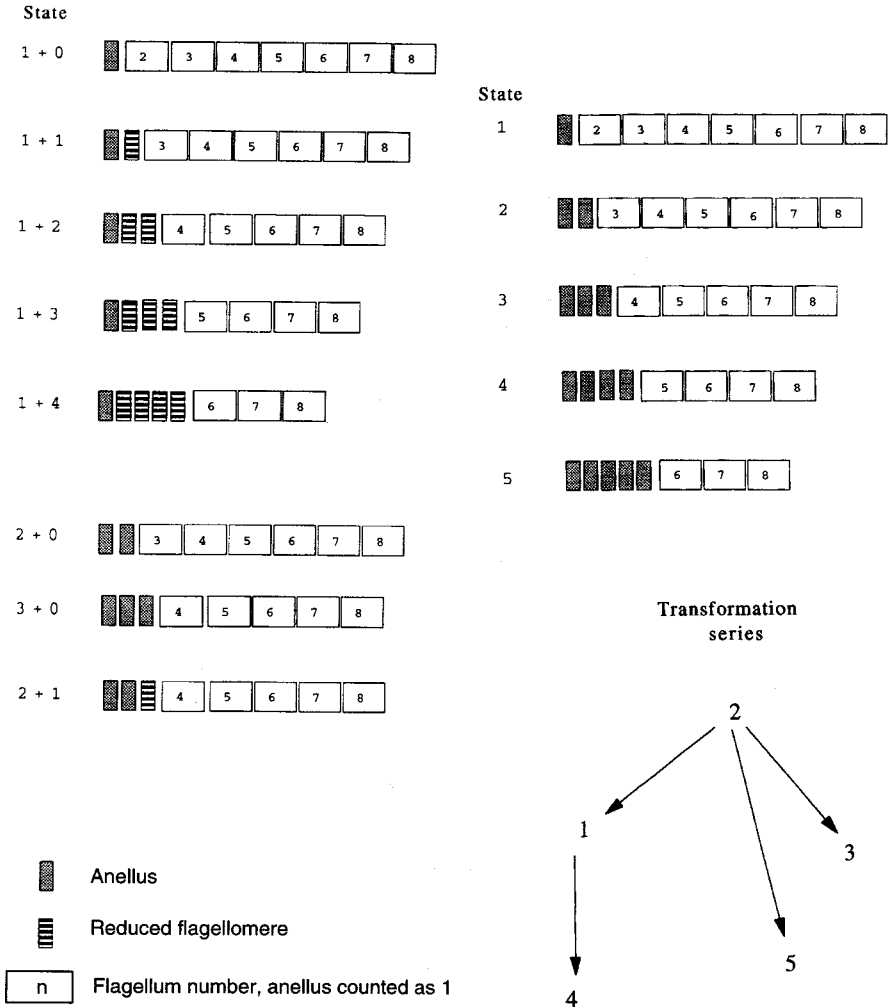


Fig. 38F . Fig. 38 cont'd, character state changes. Node 24 enlarged.

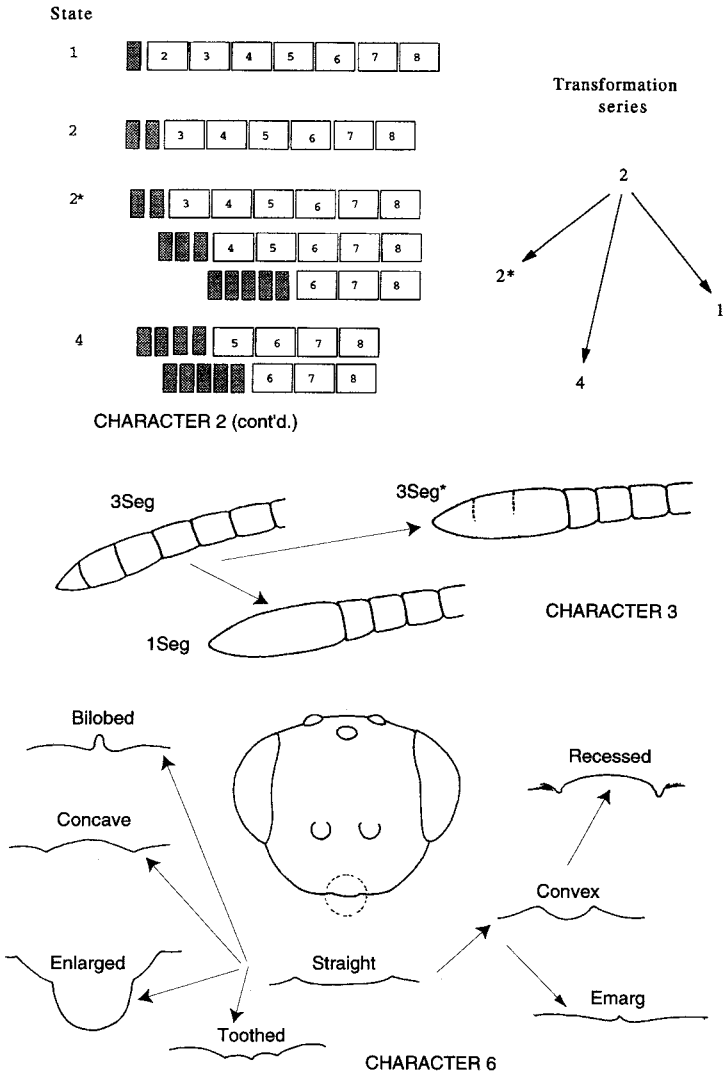


**Fig. 39.** Characters 1, 4, 5, 7 states, ending hypothesis. Character 1. Occipital carina, transformation series [Exemplars: 1 — *Glyphomerus stigma*. 2 — *Torymus* sp. 3 — *Podagrion mantis*. 3A — *Palachia* sp. 4 — *Perissocentrus argentinae*. No — *Microdontomerus anthonomi*]. Character 4. Male eye (semi-diagrammatic). Character 5. Dorsal shape of head, transformation series (semi-diagrammatic). Character 7. Malar keel (semi-diagrammatic).

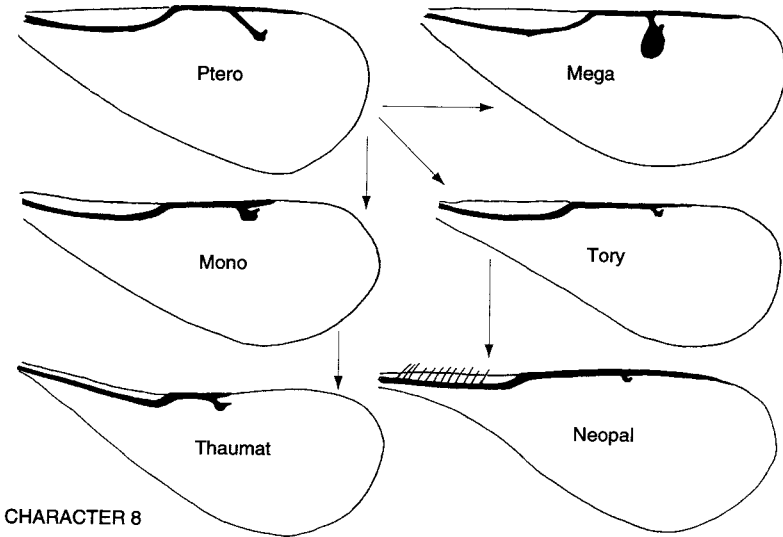


**Fig. 40.** Character 2 states. Anellus (diagrammatic). Left column, maximum hypothesized states (transformation series not used, see text for explanation). Right column, working hypothesis states (above) and their transformation series (below).

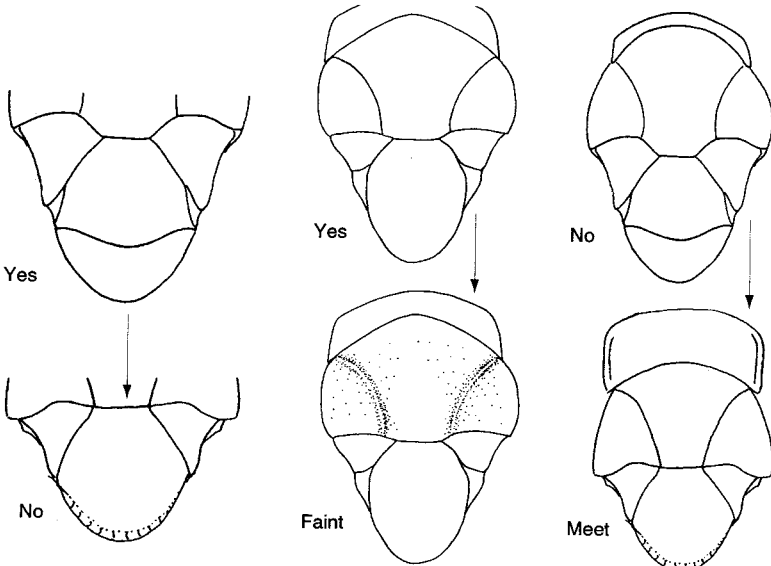




**Fig. 41.** Characters 2 (cont'd.), 3, 6 and their states. Character 2. Anellus (diagrammatic). Ending hypothesis (left) and their transformation series (right). Character 3, ending hypothesis. Antennal club, transformation series (semi-diagrammatic). Character 6, ending hypothesis. Clypeal apex, transformation series (semi-diagrammatic).



CHARACTER 8

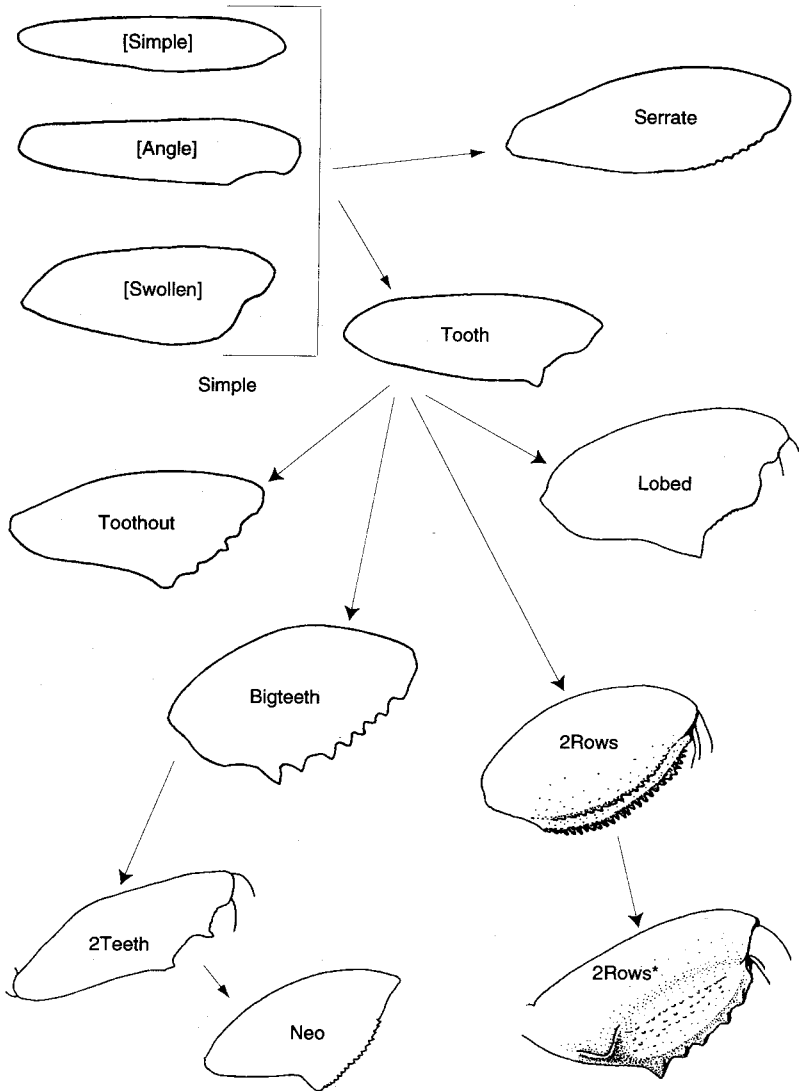


CHARACTER 15

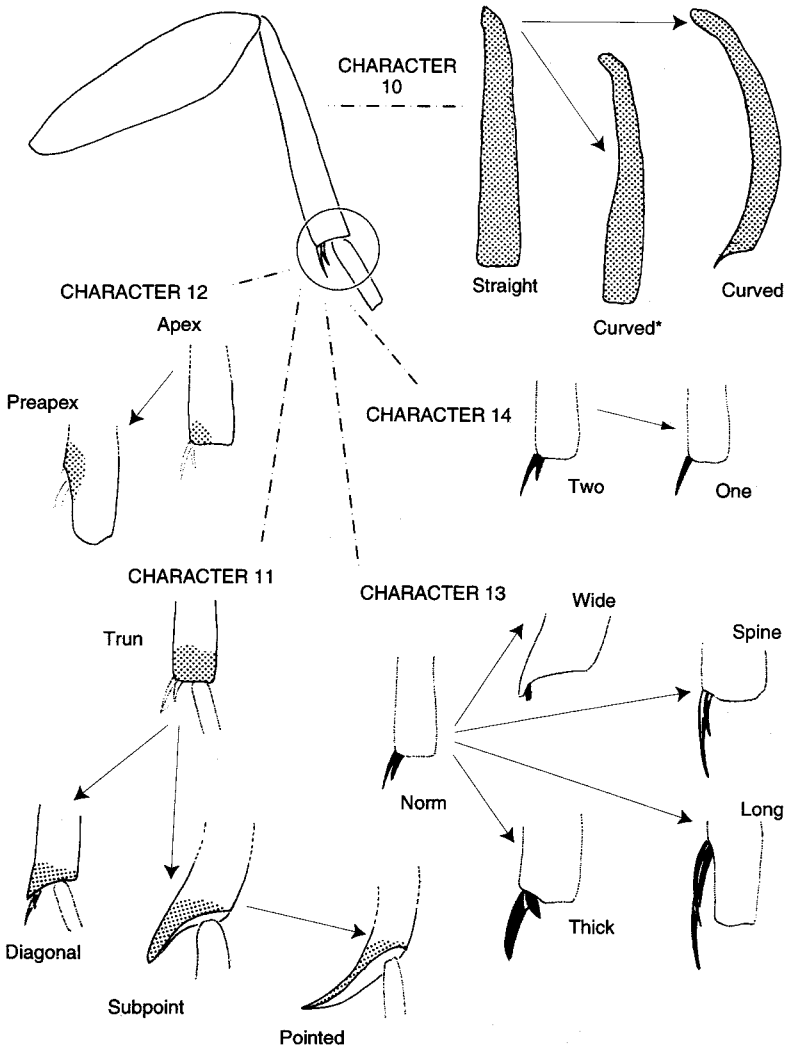
CHARACTER 16

CHARACTER 17

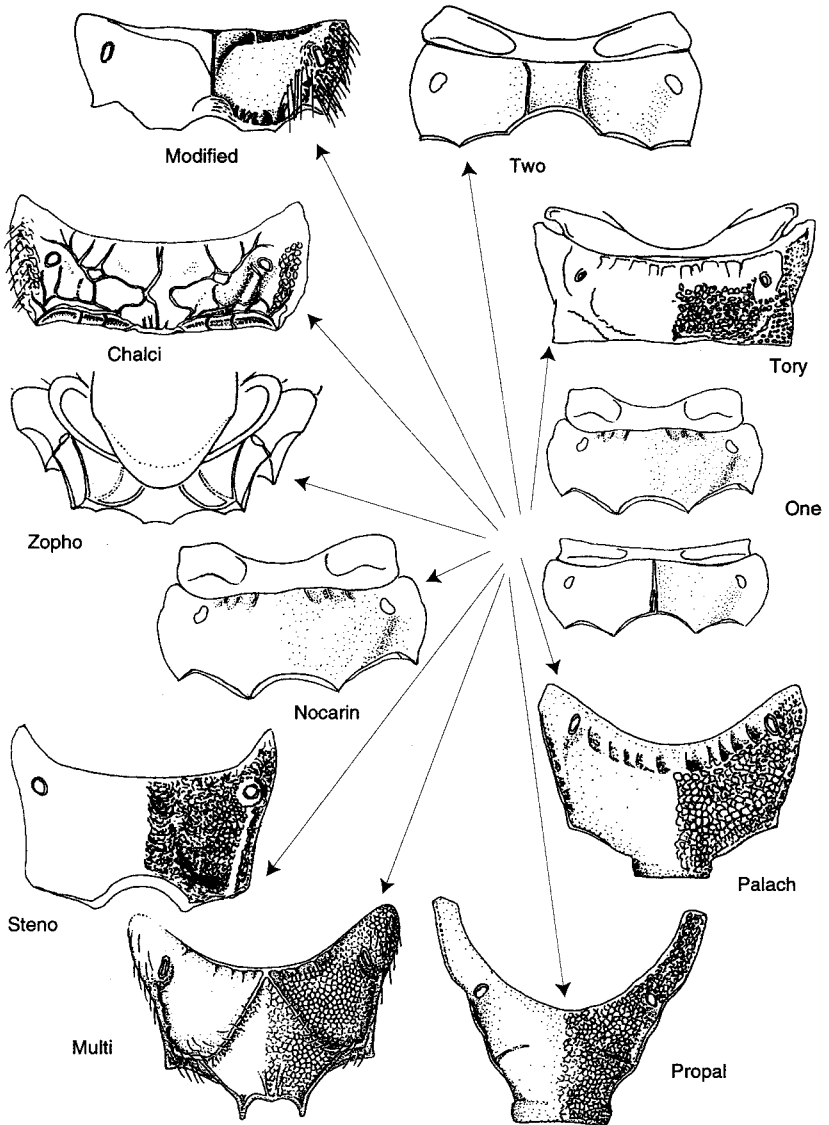
**Fig. 42.** Character 8, 15, 16, 17 states, ending hypothesis. Character 8. Forewing venation [Exemplars: Ptero — *Pteromalus*. Mega — *Megastigmus*. Mono — *Monodontomerus*. Tory — *Torymus*. Thaummat — *Thaumatomyus*. Neopal — *Neopalachia*]. Character 15. Frenal line (semi-diagrammatic). Character 16. Notaulus (semi-diagrammatic). Character 17. Relationship of notaulus to scutoscutellar suture (semi-diagrammatic).



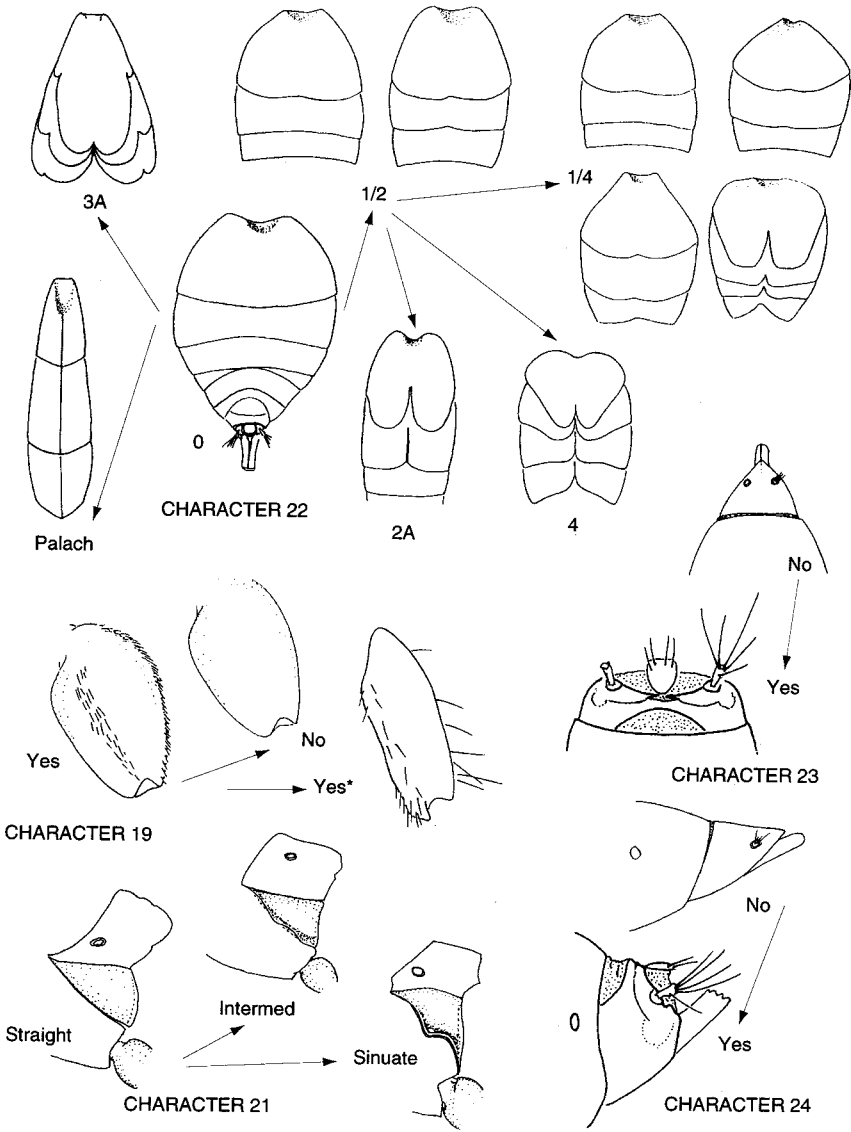
**Fig. 43.** Character 9 states, ending hypothesis. Hind femur, transformation series. [Exemplars: Simple, Angle — *Torymoides*. Swollen — *Adontomerus*. Serrate — *Ditropinotus*. Tooth — *Monodontomerus*. Toothout — *Exopristus*. Bigteeth — *Podagrion*. 2Teeth — *Palachia*. Neo — *Neopalachia*. Lobed — *Pradontomerus*. 2Rows — *Chryochalcissa*. 2Rows\* — *Rhynchotocida*.]



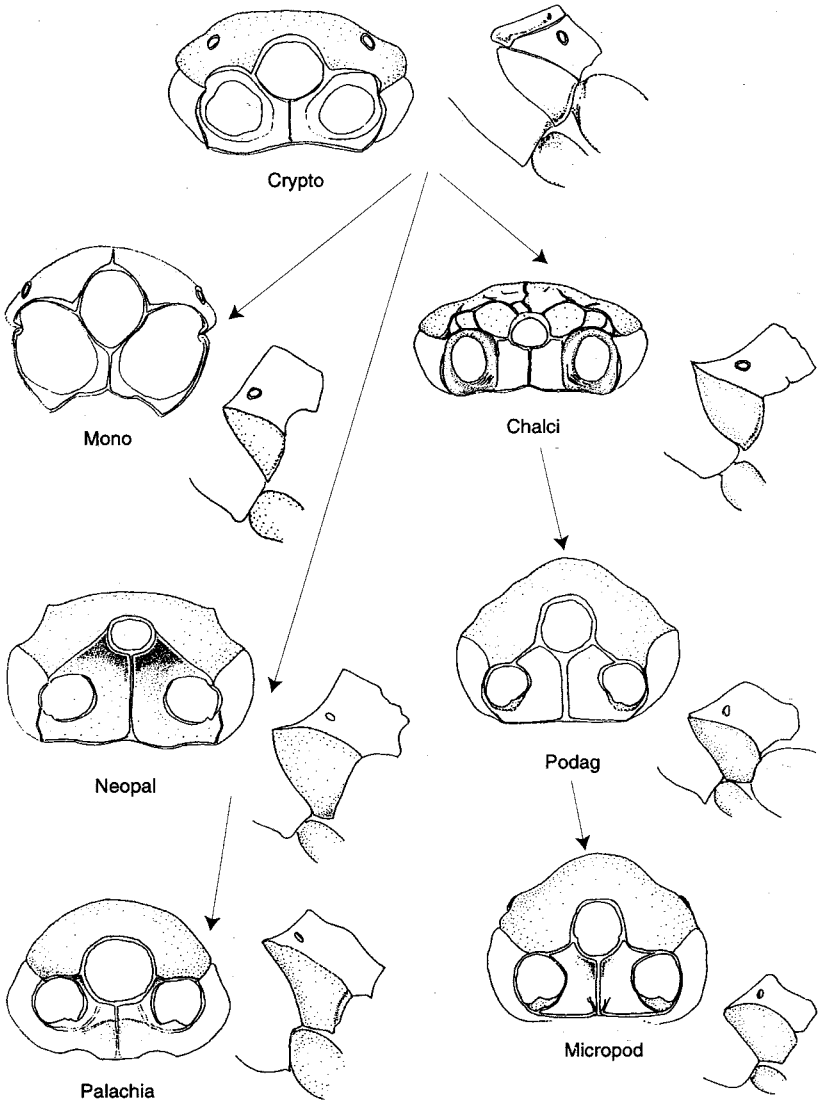
**Fig. 44.** Character 10, 11, 12, 13, 14 states, ending hypothesis. Hind tibia, transformation series [diagrammatic]. Character 10. Shape. Character 11. Apex. Character 12. Spur insertion. Character 13. Spur length. Character 14. Spur number.



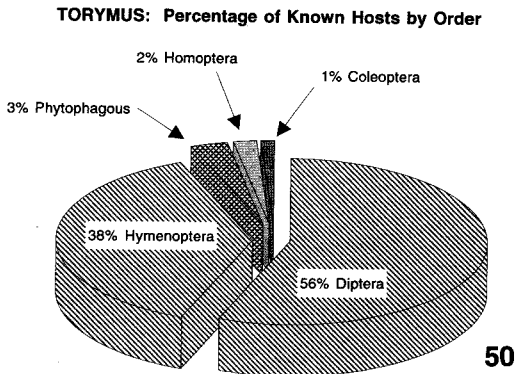
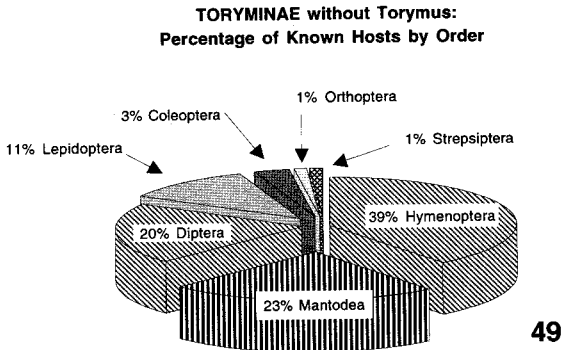
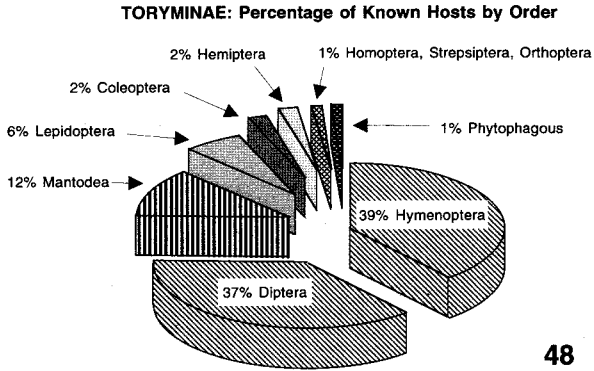
**Fig. 45.** Character 18 states, ending hypothesis. Propodeum, transformation series [Exemplars: One\* — *Microdontomerus*. Palach — *Palachia*. Propal — *Propalachia*. Multi — *Podagrion*. Steno — *Stenotorymus*. Zopho — *Zophodetus*. Chalci — *Chalcimerus*. Modified — *Monodontomerus*. Two — *Ditropinotus*. Tory — *Torymoidellus*].



**Fig. 46.** Character 19, 21, 22, 23, 24 states, ending hypothesis. Character 19. Hind-coxal setae, transformation series (semi-diagrammatic). Character 21. Metapleural margin (semi-diagrammatic). Character 22. Tergal emarginations states, transformation series (semi-diagrammatic). Character 23. Exserted cerci on metasomal tergum 8 (semi-diagrammatic). Character 24. Articulated metasomal tergum 9 (semi-diagrammatic).



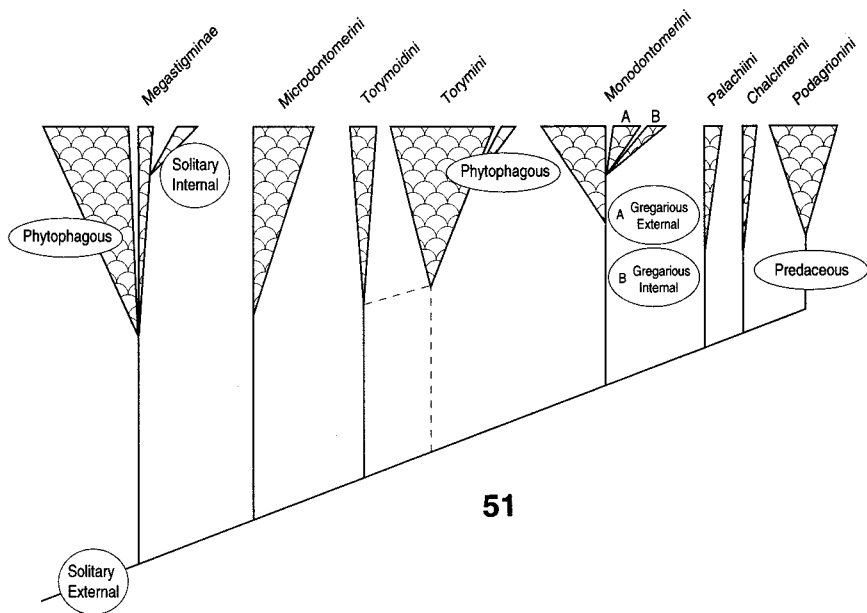
**Fig. 47.** Character 20 states, ending hypothesis. Metasternum, transformation series [Exemplars: Crypto — *Cryptopristus*. Mono — *Monodontomerus*. Neopal — *Neopalachia*. Palachia — *Palachia*. Chalci — *Chalcimerus*. Podag — *Podagrion*. Micropod — *Micropodagrion*].



**Figs. 48-50.** Diagrams of percentage of known hosts by order for Toryminae prepared from Table 3 (Appendix 5; see text, p. 58-60, for explanation). 48. Known world hosts of Toryminae including subsample of *Torymus*. 49. Known world hosts of Toryminae excluding *Torymus* (total not equal to 100%, fractional percentages ignored). 50. Subsample of hosts of *Torymus*.

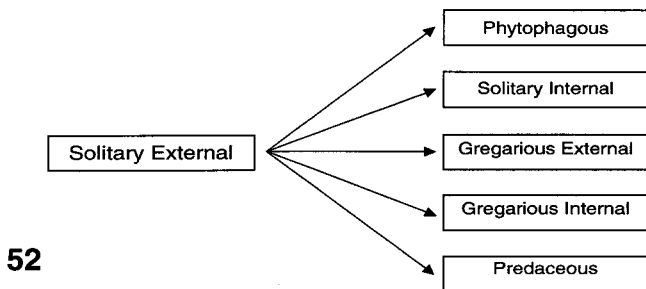


BIOLOGICAL FEEDING TYPES COMPARED TO TORYMID PHYLOGENY



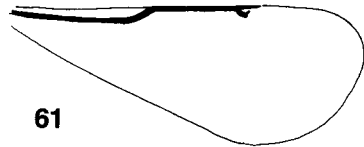
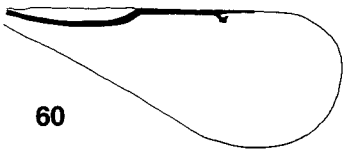
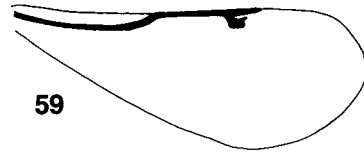
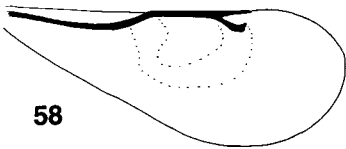
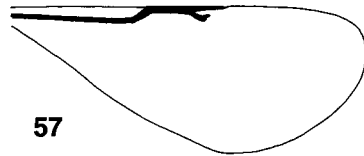
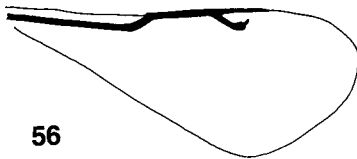
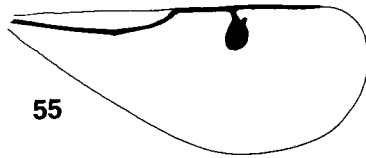
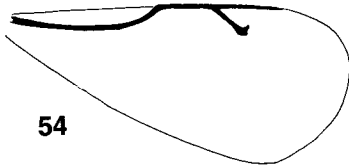
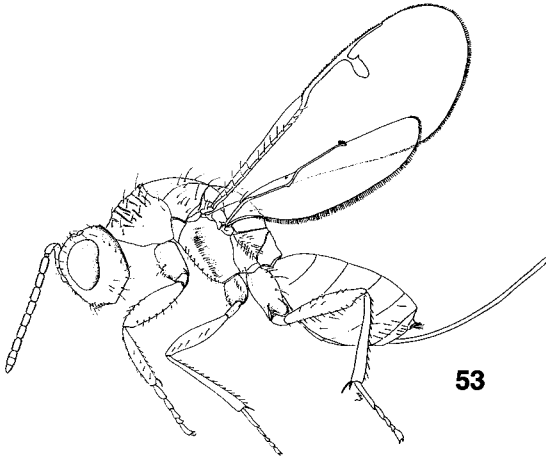
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TRANSFORMATION SERIES OF BIOLOGICAL FEEDING TYPES

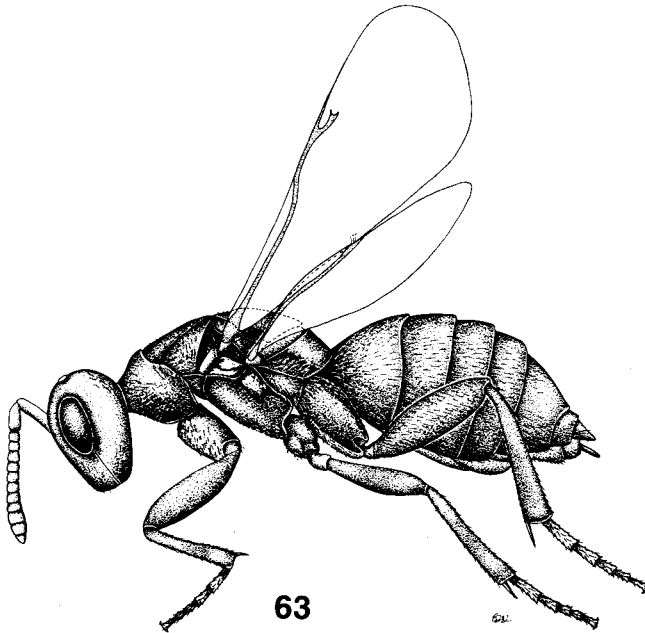
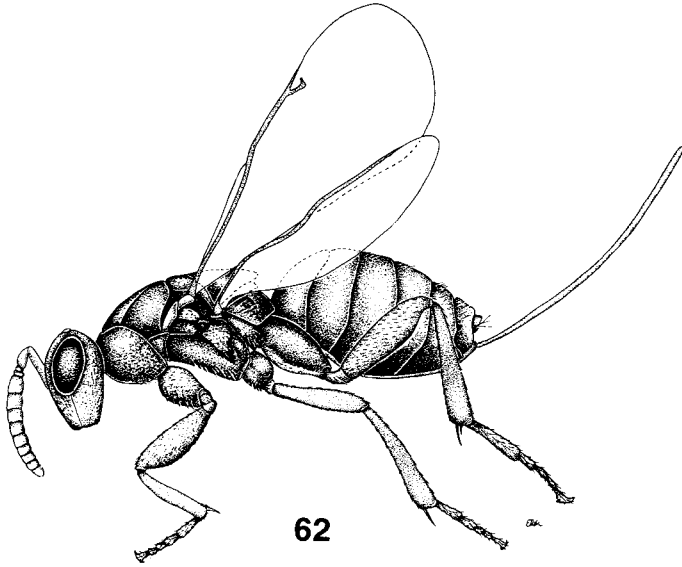


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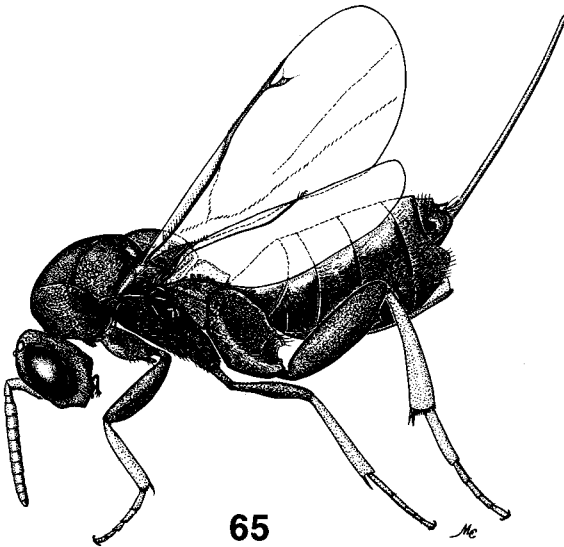
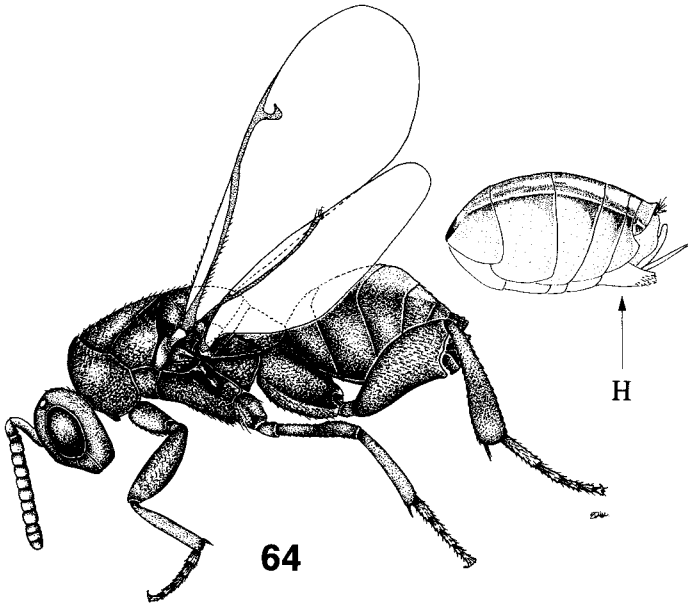
**Figs. 51-52.** Larval feeding types. 51. Feeding types placed as cladogram characters on simplified ending-hypothesis tree Fig. 38 (see text for discussion). 52. Transformation series of feeding types derived from Fig. 51 (see text for discussion).



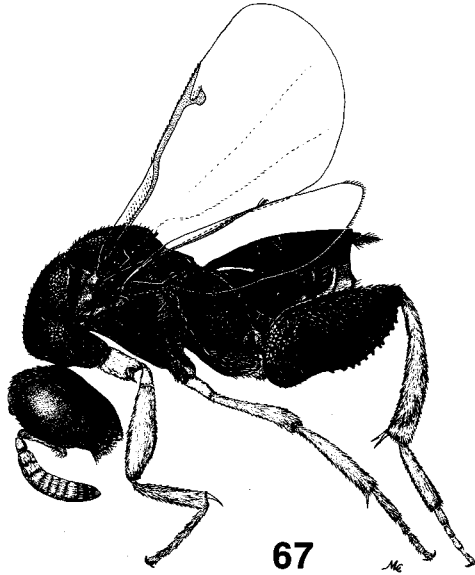
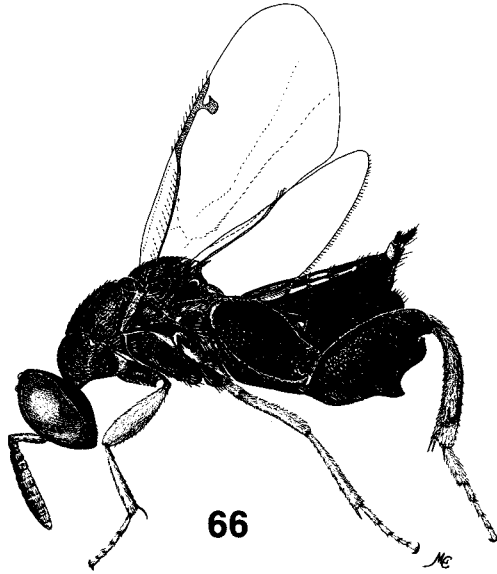
**Figs. 53-61.** Torymidae, Pteromalidae. 53. *Megastigmus floridana*, female (habitus). 54-61. Forewing, dorsal. 54. *Pteromalus puparum*. 55. *Megastigmus bipunctatus*. 56. *Glyphomerus stigma*. 57. *Adontomerus gregalis*. 58. *Idiomacromerus bimaculipennis*. 59. *Monodontomerus aeneus*. 60. *Torymus bedeguaris*. 61. *Podagrion splendens*.



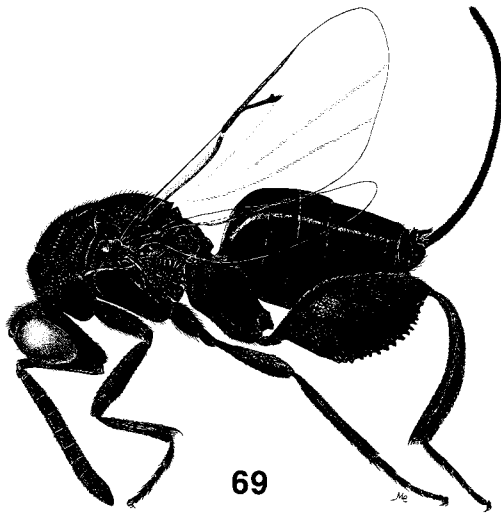
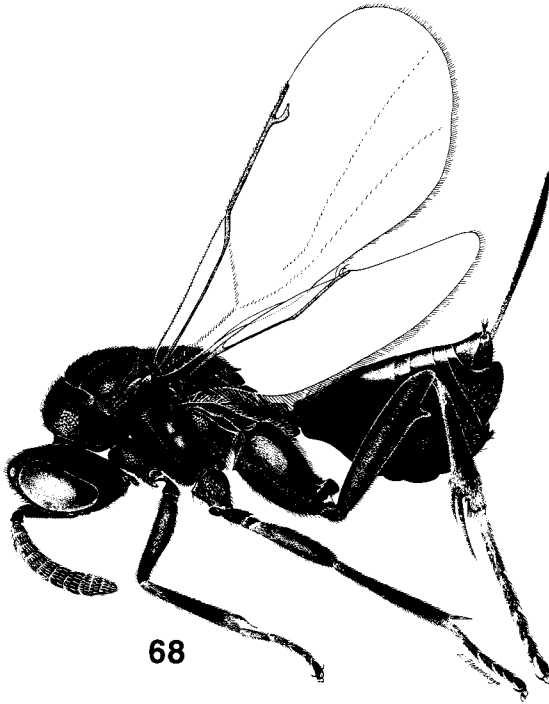
Figs. 62-63. Torymoidini, Microdontomerini, habitus. 62. *Torymoides* sp. (female). 63. *Erimerus wickhami* (male).



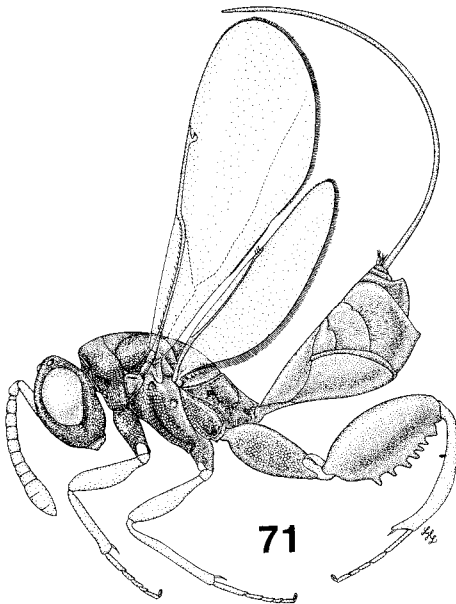
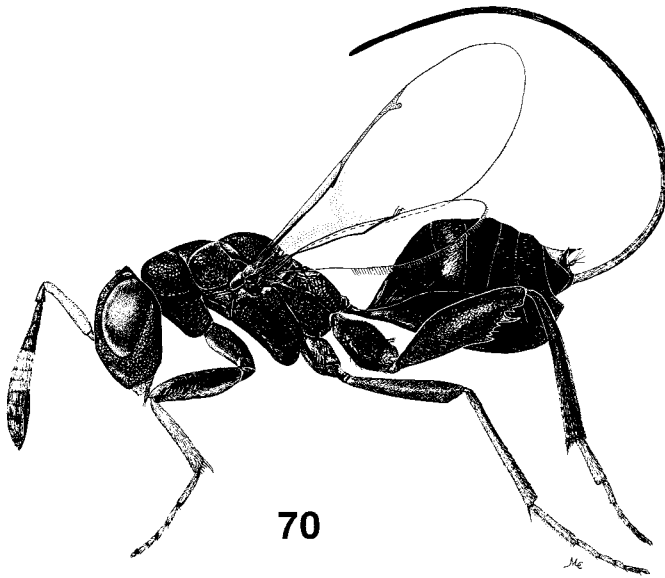
Figs. 64-65. Monodontomerini, habitus (female). 64. *Zdenekius smithi* (inset: metasoma; H: hypopygium). 65. *Monodontomerus aeneus*.



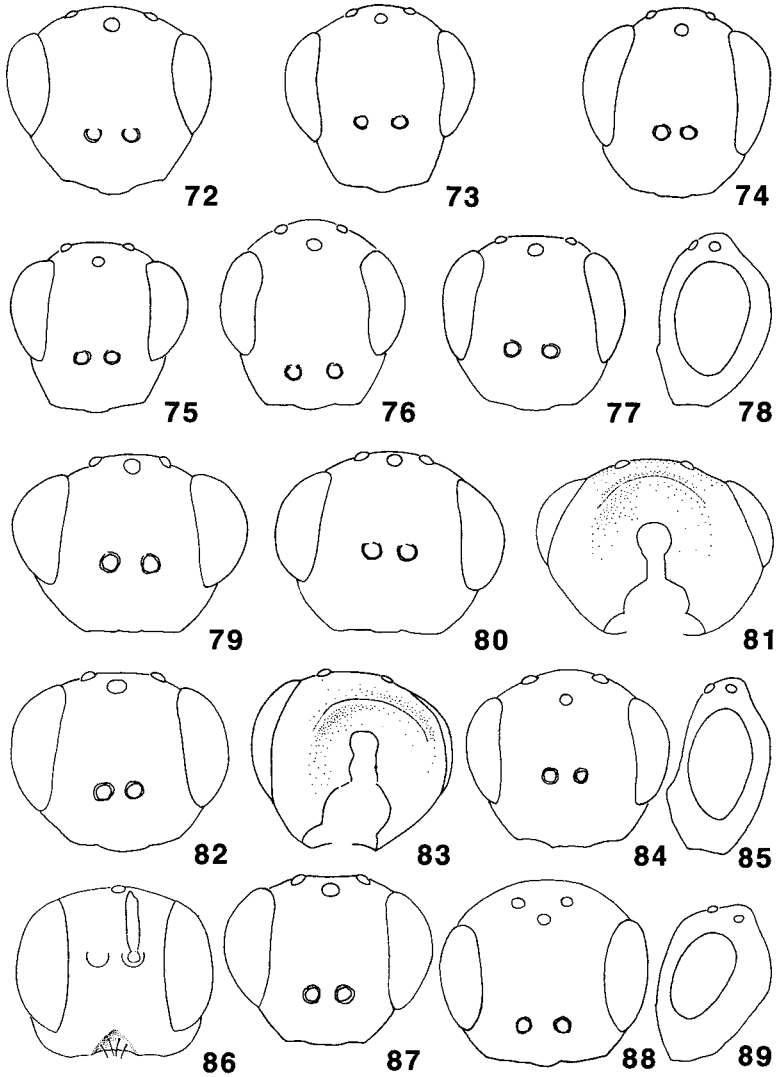
**Figs. 66-67.** Monodontomerini, habitus (female). 66. *Pradontomerus hyper*. 67. *Oopristus turkestanicus*.



**Figs. 68-69.** Monodontomerini, Chalcimerini, habitus (female). 68. *Perissocentrus striatulus*.  
69. *Chalcimerus borceai*.

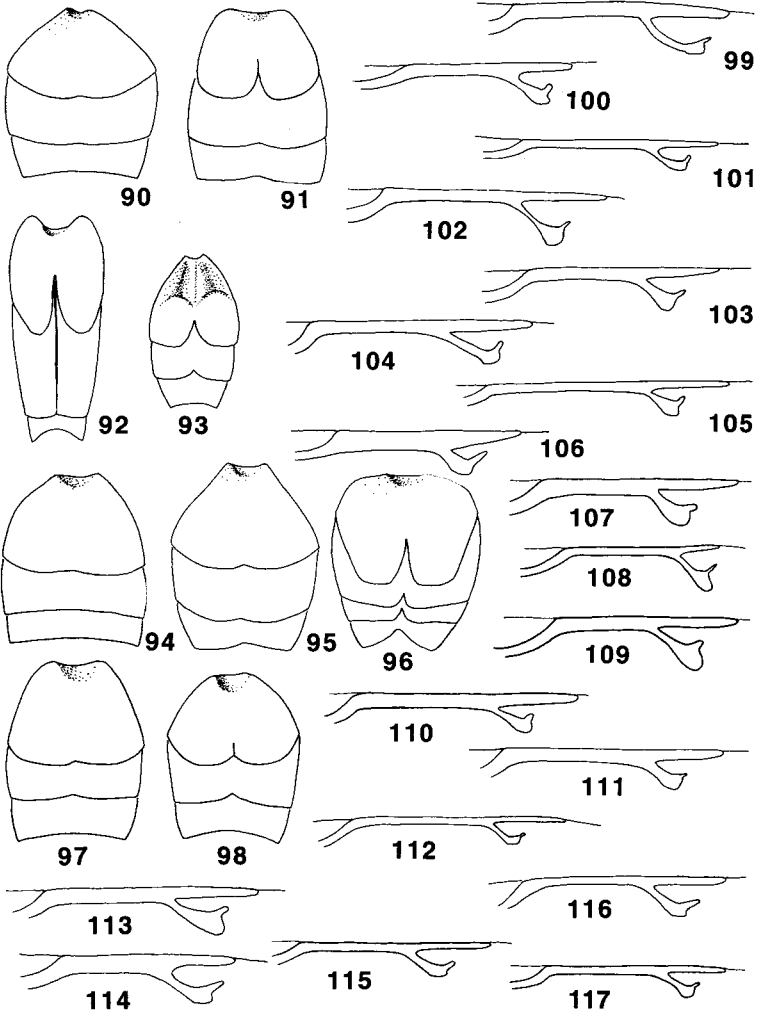


**Figs. 70-71.** Palachiini, Podagrionini, habitus (female). 70. *Palachia caudata*. 71. *Podagrion mantis*.

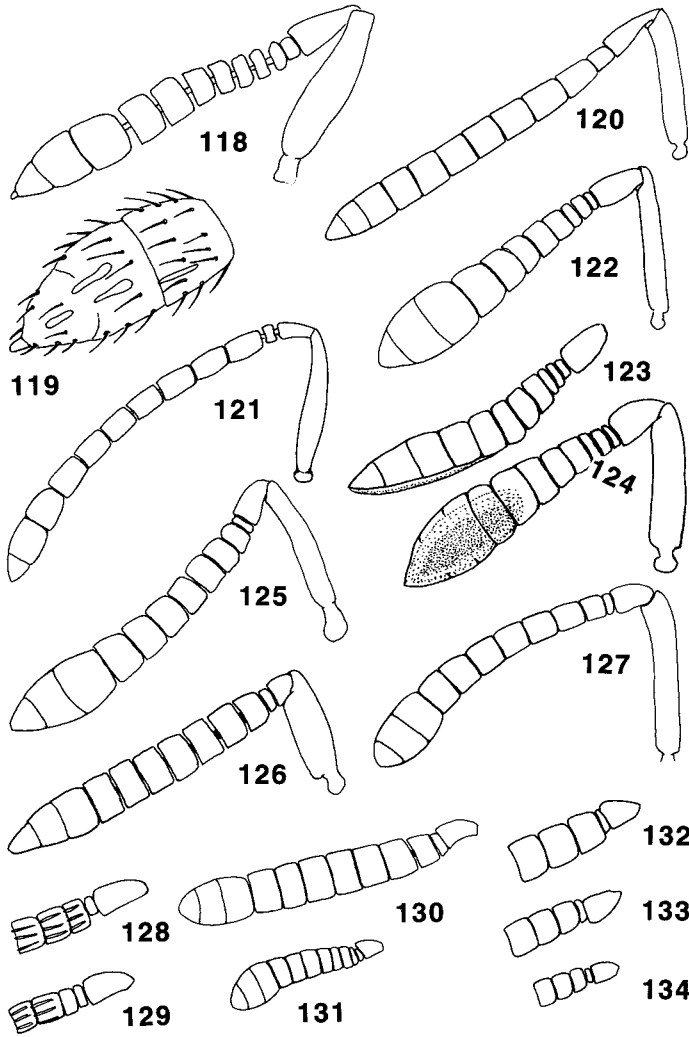


**Figs. 72-89.** Microdontomerini (female, paratype unless otherwise noted). Heads, anterior view except 78, 85, 89 side view; 81, 83 posterior view. 72. *Idiomacromerus arcus*. 73. *I. nitens*, type-species of *Conolochites*. 74. *I. papaveris* (cotype), type-species of *Lochites*. 75. *I. mayri* (non-type, France). 76. *I. balasi* (holotype), type-species of *Lochimerus*. 77-78. *I. perplexus*, type-species of *Liodontomerus*. 79. *I. regillus* (after Steffan 1962b), type-species of *Liotorymus*. 80-81. *I. bimaiculipennis*, type-species of *Idiomacromerus*. 82-83. *Adontomerus eriogasteris*. 84-85. *Idiomacromerus bimaiculipennis*, male. 86. *Zophodetus woodruffi* (holotype). 87. *Microdontomerus anthonomi*. 88-89. *Pseuderimerus mayetiolaie*, male.

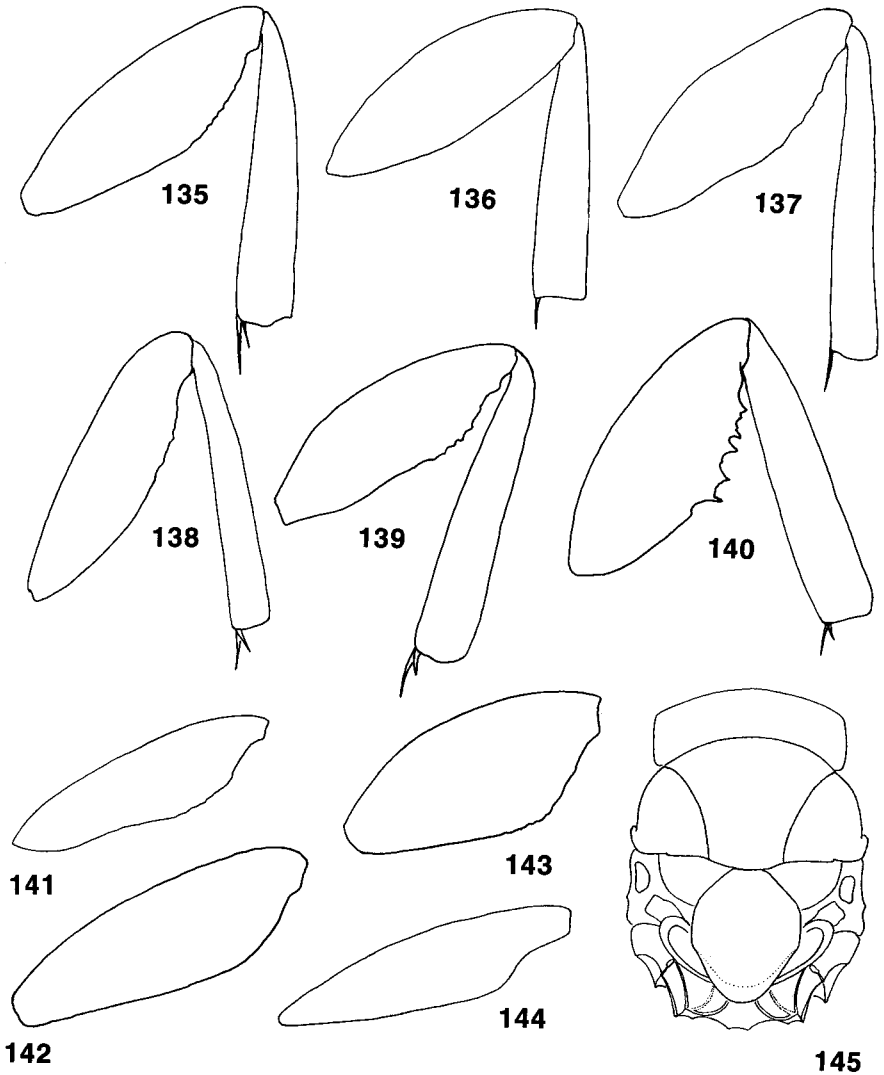




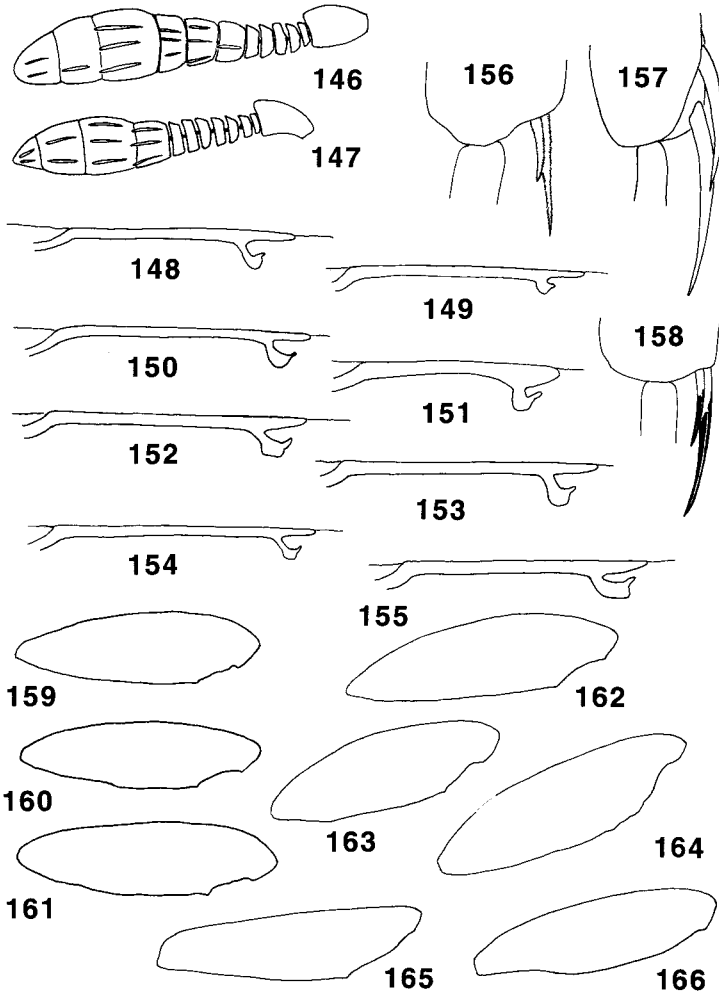
**Figs. 90-117.** Microdontomerini (female, except 93, male; compared to holotype or lectotype except as noted), 90-98. Metaterga 2 through 4 or 5, dorsal view. 99-117. Forewing venation, dorsal view. 90. *Adontomerus gregalis* (compared with paratype). 91. *A. crassipes*. 92. *Idarnotorymus pulcher*. 93. Same, male (Italy). 94. *Microdontomerus anthonomi* (paratype). 95. *M. bicoloripes* (paratype). 96. *M. annulata*. 97. *Idiomacromerus bimaculipennis*. 98. *I. papaveris* (cotype). 99. *I. bimaculipennis*. 100. *I. balasi* (holotype). 101. *I. splendidus* (Hungary). 102. *I. arcus* (paratype). 103. *I. perplexus* (paratype). 104. *I. papaveris* (cotype). 105. *I. regillus* (after Steffan 1962b). 106. *Adontomerus eriogasteris* (paratype). 107. *A. gregalis* (compared with paratype). 108. *A. impositus* (paratype). 109. *A. crassipes*. 110. *Microdontomerus anthonomi* (paratype). 111. *M. annulata*. 112. *Zophodetus woodruffi* (holotype). 113. *Erimerus wickhami*. 114. *Pseuderimerus mayetiola* (paratype). 115. *Ditropintous aureoviridis*. 116. *Eridontomerus isosomatis*. 117. *Idarnotorymus pulcher*.



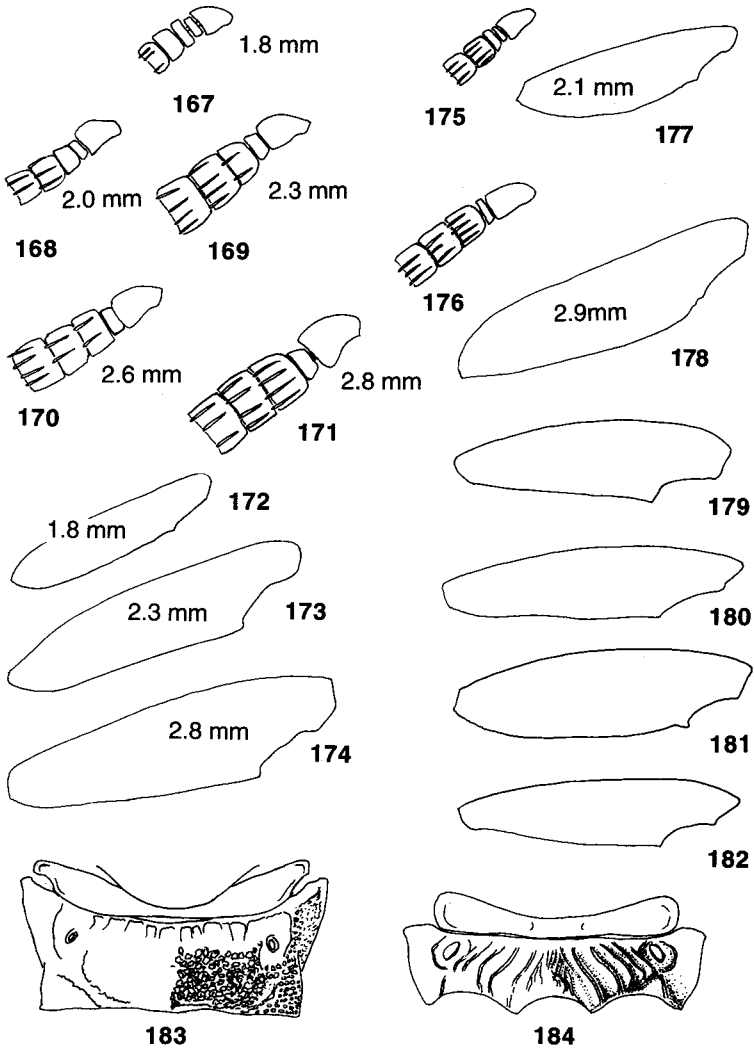
**Figs. 118-134.** Microdontomerini (female, from paratype unless otherwise noted). Antenna, side view (except 124, dorsal; 125, three-quarter ventral). 118-119. *Pseuderimerus mayetiolae* (paratype) (119, enlargement of club). 120. *Eriemerus wickhami* (compared with lectotype). 121. *Zophodetus woodruffi* (holotype). 122. *Eridontomerus isosomatis* (compared with lectotype). 123-124. *E. isosomatis*, male. 125. *Ditropintous aureoviridis* (compared with lectotype). 126. *D. aureoviridis*, male. 127. *Adontomerus eriogasteris* (paratype). 128-129. *A. impolitus*, right (128) and left (129) basal segments of same specimen (paratype). 130-131. *Microdontomerus anthonomi* (compared to holotype): 130, 3 mm specimen; 131, 1.5 mm (drawn to same scale). 132-134. *M. annulata* (compared with lectotype): 132, 4 mm specimen; 133, 3 mm; 134, 2.3 mm (all drawn to same scale).



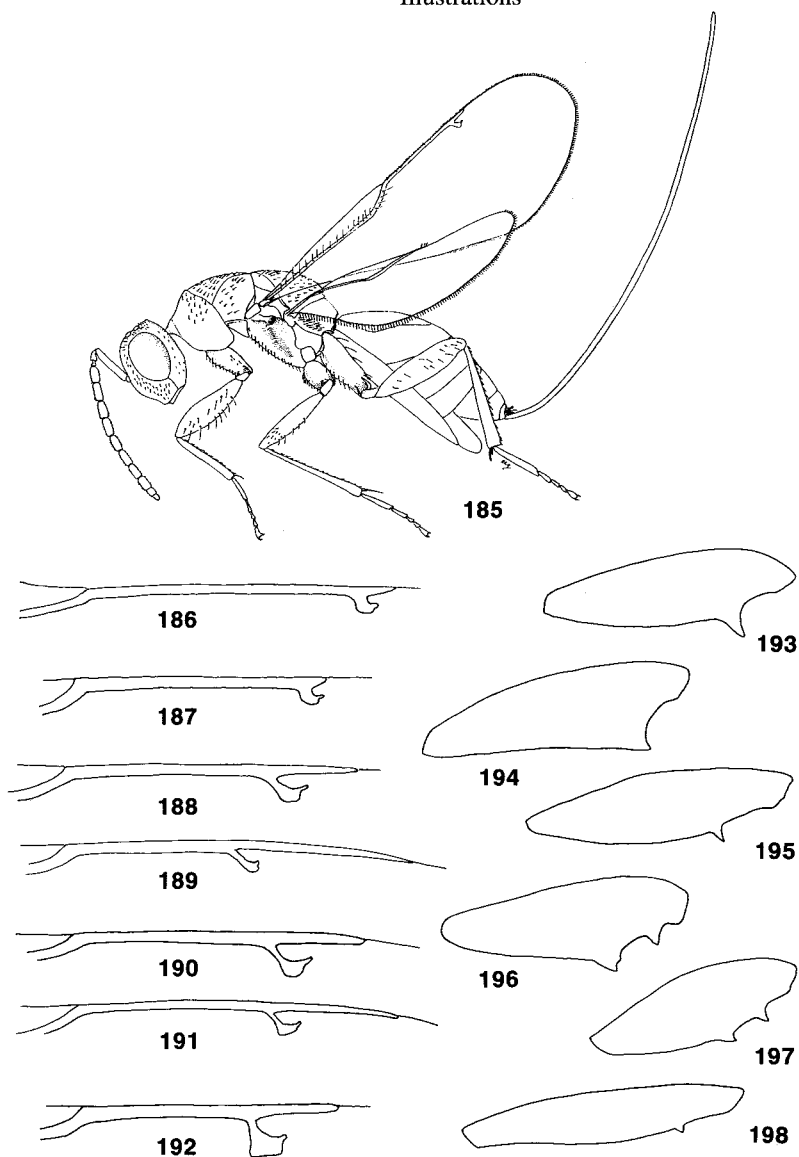
**Figs. 135-145.** Microdontomerini (female, from paratype unless otherwise noted). 135-140. Hind femur and tibia, lateral. 141-144. Hind femur, lateral. 145. Metasoma, dorsal. 135. *Microdontomerus anthonomi*. 136. *Pseuderimerus mayetiolae*. 137. *Erimerus wickhami* (compared with lectotype). 138. *Idiomacromerus bimaculipennis* (compared with holotype). 139. *Eridontomerus isosomatis* (compared with lectotype). 140. *Idarnotorymus pulcher* (compared with holotype). 141. *Adontomerus gregalis* (compared with paratype). 142. *A. impolitus* (paratype). 143. *A. crassipes* (compared with holotype). 144-145. *Zophodetus woodruffi* (holotype).



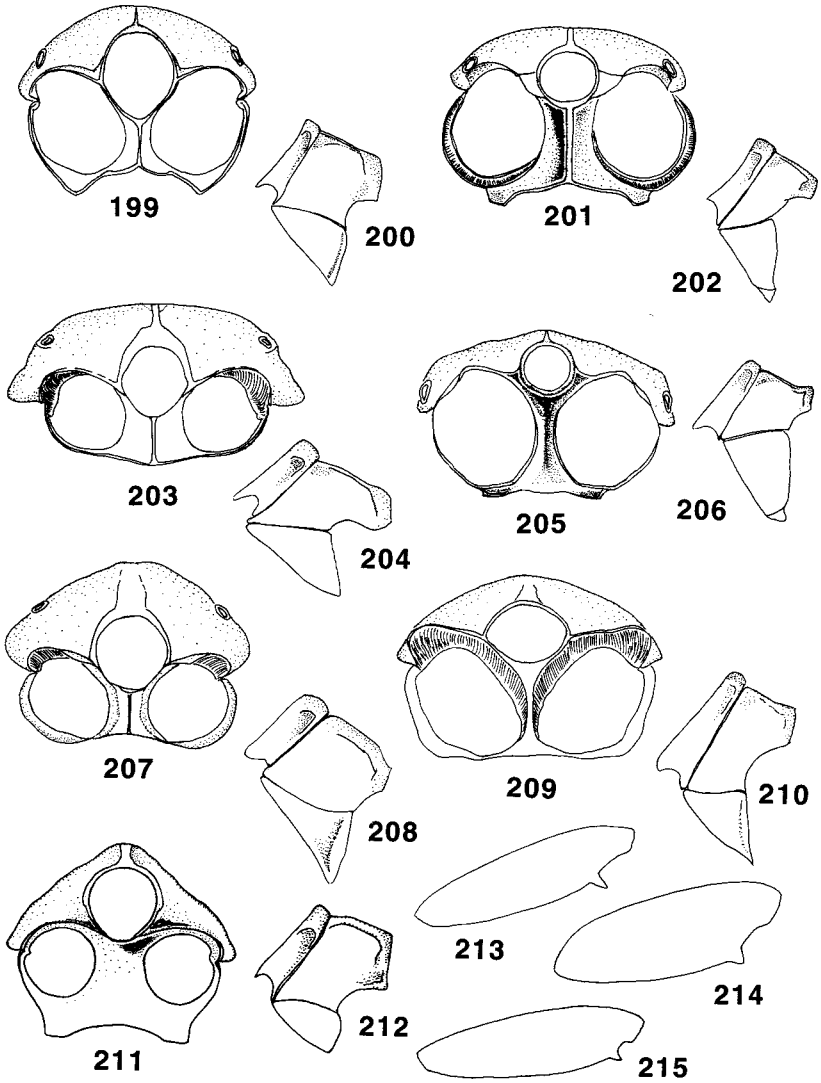
**Figs. 146-166.** Torymoidini (female, specimens compared with types unless noted). 146-147. Antenna without scape, lateral view. 148-155. Right forewing venation, dorsal view. 156-158. Hind tibial apex, spurs, and base of basitarsus, lateral view. 159-166. Left hind femur, lateral view. 146-147. *Torymoides* sp. (Arizona). 148. *Torymoidellus reticulatus* (paratype). 149. *Platykula albihirta*. 150. *Aloomba calcaris* (holotype). 151. *Torymoides latus* (holotype, type of *Pondorymus*). 152. *Pseudotorymus militaris* (not compared with type, Egypt). 153. *Pseudotorymus leguminosae*. 154. *Torymoides amabilis*. 155. *Torymoides violaceus*. 156. *Pseudotorymus leguminosae*. 157. *Aloomba calcaris* (holotype). 158. *Platykula albihirta*. 159-161. *Torymoides amabilis*, variation in hind femur (India). 162-166. *Torymoides* spp. (femur for type-species of genus [in brackets] synonymized with *Torymoides*). 162. *T.* [*Macrodontomerus*] *unimaculatus* (holotype). 163. *T.* [*Dimeromicrus*] *ashmeadi* (paratype). 164. *T.* [*Pondorymus*] *latus* (holotype). 165. *T.* [*Didactyliocerus*] *dispar*. 166. *T.* [*Ameromicrus*] *violaceus*.



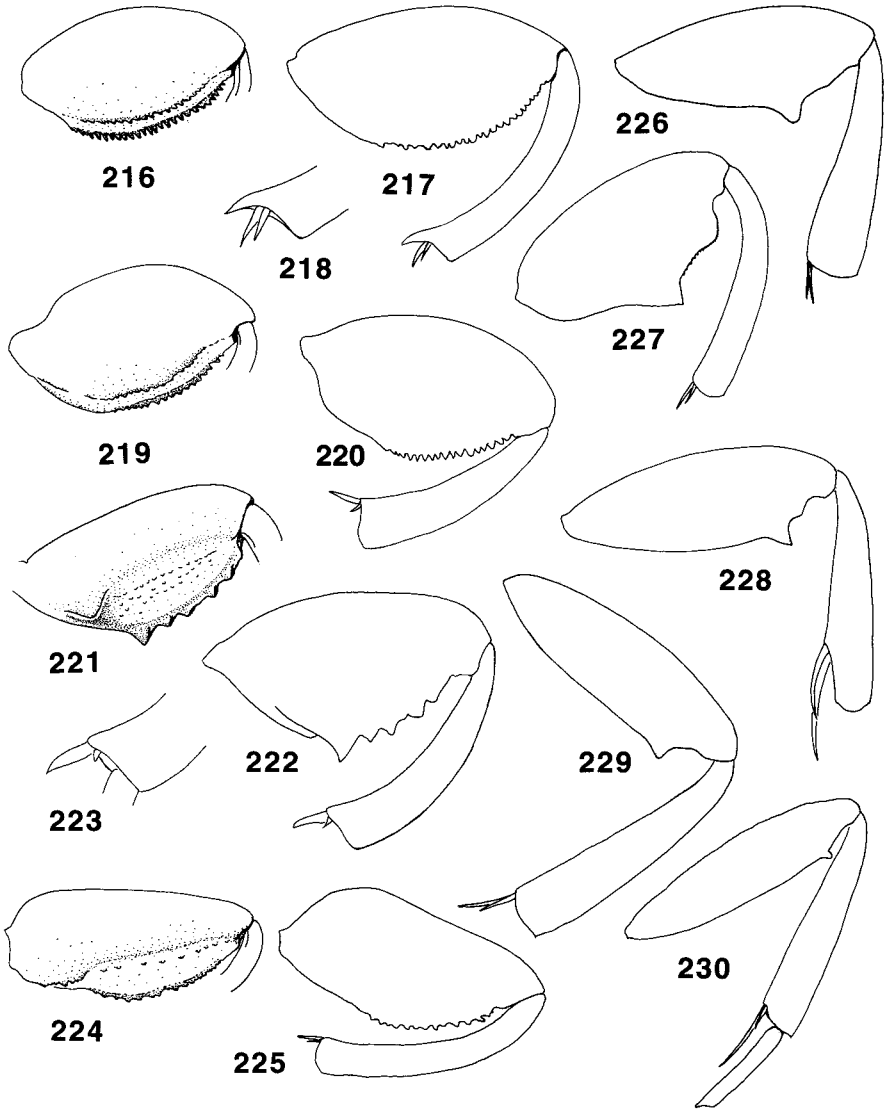
**Figs. 167-184.** Torymoidini (female, compared with type unless otherwise noted). 167-171, 175-176. Pedicel and first four flagellomeres of antenna, lateral view. 172-174, 177-182. Left hind femur, lateral view. 183-184. Propodeum, dorsal view. 167-174. *Pseudotorymus* sp., variation in size of flagellomeres and shape of hind femur relative to wasp size (in mm) (167, 169, 171 from single population with 172, 173, 174 respective hind femur of same specimen; 168, 170 single population found less than 5 miles away). 175-178. *Pseudotorymus leguminosae*, same (single population, Oman). 179. *Pseudotorymus papaveris* (not compared with type, Spain). 180. *Pseudotorymus lazulellus* (paratype). 181. *Pseudotorymus sapphyrinus* (not compared with type, Czechoslovakia). 182. *Pseudotorymus militaris* (not compared with type, Egypt). 183. *Torymoidellus reticulatus* (from paratype, modified from Bouček 1988). 184. *Aloomba calcaris* (holotype).



**Figs. 185-198.** Torymini (female, from paratype unless otherwise noted by locality). 185. *Torymus rugglesi*, habitus. 186-192. Forewing venation, dorsal. 193-198. Hind femur, lateral. 186. *Physothorax bidentulus*. 187. *Torymus warreni* (Ohio). 188. *T. bedeguaris* (Hungary). 189. *Ecdamua indica* (India). 190. *Diomorus aiolomorphi*. 191. *D. armatus* (France). 192. *D. zabriskiei* (California). 193. *D. armatus* (France). 194. *D. zabriskiei* (California). 195. *D. aiolomorphi*. 196. *Physothorax bidentulus*. 197. *P. russelli*. 198. *Ecdamua indica* (India).

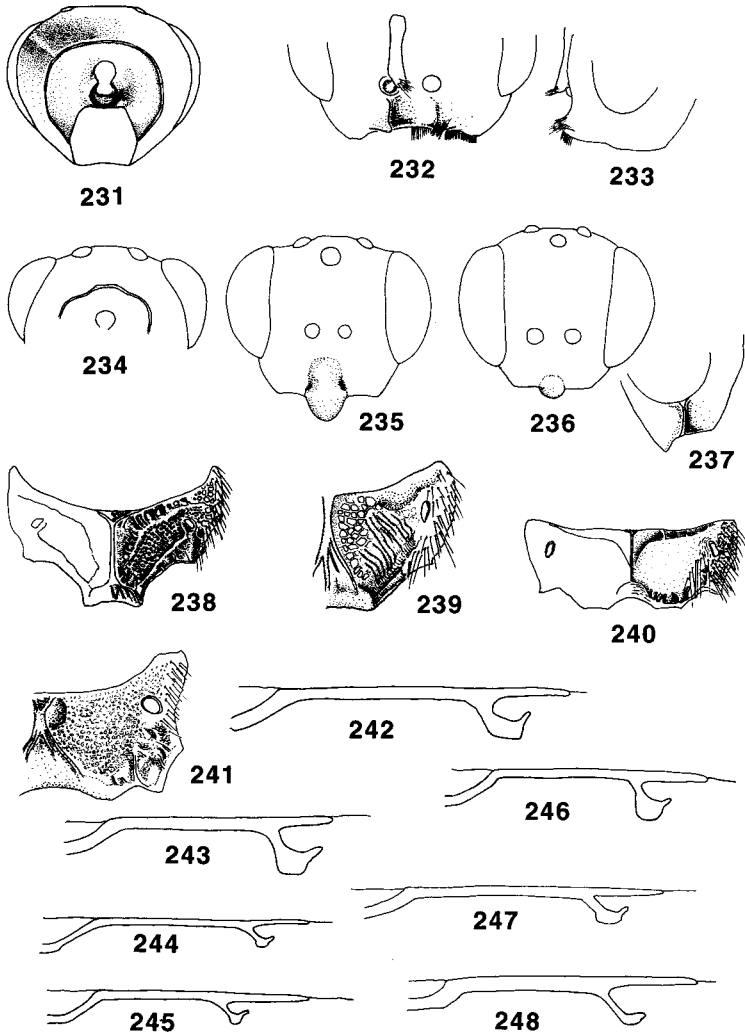


**Figs. 199-215.** Monodontomerini (female, from specimens compared with types unless otherwise noted). 199-210. Metasternum (odd numbers, ventral view), propodeum and metapleuron (even numbers, side view). 213-215. Left hind femur, lateral view. 199-200. *Monodontomerus aeneus*. 201-202. *Rhynchoticida* sp. (Philippines). 203-204. *Zdenekius smithi*. 205-206. *Anneckidea watshami*. 207-208. *Rhynchodontomerus inclusus* (Argentina, not compared with type). 209-210. *Oopristus turkestanicus* (Pakistan, not compared with type). 211-212. *Perissocentrus tumidulus*. 213. *Monodontomerus viridis*. 214. *Monodontomerus aeneus*. 215. *Monodontomerus dentipes*.

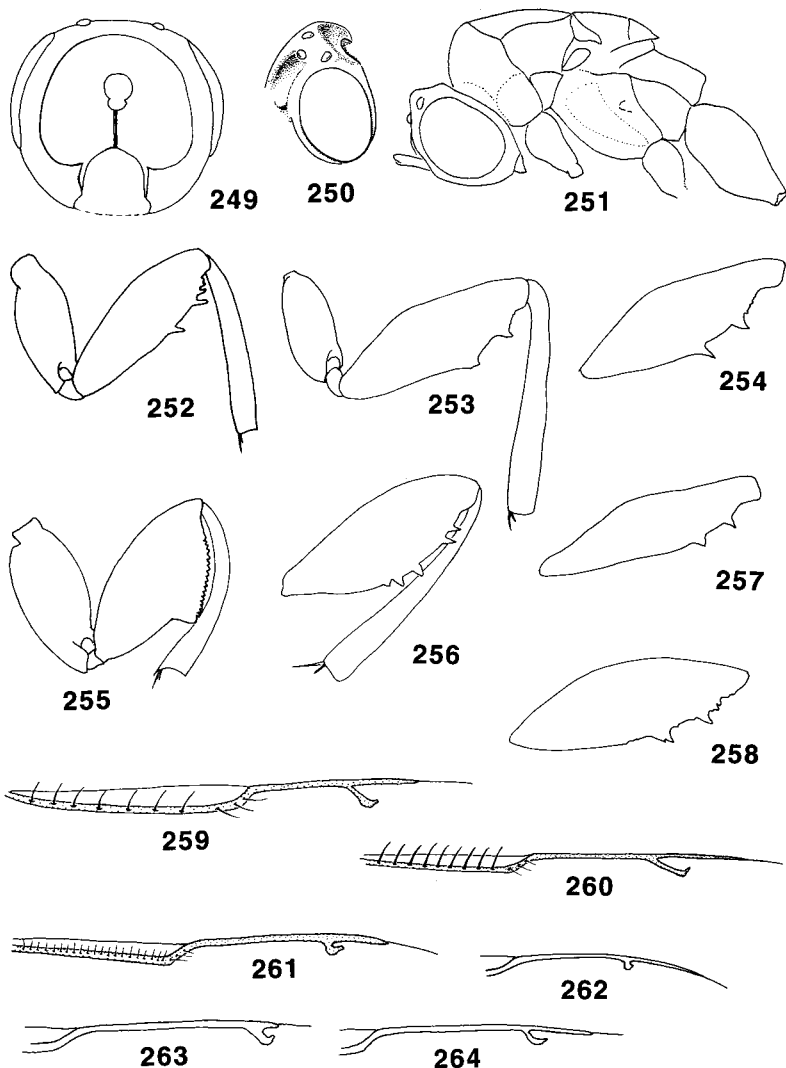


**Figs. 216-230.** Monodontomerini, hind femora, lateral except as noted (female, from specimens compared with types unless otherwise noted). 216-218. *Chrysochalcissa olivacea*, three-quarter view (216), enlarged apex of tibia (218). 219-220. *Anneckidea watshami* (paratype), three-quarter view (219). 221-223. *Rhynchotocida* sp. (Philippines), three-quarter view (221), enlarged apex of tibia (223). 224-225. *Oopristus safavii*, three-quarter view (224). 226. *Zdenekius smithi*. 227. *Pradontomerus hyper*. 228. *Perissocentrus argentinae*. 229. *Amoturoides breviscapus*. 230. *Monodontomerus strobili*.

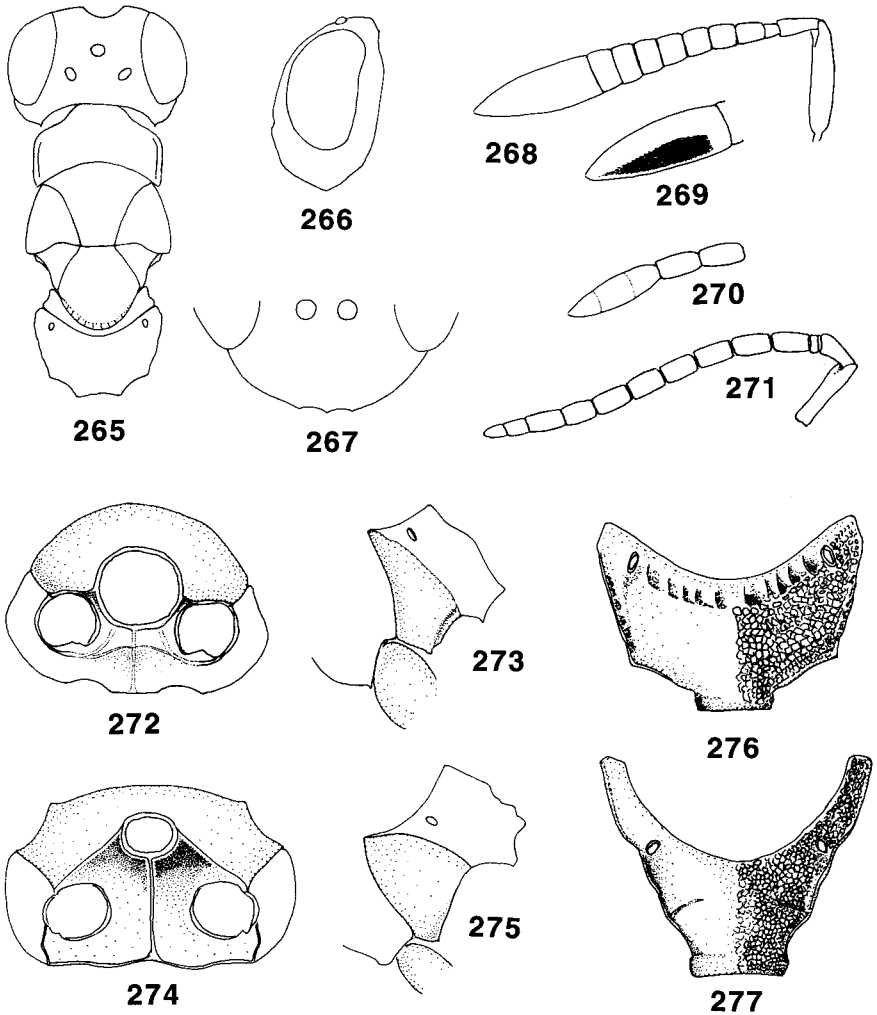




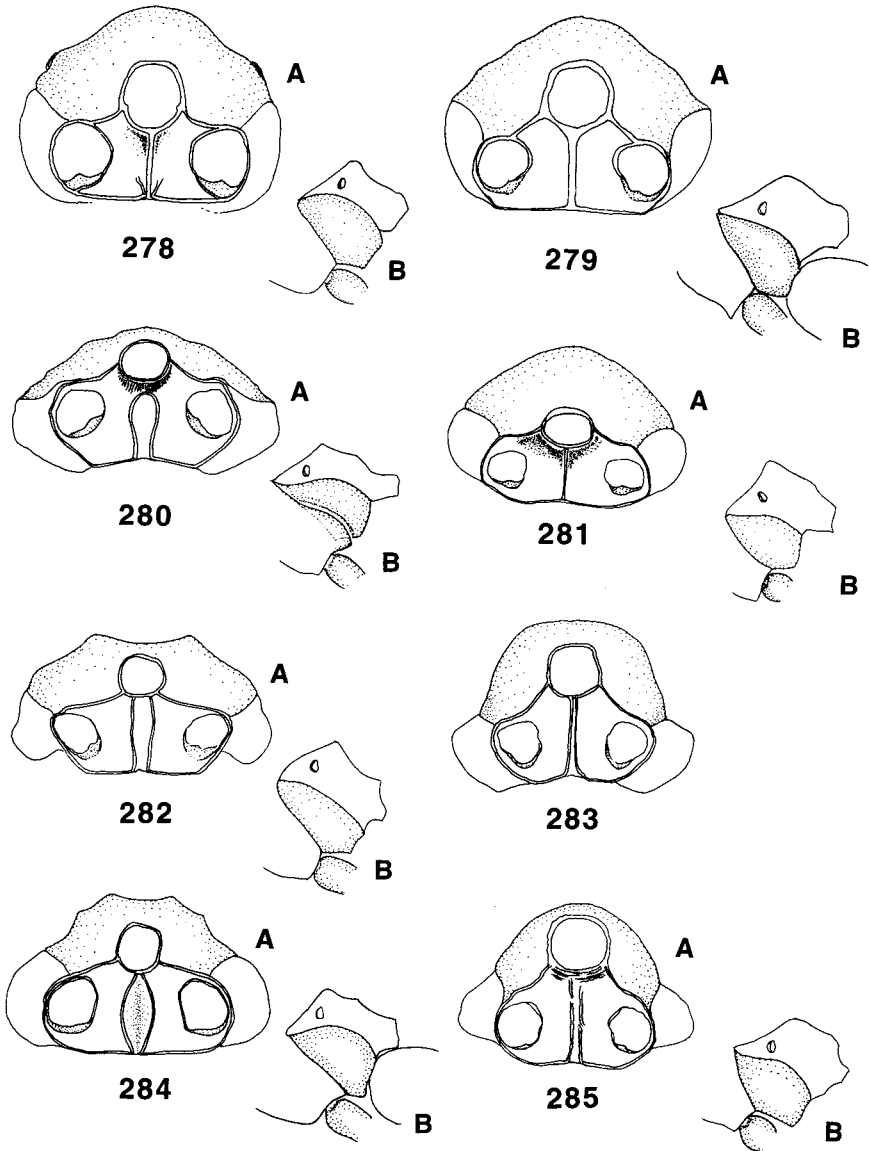
**Figs. 231-248.** *Monodontomerini* (female, from specimens compared with types unless otherwise noted by locality). 231-237. Head. 238-241. Propodeum. 242-248. Forewing veins, dorsal view (excluding submarginal). 231. *Perissocentrus argentinae* (posterior view). 232-233. *Oopristus turkestanicus* (ventral half: 232, anterior view; 233, lateral view) (Pakistan). 234-235. *Rhynchodontomerus inclusus* (234, posterior, dorsal half; 235 anterior) (Argentina). 236-237. *Rhyncoticida* sp. (236, anterior; 237, lateral, ventral half) (Philippines). 238. *Zdenekius smithi*. 239. *Perissocentrus caridei*. 240. *Monodontomerus aeneus*. 241. *Rhynchodontomerus inclusus* (Argentina). 242. *Monodontomerus aeneus*. 243. *Zdenekius smithi*. 244. *Chrysochalcisssa olivacea* (male). 245. *Rhyncoticida* sp. (Philippines). 246. *Pradontomerus hyper*. 247. *Perissocentrus chilensis*. 248. *Rhynchodontomerus inclusus* (Argentina).



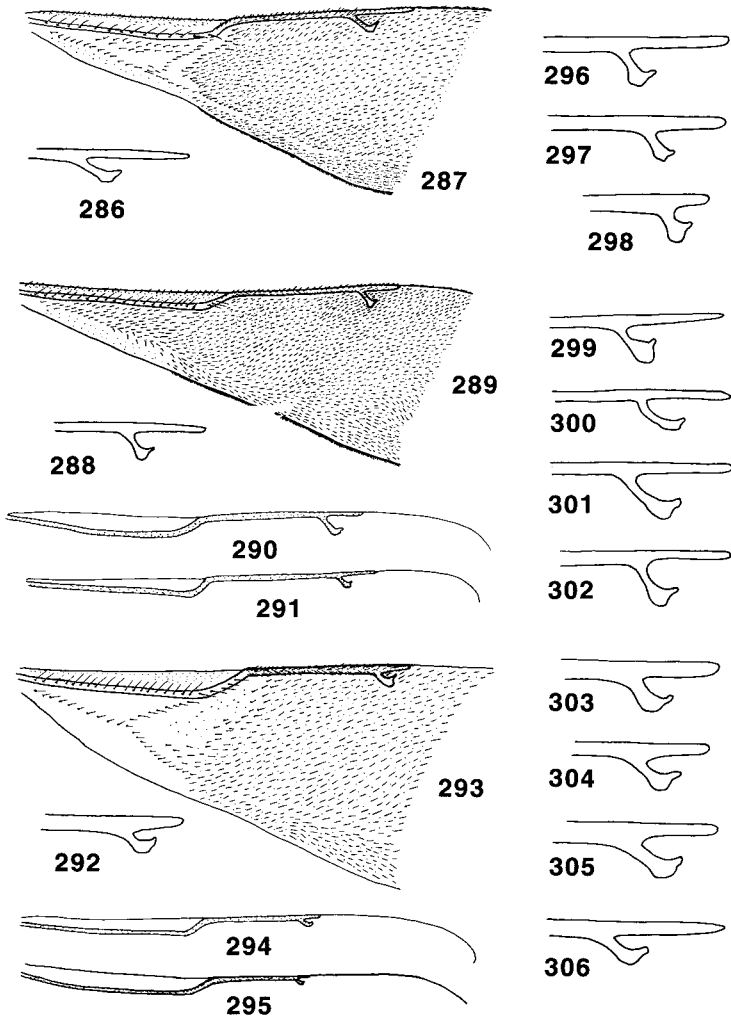
**Figs. 249-264.** Palachiini (female, from specimens compared with types, unless otherwise noted by locality). 249. *Palachia* sp. (India); back of head. 250-251. *Gummilumpus bouceki*; head, dorsal, three-quarters view (250); body, lateral view (251). 252-258. Hind femora, lateral view. 252. *Propalachia beaveri*. 253. *Palachia punctigastra* (paratype). 254. *Palachia* sp. (Uganda). 255. *Neopalachia* sp. (Peru). 256. *Gummilumpus bouceki*. 257. *Palachia pulchra*. 258. *Palachia puntifronta* (paratype). 259-264. Forewing venation, dorsal view. 259. *Propalachia beaveri*. 260. *Neopalachia* sp. (Peru). 261. *Palachia pulchra*. 262. *Palachia medleri* (after Bouček 1978). 263. *Palachia caudata*. 264. *Palachia puntifronta* (paratype).



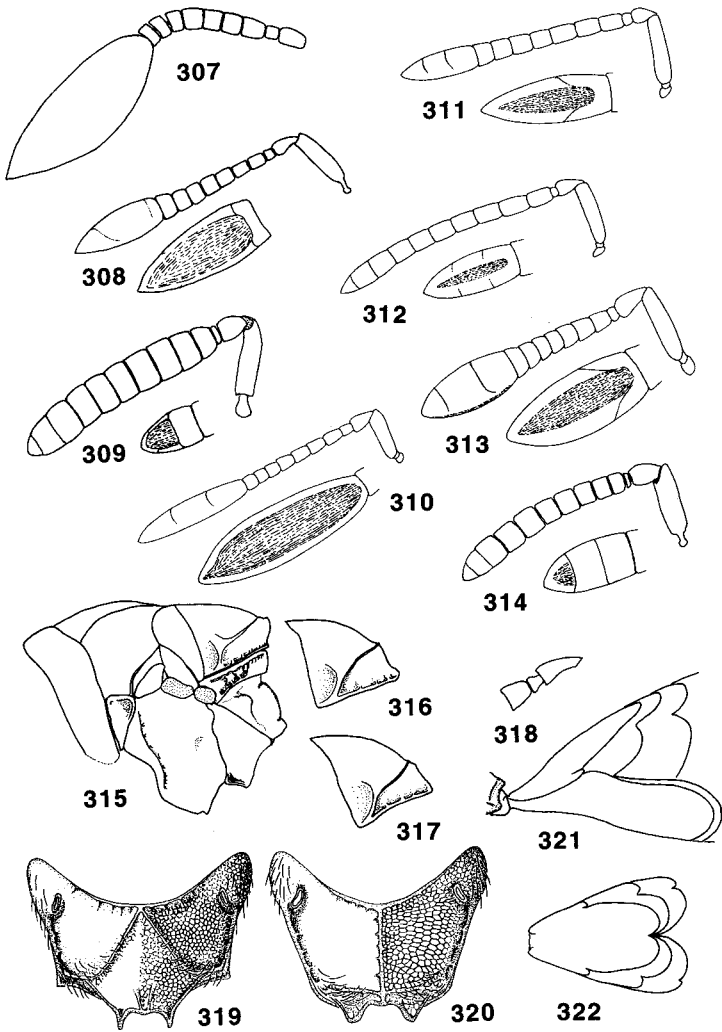
**Figs. 265-277.** Palachiini (female, from specimens compared with types, unless otherwise noted). 265-267. *Palachia pulchra*; dorsum of body (265), head, side view (266), lower margin of face (267). 268-269. *Palachia infumata*; antenna, side view (268), club, three-quarter lateral view (269) (after Bouček 1978). 270. *Neopalachia noyesi*, apex of antenna. 271. *Gummilumpus bouceki*, antenna. 272-273. *Palachia pulchra*; metasternum, ventral view (272), metapleuron and propodeum, lateral view (273) (midcoxa, metapleuron stippled). 274-275. *Propalachia* sp. (Taiwan); metasternum, ventral view (274), metapleuron and propodeum, lateral view (275). 276-277. Propodea, dorsal view, (sculpture shown on right side only). 276. *Palachia pulchra*. 277. *Neopalachia* sp. (Peru).



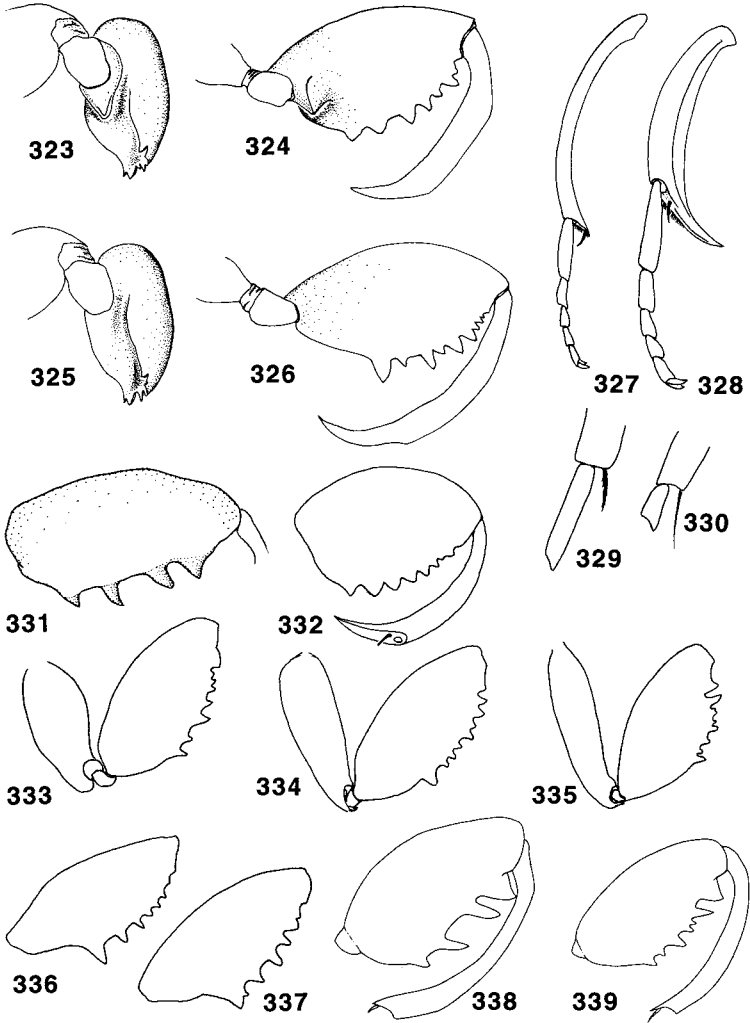
**Figs. 278-285.** Podagrionini (female, all specimens compared with types). Mesosoma: A - metasternum, ventral view (propodeum stipled); B - metapleuron and propodeum, lateral view (midcoxa, metapleuron stipled). 278. *Micropodagrion pauliani*. 279. *Podagrion mantis*. 280. *Propachytomoides spilopterion*. 281. *Podagrion brasiliense*. 282. *Mantiphaga pseudocrebrotae*. 283. *Palmon* sp. (Ecuador). 284. *Podagrionella bella*. 285. *Palmon zygas*.



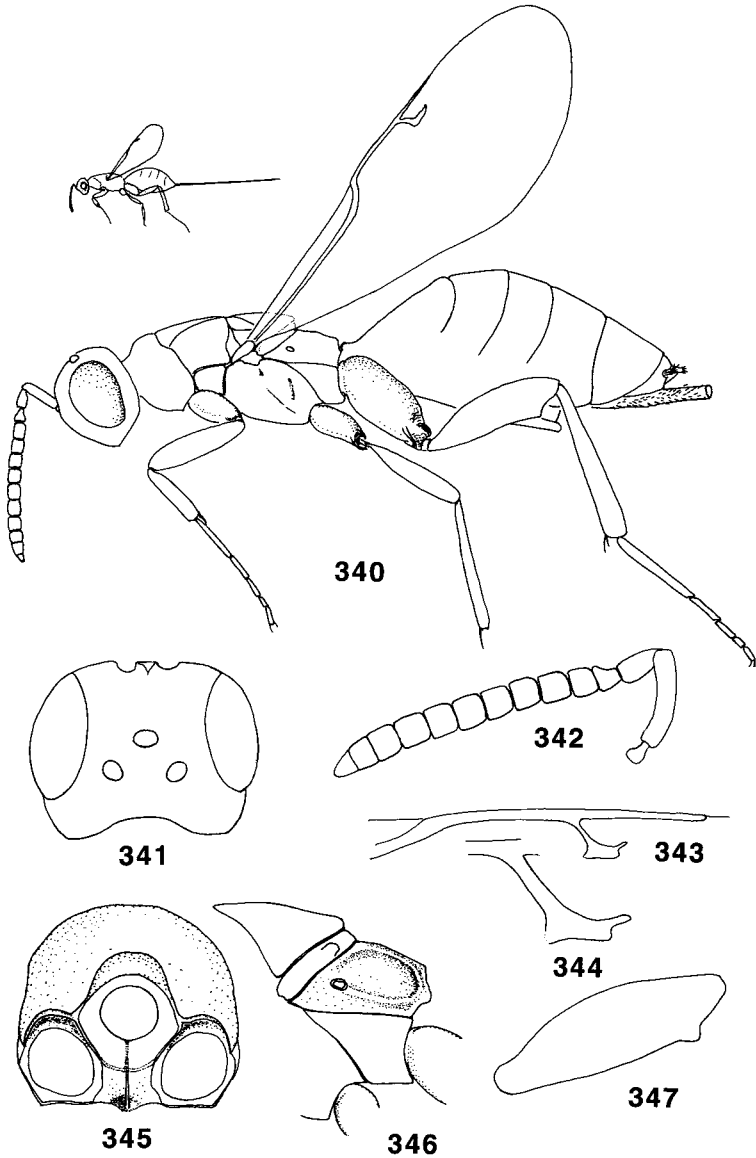
**Figs. 286-306.** Podagrionini (female), forewing venation. 287, 289, 293. Setation (part). 290, 291, 294, 295. Venation relative to wing length. 286, 288, 292, 296-306. Stigmatal and postmarginal veins. 286-287. *Podagrionella bella* (holotype). 288. *Palmon* sp. near *bellator* (Nigeria, compared with holotype). 289. *Palmon bellator* (holotype). 290. *Palmon insolens* (paratype). 291. *Palmon ashmeadi* (holotype). 292-293. *Podagrion splendens* (France). 294. *Podagrion klugianum* (compared with lectotype). 295. *Podagrion mantis* (compared with holotype). 296. *Podagrionella lichtensteini* (syntype). 297. *Podagrionella senegalensis* (syntype). 298. *Podagrionella petiolatus* (holotype). 299. *Palmon ashmeadi* (holotype). 300. *Palmon greeni* (syntype). 301. *Palmon insolens* (paratype). 302. *Palmon zygus* (paratype). 303. *Podagrion longicaudum* (Ivory Coast). 304. *Podagrion mantis* (compared with holotype). 305. *Podagrion coeruleoviride* (syntype). 306. *Podagrion mantidiphagum* (paratype).



**Figs. 307-322.** Podagrionini (female, compared with holotype unless noted). 307-314. Antennae, lateral view (inset, ventral view of club). 315-317. Mesosoma and scutellum (lateral view). 318. Antenna, pedicel, anellus. 319-320. Propodea (sculpture shown on right side only). 321-322. Metasoma, lateral (15) and dorsal (16) views. 307. *Palmon bellator* (holotype). 308. *Podagrionella bella*. 309. *Podagrionella senegalensis* (syntype). 310. *Palmon zygus* (paratype). 311. *Podagrion mantis*. 312. *Podagrion mantidiphagum* (compared with lectotype). 313. *Podagrion crassiclava*. 314. *Mantiphaga pseudocreobotrae* (compared with syntype). 315. *Podagrionella senegalensis* (syntype). 316-317. *Podagrionella* n. sp. (Somalia). 318. *Micropodagrion pauliani*. 319. *Podagrion mantis*. 320. *Palmon zygus* (paratype). 321-322. *Podagrion mantis*.

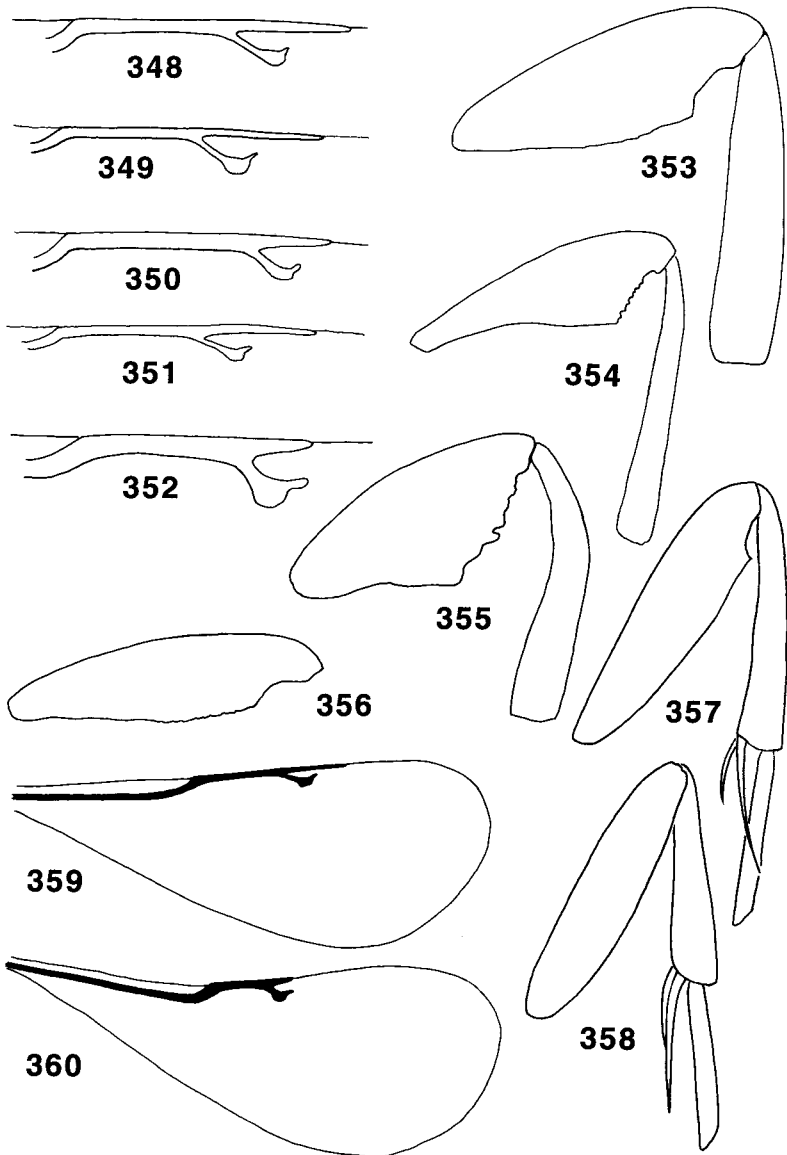


**Figs. 323-339.** Podagrionini (female, compared with holotype unless noted otherwise or with locality). 323-326. Right hind femur (323, 325: view from distal end to coxa; 324, 326: inner view). 327-328. hind tibia and tarsus. 329, 330. Midtibia and basitarsis. 331-339. Left hind femur (except 337, right). 323-324. *Podagrionella* n. sp. (Somalia). 325-326. *Podagrionella bella*. 327. *Podagrion pachymerum* (France, Spain). 328. *Podagrionella senegalensis* (syntype). 329. *Palmon zygus* (paratype). 330. *Micropodagrion pauliani*. 331. *Podagrion klugianum* (holotype, male). 332. *Podagrionella senegalensis* (syntype). 333. *Podagrion mantis*. 334. *Palmon bellator* (holotype). 335. *Palmon mirus* (holotype). 336-337. *Micropodagrion pauliani* (holotype); left (336) and right (337) hind femora. 338-339. *Podagrion mantidiphagum* (compared with lectotype); male (338) and female (339).

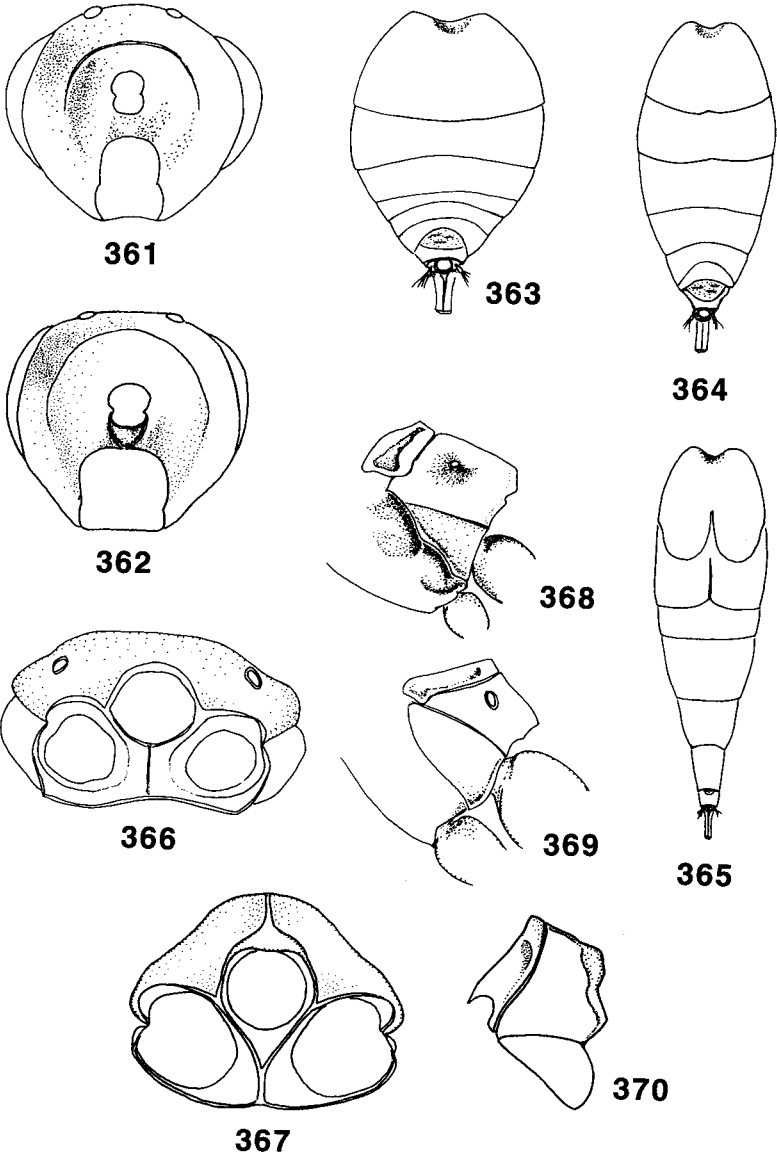


**Figs. 340-347. *Insertae sedis. Stenotorymus linearis* (holotype female, except 345). 340. Habitus, ovipositor excluded (inset to show reduced overview of entire specimen). 341. Head, dorsal. 342. Antenna, lateral. 343. Forewing venation, dorsal. 344. Stigmal vein, enlarged. 345. Metasternum, ventral (undescribed species, India). 346. Propodeum, mesopleuron, lateral. 347. Hind femur, lateral.**



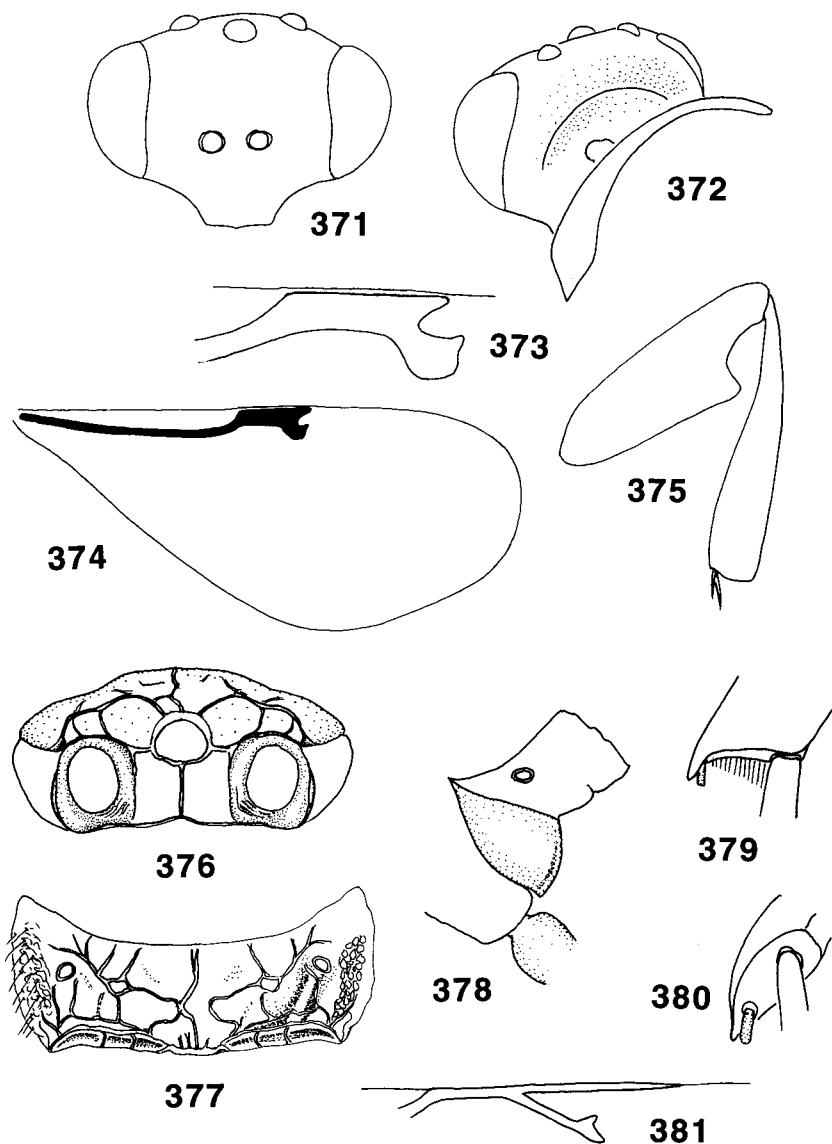


**Figs. 348-360. *Insertae sedis*** (female, from specimens compared with types unless otherwise noted). 348-352. Forewing venation, dorsal. 353-358. Left hind leg (part), lateral. 359-360. Forewing, dorsal. 348, 355. *Exopristus trigonomerus*. 349, 356. *Glyphomerus stigma* (syntype, sex unknown). 350, 357. *Zaglyptonotus mississippiensis*. 358. *Zaglyptonotus* n. sp. (Chile). 351, 353, 359. *Cryptopristus caliginosus*. 352, 354, 360. *Thaumatorymus notanisoides* (male, Hungary).

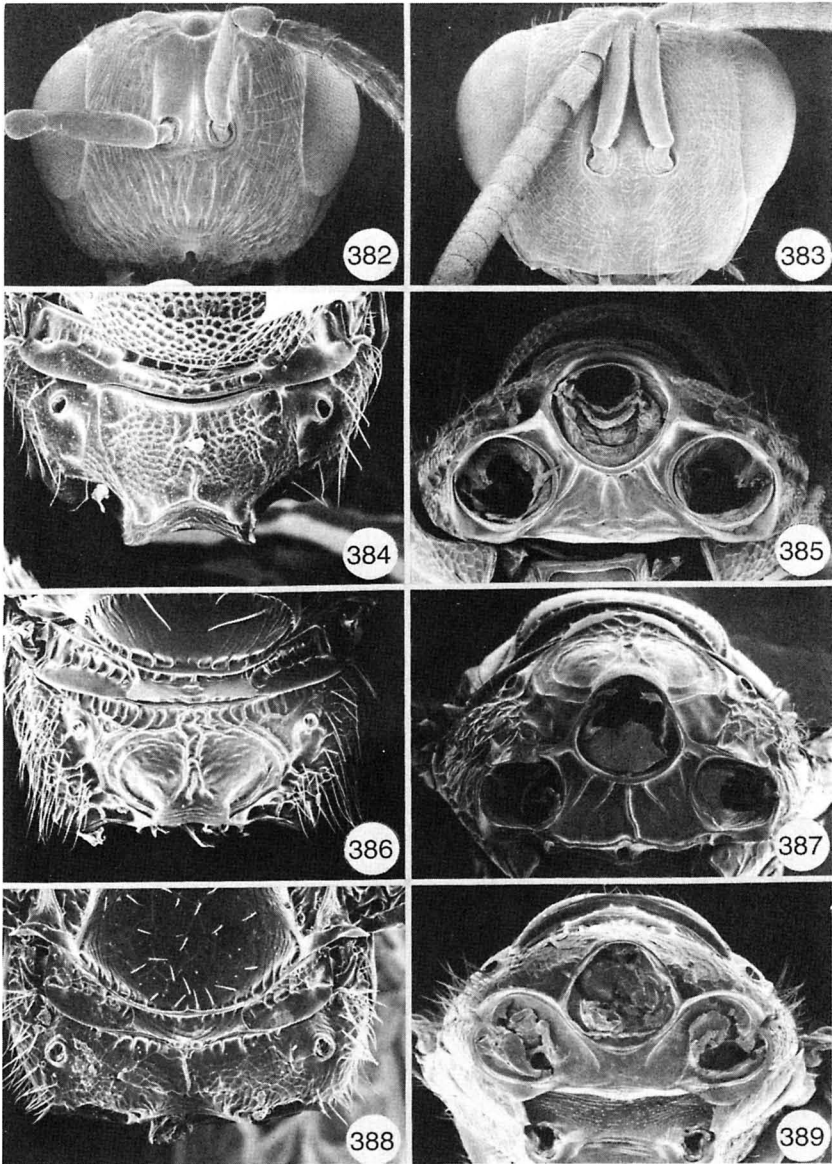


**Figs. 361-370. *Insertae sedis*** (female, from specimens compared with types unless otherwise noted). 361-362. Head, posterior. 363-365. Metasoma, dorsal. 366-367. Measternum, ventral. 368-370. Mesosoma, posterior. 361, 363. *Glyphomerus stigma*. 362, 367, 370. *Zaglyptonotus schwarzi*. 364. *Exopristus trigonomerus*. 365, 366, 369. *Cryptopristus caliginosus*. 368. *Thaumatorymus notanisoides* (male, Hungary).

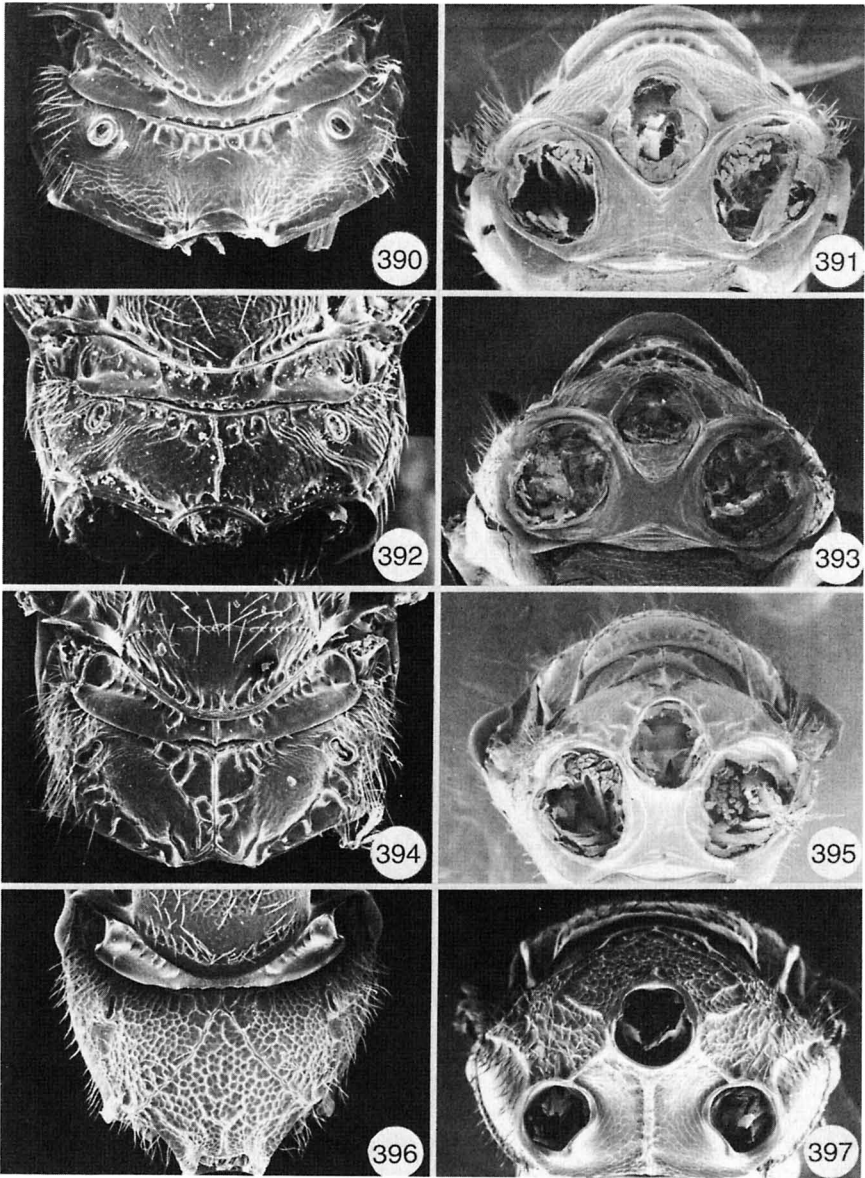
World Toryminae



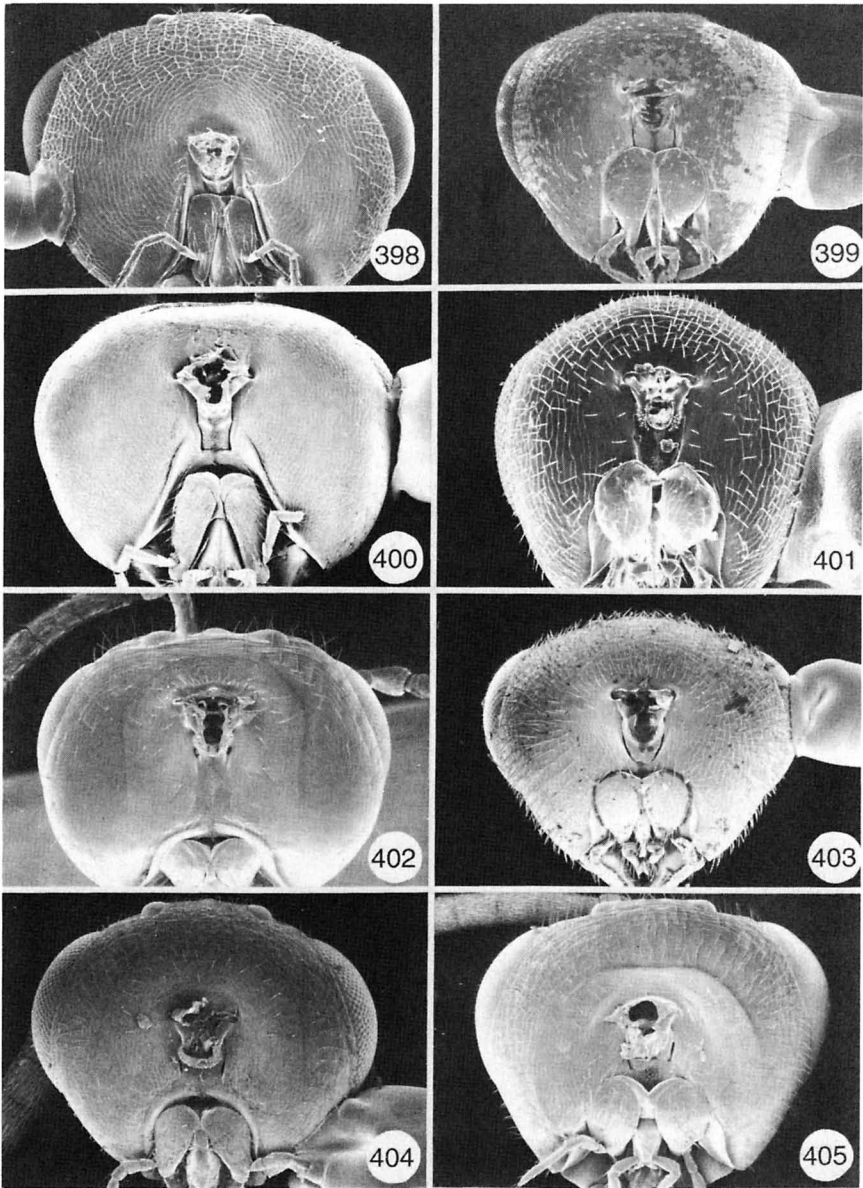
**Figs. 371-381. *Insertae sedis*.** 371-375. *Echthrodape africana* (holotype female). 371. Head, anterior. 372. Head, three-quarter, posterior. 373. Forewing venation, dorsal. 374. Forewing, dorsal. 375. Hind femur and tibia, lateral. 376-381. Chalcimerini, *Chalcimerus borceai* (female). 376. Metasternum, ventral view. 377. Propodeum, dorsal view. 378. Metapleuron and propodeum, lateral view (midcoxa, metapleuron stippled). 379-380. Apex of hind tibia: lateral view (379); ventral view (380). 381. Forewing venation.



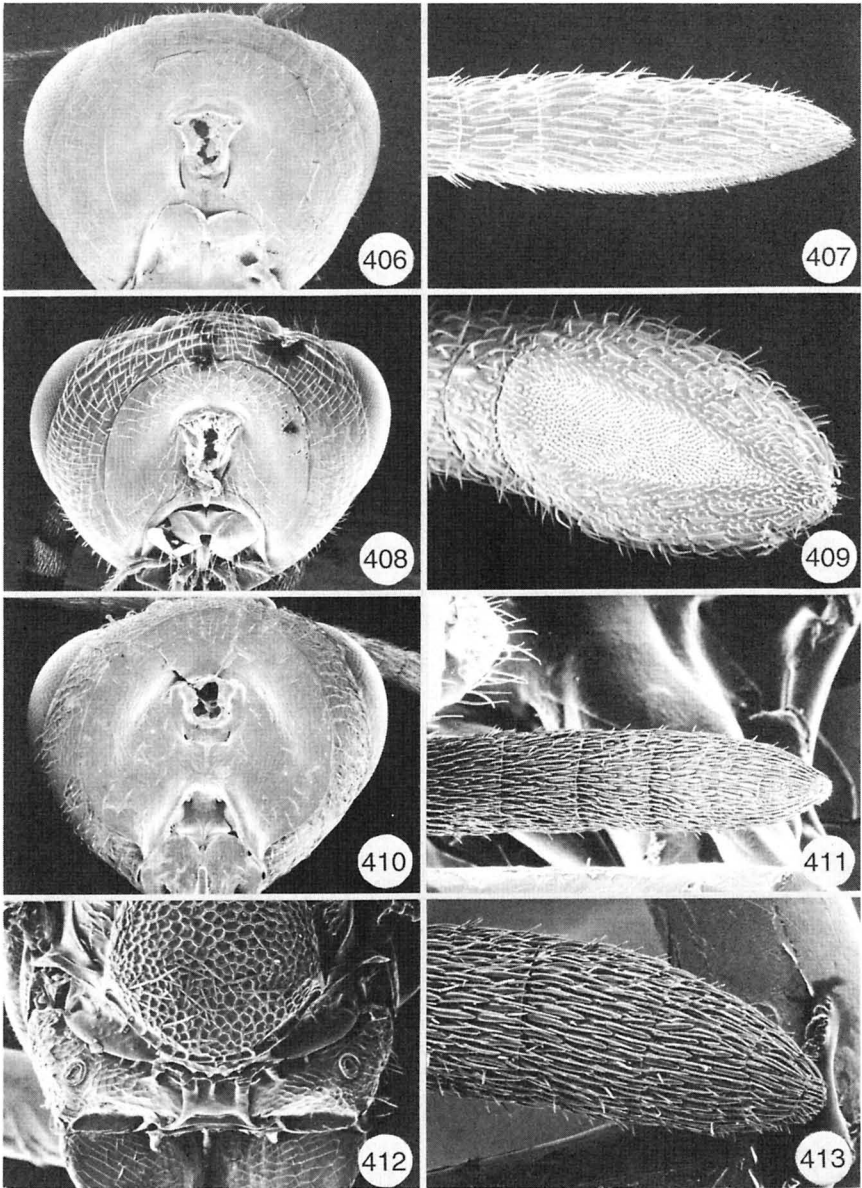
**Figs. 382-389.** Scanning electron micrographs. Head (382, 383), anterior; propodeum (384, 386, 388), dorsal; metasternum (385, 387, 389), ventral. 382. *Megastigmus aculeatus nigroflavus*. 383. *Monodontomerus* sp. 384-385. *Pteromalus* sp. 386-387. *Megastigmus aculeatus nigroflavus*. 388-389. *Microdontomerus anthidii*.



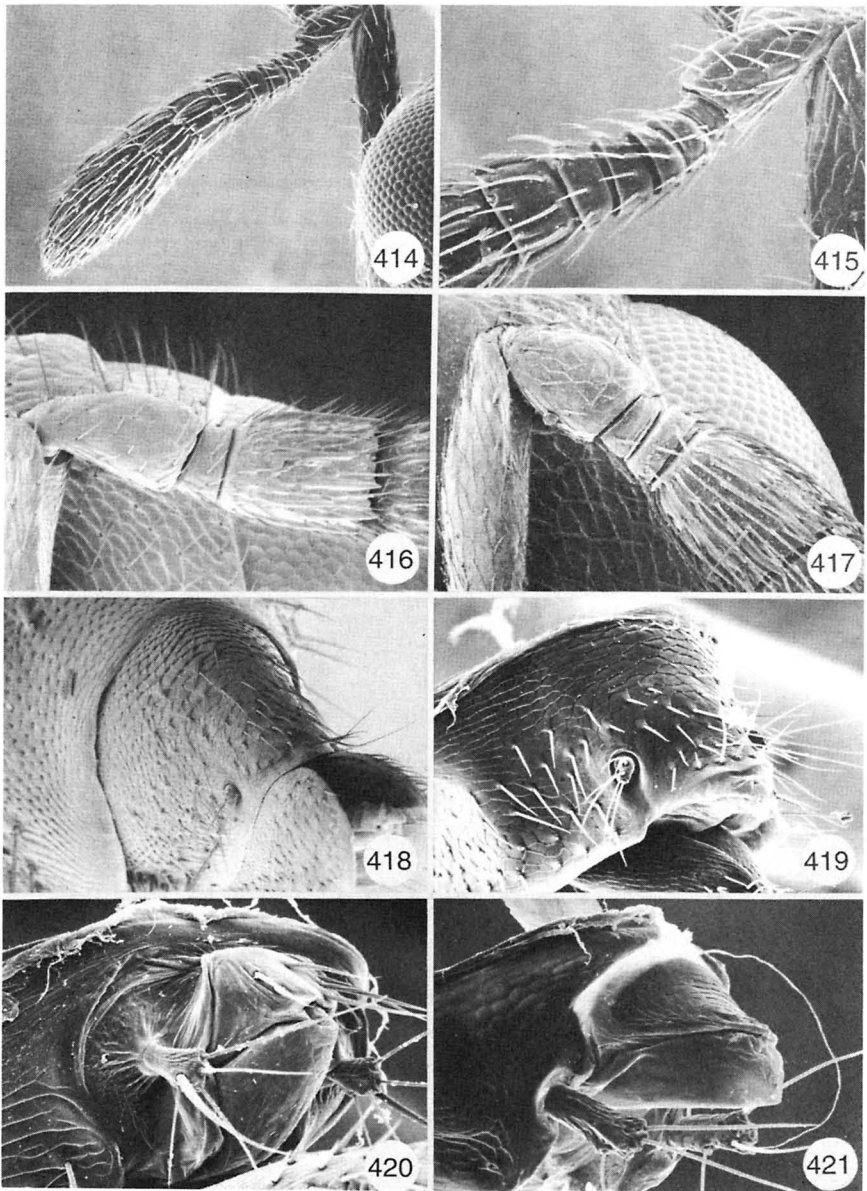
**Figs. 390-397.** Scanning electron micrographs. Propodeum (390, 392, 394, 396), dorsal; metasternum (391, 393, 395, 397), ventral. 390-391. *Torymus* sp. 392-393. *Torymoides amabilis*. 394-395. *Monodontomerus* sp. 396-397. *Podagrion mantis*.



**Figs. 398–405.** Scanning electron micrographs. Head, posterior view. 398. *Pteromalus* sp. 399. *Microdontomerus anthidii*. 400. *Roptrocerus* sp. 401. *Idiomacromerus perplexus*. 402. *Megastigmus aculeatus nigroflavus*. 403. *Ditropinotus aureoviridis*. 404. *Torymoides amabilis*. 405. *Monodontomerus* sp.

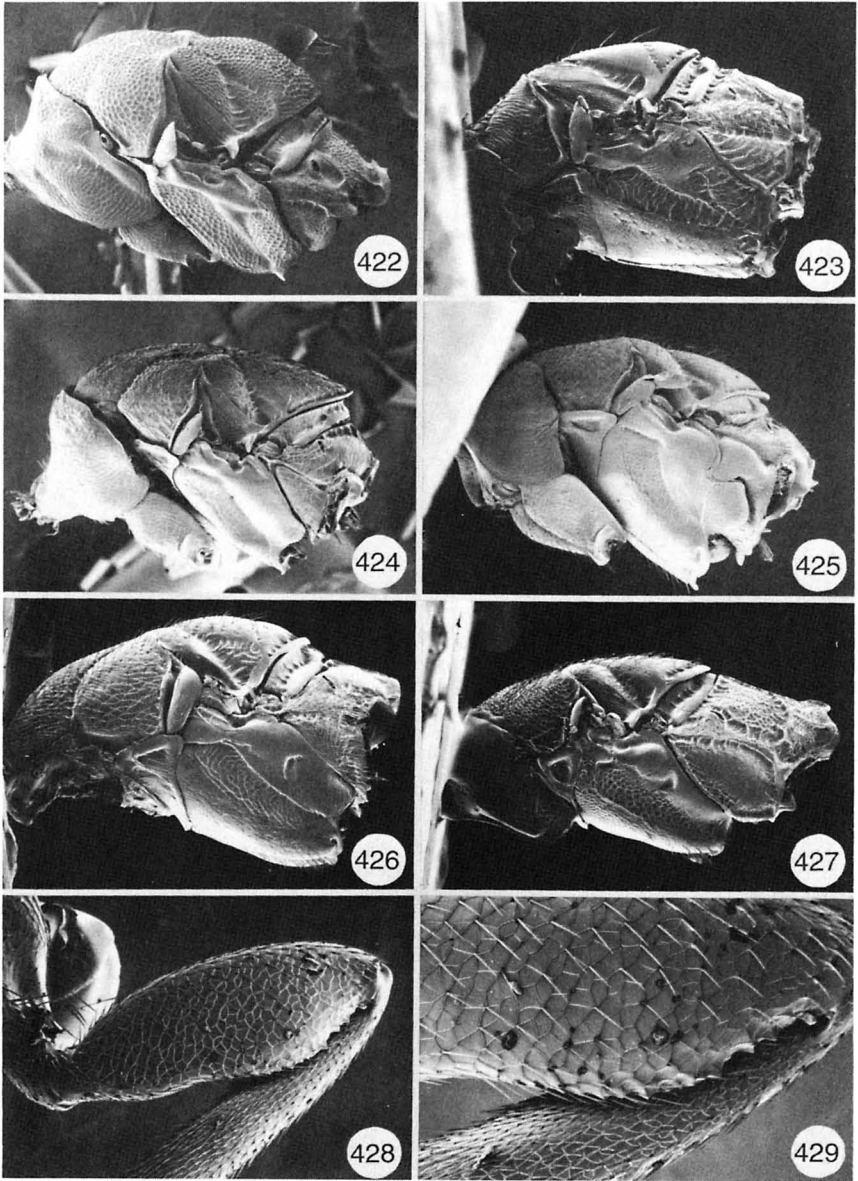


**Figs. 406-413.** Head (406, 408, 410), posterior; antennal club (407, 409, 411, 413), lateral (407, 411), ventral (409, 413); propodeum (412), dorsal. 406. *Torymus* sp. 407, 409, 410. *Podagrion mantis*. 408, 411, 413. *Diomorus zabriskiei*. 412. *Ditropinotus aureoviridis*.



**Figs. 414-421.** Antenna (414-413), lateral; apex of metasoma (418-421), three-fourths lateral. 414-415. *Torymoides* sp. 416. *Torymus* sp. 417. *Torymoides amabilis*. 418. *Ormyrus* sp. 419. *Pteromalus* sp. 420. *Diomorus zabriskiei*. 421. *Podagrion mantis*.





**Figs. 422-429.** Mesosoma (422-421), lateral; hind femur (428-429), lateral. 422. *Pteromalus* sp. 423. *Megastigmus aculeatus nigroflavus*. 424. *Torymoides amabilis*. 425. *Torymus* sp. 426. *Monodontomerus* sp. 427. *Podagrion mantis*. 428-429. *Ditropinotus aureoviridis*.

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## INDEX OF TORYMID NAMES

Higher taxa and invalid species and genus names (i.e., synonyms or misspellings) are in Roman type; valid names are in *italics*; main page references are in **bold**; page numbers for the key are in **bold italic**. Species names are cited in their original generic combination, and if only one genus name is given that is the current placement. If more than one name is cited, then transfers are listed in chronological order with the last being the currently accepted combination. Author's names for species are not placed in parentheses to indicate changes of combination. Names preceded by an asterisk (\*) are *nomina nuda*. Subspecies names are listed both under their own name and also under the name of the nominal species.

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## ADDENDA

Two papers were discovered too late to include all information in the main text without substantially altering the finished camera-ready copy: Bouček 1994b and Zerova and Seregina 1994. Both are included in the literature cited section (p. 411). One comment on type information given by Bouček (1994b) is incorporated under *Diomorus calcaratus* (see p. 184). *Pseuderimerus bouceki* Zerova and Seregina (1994) is described as a new taxon. According to Bouček (1994b), *Pseudotorymus brassicae* Ruschka is a synonym of *Pseudotorymus napi* (Amerling and Kirchner). These changes, as detailed below, will bring the text up to date. Recalculations of species numbers have not been made in the text but one species of *Pseuderimerus* is gained and one species of *Pseudotorymus* is lost.

*Pseuderimerus*

The next entry should be added in its entirety to page 252 before *femoratus* Gahan.

***bouceki*** Zerova and Seregina. PALEARCTIC: CIS (Turkmenistan).

*Pseuderimerus bouceki* Zerova and Seregina 1994:124 (Fig. 3:1-3). Holotype ♀, near Ashkhabad, Turkmenistan (IZU).

HOST. - The type was reared from an unknown host associated with stems of *Centaurea belangerana* (Asteraceae).

*Pseudotorymus*

In the main text the entry for *P. brassicae* (p. 255) should be removed and the entry for *P. napi* (p. 259) should be replaced with the following:

***napi*** (Amerling and Kirchner). PALEARCTIC: Czechoslovakia, Germany, Austria; Italy (Solinas and Bucci 1982).

*Torymus napi* Amerling and Kirchner, in Kirchner 1860:72. Lectotype ♀ [designated by Bouček 1994b:119], Prague, Czechoslovakia [NMP, confirmed by Bouček 1994b:119].

*Pseudotorymus brassicae* Ruschka 1923:404-406 (Figs. 3-6). Lectotype ♀ [designated by Bouček 1994b:119; syntype number unstated], Prague, Czechoslovakia; Vienna, Austria; Naumburg, Germany (NMW, confirmed by Bouček 1994b:119). [Synonymized by Bouček 1994b:119.]

TAXONOMY. - Hoffmeyer (1931:261) apparently was the first to use this combination for *napi*. Bouček (1994b:119) discussed the types.

HOST. - All records are from Cecidomyiidae. The type of *napi* was reportedly reared from "*Diplosis ochracea*" apparently in rape seed (*Brassica napus*: Cruciferae). According to R. Gagne (pers. comm.) it is highly likely that the true host is the cecidomyiid *Dasineura brassicae*. The type series of *brassicae* was reared from *Dasineura brassicae* on *Brassica napus oleifera* (Cruciferae) in Czechoslovakia and *Dasineura sisymbrii* in Austria. Solinas and Bucci (1982) reported the species (as *brassicae*) as an ectoparasite of *Gephyraulius* (as *Paragephyraulius*) *diplotaxis* and *Contarina* sp. in flowers of *Diplotaxis muralis* (Cruciferae) in Italy.