2005

Phylogenetic revision of the genus Mesynodites Reichardt (Coleptera: Histeridae: Hetaeriinae)

Alexey K. Tishechkin
Louisiana State University and Agricultural and Mechanical College

Recommended Citation

Tishechkin, Alexey K., "Phylogenetic revision of the genus Mesynodites Reichardt (Coleptera: Histeridae: Hetaeriinae)" (2005). *LSU Doctoral Dissertations*. 1605.
https://repository.lsu.edu/gradschool_dissertations/1605

PHYLOGENETIC REVISION OF THE GENUS *MESYNODITES* REICHARTD (COLEOPTERA: HISTERIDAE: HETAERIINAE)

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

In

The Department of Entomology

by
Alexey K. Tishechkin
M.S., Belarusian State University, 1983
May 2005

ACKNOWLEDGEMENTS

A long-term research endeavor such as this project that includes such dramatically different activities as extracting genitalia out of a millimeter-long beetle on a fingertip and walking long night-time tracks in Amazonian rainforest, always will depend on expertise, collaboration and help from numerous people. The following are words of my deep appreciation to everybody who was around to help.

First and foremost, I would like to thank my major professor, Dr. Chris Carlton. His encouragement, timely and wise suggestions and patience made this work possible. Chris enthusiastically supported my research and provided important discussion and guidance that served to lead my professional development. I am grateful for his mentorship and friendship throughout my time at Louisiana State University.

I thank my graduate committee members Drs. Dorothy Prowell, Fred Sheldon and Bruce Williamson for their insightful discussion and wise counsel during the course of my study at LSU. All of them read and provided valuable suggestions and improvements to the draft of this dissertation. I learned a multitude of important things from our conversations in classrooms, offices and next to a bon fire.

I am grateful to numerous curators who loaned material used throughout this study (listed in Chapter 2). Several persons from this list deserve special mention. My simple innocent question about his work on Heateriinae in a letter to Nicolas Dégallier lead to the onset of this project and our long-term cooperation and friendship. Nicolas' encouragement, constant flow of knowledge and numerous important specimens going my way were critical for the completion of this study. I thank Pete Kovarik for sharing his friendship as well as histerid knowledge and enthusiasm over the last decade. After all, Pete made the first move that resulted to my long trip to LSU and writing this dissertation. Michael Schmitt was the perfect curator of a foreign museum to meet in person first during your career. He was very instrumental in arranging my 1996 trip to the Alexander König Museum, crucial for this project, and he still is a good colleague and friend.

My old friends from Belarusian State University times, Nickolai Davidovich, Wasilij Gritschik and Alexander Konstantinov, all were always available with suggestions, discussions, inspiration and any other possible help. I also wish to thank a nice group of Louisiana State Arthropod Museum's people, in particular, Andy Cline, Dee Colby, Mel Dean, Stephanie Gil, Debbie Landau, Victoria Moseley Bayless, Debra Murray and Lisa Peri. These folks provided interesting, stimulating conversation, companionship and friendship throughout my years in Baton Rouge. My deep gratitude goes to Dr. Bill Henk, LSU School of Veterinary Medicine, who prepared scanning electron microscopic images.

Various institutions and agencies generously supported my graduate research endeavors. The National Science Foundation provided important support through Grant DEB-9815394 awarded to Chris Carlton. Funding through this NSF grant provided me with funds for field trips, visits to museums and symposia and various other research activities. Additional funds for fieldwork in Costa Rica, Ecuador and Panama and visits to collections in Europe and North America came from CanaCol Foundation, Deutsche Forschungsgemeinschaft (grant 436 WER 17/5/96), Field Museum of Natural History, Global Canopy Program, LSU Agricultural Center, Organization for Tropical Studies, Smithsonian Tropical Research Institute, Solvin/Solvay and

United Nations Environmental Program. I would like to thank numerous people in Latin American countries visited, especially Yves Basset, Luis Diego Gomez and Giovanni Onore, for the logistic support, hospitality and companionship. Special thanks go to all my friends in the IBISCA Project team.

On a personal level, I would like to thank my parents, Stepanida Tishechkina and late Konstantin Tishechkin, who provided encouragement and support during my entire career in field and systematic biology. They instilled in me a love of Nature’s wonders and learning and supported me completely from the very beginning of my teenage outdoor wanderings despite having completely different original plans for my career. Finally, I could not have written this dissertation without the support and love of my wife Irina and son Mikhail. They had to become a part of a research team, were patient and helpful with their ‘roles’ in it and provided essential inspiration, encouragement and love. Thank you all.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Mesynodites is the largest genus within the exclusively inquilinous (social insect-associated) histerid beetle subfamily Hetaeriinae (Insecta: Coleoptera: Histeridae). The 44 described species are systematically revised, and new taxa are described based on newly discovered species and the results of a cladistic analysis. The work was based on available type specimens representing 42 species and approximately 2500 specimens of non-type material. Phylogenetic hypotheses were based on maximum parsimony analysis of 150 morphological characters derived from a selection of *Mesynodites* species and representatives of related genera. This analysis confirmed that, in its current concept, *Mesynodites* is not a monophyletic taxon. Species included currently in *Mesynodites* were scattered among 11 distinct lineages. As a result, in the revised sense, *Mesynodites* includes only nine species, two of which are of uncertain affinities (type specimens of these species were not located).

Revision of *Mesynodites* species in the context of the phylogenetic analysis allowed numerous taxonomic changes to the Hetaeriinae. Presentation of those changes in this dissertation does not constitute formal publication. The following taxonomic changes are introduced: two new tribes are described and all genera of Hetaeriinae, excluding 12 genera of doubtful affinities, received tribal assignments; eight new genera and three new species are described; 37 new combinations and five new synonimities are established.

The phylogenetic hypothesis of relationships within *Mesynodites* and allies (tribe Nymphisterini) provided some insight into evolution of host use in the lineage. This group evolved with army ants (Hymenoptera: Ecitoninae) and are known to occur with several species within the genera *Eciton*, *Labidus*, *Neivamyrmex* and *Nomamyrmex*. The ancestral host genus was hypothesized to be either *Eciton* or *Labidus*. Contrary to previous opinions, species in several genera of Nymphysterini live with multiple host ant genera. Two separate host switches from army ants (*Nomamyrmex* and possibly *Neivamyrmex*) to leaf cutter ants *Atta* are hypothesized for species in *Mutodites* and *Mesynodites*. Analysis of host use and speciation revealed a trend of 1.5-2.5 times fewer species per strictly specialized (single host genus) guest genus, and this trend was consistent across different levels of analysis (Nymphysterini, all ecitophiles and all Hetaeriinae).

CHAPTER 1. INTRODUCTION

1.1 Introduction to the Subfamily Hetaeriinae

The beetle family Histeridae includes about 4,000 described species distributed worldwide with the exception of Arctic and Antarctic regions (Mazur 1997). Histerids are small to medium-sized beetles (0.7-25 mm) and occur in many habitats, from dense forests to deserts and dunes, where most are predators of beetle, fly and flea larvae. They live in a variety of decomposing organic materials (dung, carrion, rotten wood, seaweed, and forest litter), under loose bark of woody plants, in galleries of wood-boring insects, vertebrate nests, rhizospheres of desert plants, and in nests of social insects (ants and termites). Several specialized soil and cave-dwelling species also exist (Kryzhanovkij & Reichardt, 1976; Dégallier & Gomy, 1983). Taxonomy of Histeridae is relatively well worked out and was recently summarized at the Worldwide level (Table 1). Eleven subfamilies are recognized traditionally, with modest numbers of tribes recognized within three of them. Studies of higher level phylogenetic relationships of histeridae are in their infancy, but an indication of coming taxonomic changes within the family to better reflect evolutionary relationships are apparent (Ôhara, 1994; Ślipiński & Mazur, 1999; Caterino & Vogler, 2002).

Myrmeco- and termitophily (ant- and termite-associated, respectively,) has evolved several times in Histeridae (Caterino & Vogler, 2002). These life habits are collectively referred to as “inquilinism.” Inquilionous associations occur among the representatives of seven out of 11 traditionally recognized subfamilies (Table 1). Two of them, Chlamydopsinae and Hetaeriinae, consist exclusively of inquilinous species. Other subfamilies contain a few specialized genera and several ant-associated species occur in otherwise non-inquilinous genera (*e.g.*, Caterino, 1999). Both exclusively inquilinous subfamilies contribute considerably to the species richness of histerid faunas in their respective zoogeographical realms, Australasian and neotropical.

Table 1. Summary of taxonomy (after Mazur, 1997) and occurrence of inquilinism in Histeridae.

Subfamily	Tribes	No. of Genera	Presence of inqulinism
Abraeinae	Abraeini, Acritini, Acritomorphini, Plegaderini, Teretriini	24	Occasional
Chlamydopsinae	No tribes recognized	9	Obligate
Dendrophilinae	Anapleini, Bacaniini, Dendrophilini, Paromalini	26	Occasional
Hetaeriinae	No tribes recognized	102	Obligate
Histerinae	Exosterninae, Histerinae, Hololeptinae, Omalodinae, Platysomatinae	104	Regular
Niponiinae	No tribes recognized	1	Absent
Onthophilinae	No tribes recognized	7	Occasional
Saprininae	No tribes recognized	42	Occasional
Tribalinae	No tribes recognized	11	Absent
Trypanaeinae	No tribes recognized	3	Absent
Trypeticinae	No tribes recognized	3	Absent

The Hetaeriinae is a diverse, almost exclusively neotropical subfamily containing about one-third of the World and two-thirds of neotropical histerid genera and about 20% of all described neotropical species (Mazur, 1997). Approximately 100 genera with 240 described species occur in the neotropics. In addition, the subfamily contains one Holarctic genus with 26 species in North America and six in the Palearctic region, and three nearly exclusively Mediterranean genera containing 50 species. Four genera are shared between neotropical and nearctic regions (Dégallier, 1994, 1998a, b, c; Mazur, 1997; Yélamos, 1997; Lackner and Yélamos, 2001). At present, the striking diversity of neotropical hetaeriine genera is characterized by the large proportion of genera containing few or single species. Only 8% of hetaeriine genera contain four or more species. Indeed, about 65% are monotypic (Mazur, 1997). In fact, Hetaeriinae may be the most diverse obligately inqulinous monophyletic lineage of insects, with rivals potentially found only among some inquilinous lineages of Staphylinidae and Phoridae (Seevers, 1965; Kistner, 1982).

Description of the first hetaeriine species dates back to Linnaean times. Before the 1920s, random species and genus descriptions were done by several major histerid researchers, *i.e.*, H.

Bickhardt, S. de Marseul, G. Lewis, J. Schmidt, with heavy emphasis on Mediterranean genera *Eretmotus* Lacordaire, *Satrapes* Schmidt and *Sternocoelis* Lewis (Mazur, 1997). Studies of the neotropical Hetaeriinae at that time were sketchy and only 29 genera and 62 species were described before 1922 (Mazur, 1997). During the early 1920s, the first papers on neotropical hetaeriines were published by Carlos Bruch (1922) and August Reichensperger (1923), signaling the beginning of the 'golden age' of hetaeriine systematics. In the 1920-30s, these two authors, along with Thomas Borgmeier (1929, 1930), published numerous papers describing the bulk of known neotropical hetaeriine diversity. A couple of final papers of these authors appeared during the post World War II period (Borgmeier, 1948; Reichensperger, 1958).

Since 1958, Hetaeriinae systematics has remained untouched despite numerous behavioral investigations of army ants and their guests, including histerids (Rettenmeyer, 1961; Akre, 1968; Akre & Rettenmeyer, 1966, 1968; Schneirla, 1971). This situation remained stable until Helava *et al.*'s (1985) revisionary treatment of New World Hetaeriinae. In this work, 77 genera were included, illustrated by means of scanning electron microscopy and the first comprehensive generic key was provided. The male genitalia were used as diagnostic characters for the first time for the subfamily, and a phylogeny of the included genera was generated using parsimony analysis of morphological characters. Helava *et al.* (1985) concluded that Hetaeriinae is a monophyletic taxon with five distinct supra-generic lineages called 'Groups A-E'. Unfortunately, this study has several weak points. First, the authors did not study material of all genera. Even within the genera studied, there were no attempts to examine material deposited outside North American institutions. As a result, the key and the phylogeny provided are of limited application. Second, the phylogenetic analysis was admittedly preliminary. Only 31 characters were used for 77 genera, and almost all major branches in their tree were supported by single synapomorphies. Finally, Helava *et al.* (1985) contains a substantial number of errors. A preliminary analysis indicates that the Group A belongs to Histerinae: Exosternini, not

Hetaeriinae. Their concept of at least four genera is wrong and two genera described as new are most probably synonyms of previously described genera (Dégallier, 1998c; Dégallier & Tishechkin, unpublished). In addition, mistakes and gaps in host identity are relatively numerous.

Regardless of its shortcomings, Helava *et al.*'s (1985) work has inspired recent hetaeriine research. Since its publication, six genera have been described as new and redescriptions of 12 genera not previously treated have been published (Helava, 1989; Dégallier, 1997, 1998a, b, c).

The oldest known fossils of recent genera of Hetaeriinae and their most frequent hosts, army ants, are from middle Tertiary Dominican amber (Wilson, 1985). Termites and ants are believed to have originated during middle to lower Cretaceous (Krishna & Weesner, 1970; Carpenter & Hermann, 1979; Agosti *et al.,* 1997; Grimaldi & Agosti, 2000; Brady, 2003). Termites, a more basal group, are presumably the older of the two. Because all hetaeriines are obligate inquilines of social insects, parsimony implies associations dating back to the group's origin.

Diverse host taxa are represented among the hetaeriines. Host termite genera in the Neotropics include *Cornitermes*, *Nasutitermes*, *Syntermes*, and *Termes* (Nasutitermitinae and Termitinae in Termitidae). Ant genera are more numerous as hosts of hetaeriines, including *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex* within the Ecitoninae (army ants); *Acromyrmex*, *Atta, Pheidole*, and *Solenopsis* within the Myrmicinae; *Ectatomma, Holcoponera,* and *Pachycondyla* within the Ponerinae (Reichensperger, 1926; Helava *et al.*, 1985 and references therein). Army ants harbor the most diverse hetaeriine assemblages. Host specificity at the generic level is high in neotropical Hetaeriinae, with only one genus reported from more than one host genus (Helava *et al.*, 1985). Ant genera that serve as hosts of hetaeriines outside the Neotropics include *Tapinoma* within the Dolichoderinae, *Acantholepis, Formica* and *Lasius* within the Formicinae, and *Aphaenogaster* and *Tetramorium* within the Myrmicinae (Kryzhanovskij & Reichardt 1976; Helava *et al.* 1985; Yélamos 1992, 1995, 1997).

Hetaeriine genera display a wide spectrum of degrees of integration into host colonies. Hetaeriines are predators of soft-bodied insect larvae, like almost all histerids. Some are known to prey on other colony associates, such as fly larvae in refuse deposits, and others are known to scavenge ant prey, attack and consume weakened adult ants and ant larvae, or even to be fed directly by the ants via trophallaxis (Akre, 1968; Akre & Rettenmeyer, 1968; Kistner, 1979). In Wasmann's (1903) classification they range from synechtrans (persecuted guests) to symphiles (welcome guests). These correspond, for the most part, to Kistner's (1979) ‘poorly specialized, non-integrated species’ and ‘completely integrated species’, respectively.

1.2 *Mesynodites* Complex Introduction

The genus *Mesynodites* was described originally by J. Schmidt (1893) under the name *Synodites*. Thirty two years later, the homonymy of the latter name, preoccupied by a genus of ichneumonid parasitic wasps (Foerster, 1868), was discovered by A. Reichardt (1924) and published as a brief paragraph at the bottom of the paper, describing two new histerid species from Russian Turkestan.

In Schmidt’s original paper, six *Mesynodites* species were described. By 1939, descriptions of all *Mesynodites* species has been performed by five authors, Lewis, Bruch, Reichensperger, Mann and Schmidt (Lewis, 1893; Schmidt, 1893; Bruch, 1923, 1926 a, b, 1933; Reichensperger, 1923, 1924 a, b, 1925, 1931, 1933, 1935 a, b, 1938, 1939; Mann, 1925; Table 2). As a result, *Mesynodites*, with 55 described species arranged into four subgenera, became the largest genus of Hetaeriinae, approached only by the Holarctic and Palearctic genera *Eretmotus* (18 species), *Hetaerius* (30 species) and *Sternocoelis* (26 species) (Mazur, 1997). In the neotropics, where all *Mesynodites* species are distributed, closest rival genera are *Homalopygus* (12 species), *Reninus* (13 species), and *Terapus* (11 species) (Mazur, 1997). This outstanding number of *Mesynodites* species is especially striking given the fact that only 8% of hetaeriinae genera contain more than 4 species and about 65% are monotypic (Mazur, 1997).

The reason for extreme species richness of *Mesynodites* species has at least one obvious component. From the very beginning it became a dumping ground for hetaeriines of generalized appearance, with no striking morphological specializations, so characteristic for many subfamily members. Reichensperger, in his later papers (1938, 1939), was the first who gave a few brief comments on this issue. But only Helava *et al.* (1985) discussed the complexity and probable polyphyly of the genus in some detail. They catalogued all the species, illustrated male genitalia for four of them (*M. elegantulus* Reichensperger, *M. geminus* Reichensperger, *M. novaeteutoniae* Reichensperger, *M. virgatus* Reichensperger) and made several taxonomic re-arrangements. Their concept of *M. verruculosus* Reichensperger, the type species of *Oudaimosister*, was wrong, and this name soon fell into synonymy with *Hemicolonides* Lewis (Dégallier, 1997, 1998c). However, they seem to be completely correct in stating: "The limited material which has been seen indicates that *Mesynodites* is in fact composed of a number of genera. ... The division of *Mesynodites* into its component genera will require a reevaluation of the proposed phylogeny [of Hetaeriinae]" (Helava *et al.*, 1985: 334-335).

Table 2. Taxonomic history of the genus *Mesynodites* Reichardt, 1924. See References for complete list of citations

Author	Years	Contribution
J.Schmidt	1893	Described genus *Synodites* with six species
G.Lewis	1893	Described one species
C.Bruch	1923-33	Described six species
A.Reichensperger	1923-39	Described three subgenera (*Alloiodites, Metasynodites, Monotonodites*) and 41 spp.
A.Reichardt	1924	Replaced preoccupied name *Synodites* with *Mesynodites*
W.Mann	1925	Described one species
J.Helava	1985	Described two genera (*Daitrosister* and *Oudaimosister*) for two Reichensperger's species and elevated rank (up to genus) of three his subgenera
S.Mazur	1997	Transferred one Bruch's species to *Daitrosister*

The task of the "division of *Mesynodites* into its component genera" was suggested to me by N.Dégallier in the mid 1990s when he decided to continue the revisionary work on hetaeriine genera not finished by Helava *et al.* (Dégallier, 1997, 1998a, b, c) and realized that, as these authors, he would not be able to deal with the large numbers of *Mesynodites* species in a proper way. Thanks to his inspiration and a series of coincidences, I am able to do that in this work.

1.3 Statement of Problem

The current concept of the genus *Mesynodites* (Helava *et al*., 1985; Mazur, 1997), an unusually large genus of the subfamily Hetaeriinae, has not changed significantly since the last treatment more than 60 years ago (Reichensperger, 1939). In its current status, *Mesynodites* is the major obstacle in understanding evolutionary relationships within Hetaeriinae and establishing a higher classification of the subfamily. However, no comprehensive attempt has been made to test the doubtful monophyly of *Mesynodites* and to resolve relationships of its species groups and their relationships with other genera by means of phylogenetic analysis.

Without a systematic revision of the genus and a phylogenetic analysis of relationships of its members and members of related genera, a context for understanding the origins of groups, modes of speciation, character trait and host use evolution within Hetaeriinae is lacking.

1.4 Research Objectives

Following are the objectives of this *Mesynodites s.l.* monographic study:

1. Revision of all material available in collections Worldwide for validation of described species-level taxa, recognition of synonyms, and description of new species where necessary.

2. Phylogenetic cladistic analysis of all species under consideration to elucidate monophyletic species-group lineages and develop modern generic concepts for the included species.

3. Preparation of identification keys for all the genera treated.

4. Investigation of host use evolution in *Mesynodites* and Hetaeriinae using the results of the phylogenetic analysis.

CHAPTER 2. MATERIALS AND METHODS

2.1 Introduction

This study is based exclusively on a large set of morphological characters derived from examination of most neotropical hetaeriine specimens preserved in scientific collections Worldwide. The following is the description of the procedures and methods relevant to examination and preparation of specimens, choice of taxa and characters for phylogenetic analysis and methods of this analysis.

2.2 Specimens and Taxonomic Material

About 2500 specimens from 24 institutions and private collections were examined during this study. Acronyms for the collections are used throughout the text below. Names in parentheses are those of the individuals who made the material available to me.

CMN	Canadian Museum of Nature, Ottawa, Canada (R.S. Anderson and F. Génier)
DEI	Deutsches Entomologisches Institut, Eberswalde, Germany (L. Zerche)
FSAC	Florida State Arthropod Collection, Gainesville, FL (P. Skelley)
FIMAK	Zoologisches Forschungsinstitut und Museum Alexander König, Bonn, Germany (M. Schmitt)
FMNH	Field Museum of Natural History, Chicago, IL (A.F. Newton, Jr.)
HUB	Museum für Naturkunde der Humbolt Universität zu Berlin, Berlin, Germany (F. Hieke and M. Uhlig).
INBIO	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (A. Solís).
LSAM	Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, LA (V.L. Bayless and C.E. Carlton).
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (A. Oliva).

MHNG	Musée d'Histoire Naturelle, Geneva, Switzerland (G. Cuccodoro).
MZSP	Museu de Zoologia, Universidade do São Paolo, São Paolo, Brazil (S. A. Casari).
NHMB	Naturhistorisches Museum, Basel, Switzerland (E. Sprecher)
NHML	Department of Entomology, Natural History Museum, London, UK (M. Brendell and E. DeBoise)
NMM	Natuurhistorisch Museum, Maastricht, Netherlands (F.M. Dingemans-Bakels)
SEC	Division of Entomology, Natural History Museum, University of Kansas, Lawrence, KS (formerly the Snow Entomological Collection) (B. Beatty, R. Brooks and Z. Falin)
TAMU	Entomological Collection, Texas A & M University, College Station, TX (E.G. Riley)
USNM	National Museum of Natural History, Washington, DC (D. Furth and G. House).
ZIN	Zoological Institute, Russian Academy of Sciences, St.Petersburg, Russia (A.K. Chistyakova and G.S. Medvedev)
AKT	Collection of A.K. Tishechkin, Baton Rouge, LA (currently housed in LSAM)
BDG	Collection of B.D. Gill, Ottawa, Canada
FP	Collection of F. Penati, Morbegno, Italy
ND	Collection of N. Dégallier, Paris, France
PWK	Collection of P.W. Kovarik, Columbus, OH
SM	Collection of S. Mazur, Warsaw, Poland

2.3. Specimen Preparation and Examination

During the course of the study specimens were observed under a dissecting microscope (25x – 50x) properly pointed on cardboard points (hereafter referred to as points) to make observations and descriptions of external cuticular morphology possible. Observations of mouth parts and genitalia required special dissections and clearing.

Recent taxonomic literature on Histeridae, *e.g.*, Kryzhanovskij & Reichardt (1976), Mazur (1981), Vienna (1981), Ôhara (1994), Kanaar (1997), contains descriptions of specimen preparation methods, which are mostly conventional for small Coleoptera. Most histerids, and hetaeriines in particularly, are more or less convex beetles with dark and solid cuticles, so total slide mounting is not used for routine study. Histerid specimens for scientific collection preservation are glued laterally to a point or cardboard square in the way allowing observation of a lower body surface. Extracted and prepared genitalia are either glued next to specimens or kept in a microvial on the same pin as a beetle. The following is a description of preparation procedures used in the course of this study.

Specimens stored in alcohol did not require relaxation. However, dried non-pointed specimens were relaxed before processing by placing them in a water vapor chamber for several hours, usually overnight. Small Petri dishes with a flat piece of foam were use as chambers, beetles being stored there individually or in short series from the same locality. Occasionally, to accelerate the process, especially in cases of greasy or dirty specimens, relaxation was achieved by placing specimens into hot soapy water for several minutes.

Dissection of point- or card-mounted specimens required removing them using procedures that depended on the type of glue used originally to mount specimens. For water-soluble glues, a vapor chamber was used with 10-30 minute exposure. Specimens attached by organic solvent-based glues were placed for several seconds into an acetone vapor-rich volume, *i.e.*, over a solvent surface in medium sized jar. When the glue softened, specimens were carefully released from it.

Mouthpart dissections were performed for a single male specimen for each exemplar taxon used in the phylogenetic analysis. First, the head was removed from a softened specimen and placed in cold 10% KOH for several hours or overnight for large specimens. It was then rinsed in 3 changes of water, for 20-40 minutes in each. Then, it was transferred into a droplet of glycerol placed on preparate glass for actual dissection. Fine sandstone sharpened insect pins, sizes “1” or “0”, depending on the size of dissected specimens, were used as tools. The entire complex of labia, labrum and mentum was carefully cut out from the inside. Then, constituent parts were separated. In the case of specimens smaller than 2 mm, the right mandible was also removed. Prepared mouthparts were stored in a glycerol-filled microvial with prepared genitalia and pinned together with the specimen. After the completion of the dissection, the head was glued on the point or cardboard next to the beetle or back into head socket of the prothorax in case of large specimens.

Genitalic dissections of male specimens were required because genitalic structures provide important diagnostic characters, both at specific and generic levels. Female genitalia were prepared and studied for each exemplar taxon, except *Mesynodites speculum* Reichensperger, known only from the male holotype. If possible, several species per genus (or species group, see below) were scanned for female genital morphology to get an idea of variability within supraspecific taxa.

Sharp size “0” insect pins were used to remove genitalic sclerites from the abdomen. A pin with a straight tip was used occasionally to open up the pygidium in case it was tightly closed. When the pygidium was elevated enough and a cloacal opening was clear, a pin with a hooked tip was used to anchor and remove a set of genitalic sclerites (as is shown in cartoon form in Kryzhanovskij & Reichardt, 1976). All the procedures were done on a tip of a finger, in most cases leaving the specimen intact. Occasionally, if the pygidium or prothorax was broken off, the pygidium was glued to a point next to the specimen and other body parts were glued together or separately to the point. In a few cases, small specimens were not handled by fingers, but fixed by elastic glue to some kind of surface, a point as a rule.

Removed sets of genitalic sclerites, tightly packed and compact in both sexes, were transferred to a vial with 10% KOH and were heated at 60-80^{o} C for 10-25 minutes depending on size and degree of sclerotization. Lightly sclerotized genitalia of small beetles were soaked in cold KOH overnight. Cleared genitalia were rinsed in an excess of water for several hours.

Shape and structure of female spermathecae have been used in histerid studies in comparative and phylogenetic contexts (De Marzo & Vienna, 1982; Ôhara, 1994). However, they are often very hard to find while dissecting old and dry specimens (De Marzo & Vienna, 1982; Caterino & Vogler, 2002). As this study deals with numerous rare species, often known only from very few type specimens and collected mostly 70-80 years ago, I did not look for spermathecae in females.

Cleared male genitalia were prepared to separate aedeagus and genitalic sclerites into 4 pieces: aedeagus and three sclerites, 8th sternite and tergite together, 9th and 10th (if present) tergites together and 9th sternite (spiculum gastrale). This was done in a droplet of glycerol using sharp size "0" pins. In female genitalia, all the sclerites were left unseparated. Prepared genitalia were stored in glycerol in a microvial pinned together with the specimen.

2.4 Examination of Type Material

The holotype or type series were examined as a necessary prerequisite for association of published names with actual specimens. Many *Mesynodites* species were described without adequate details that could be used to distinguish them from closely related taxa. Fortunately, only five authors described all the species under study, and type specimens for almost all species were studied through loans and/or visits to museums.

Studying the type specimens of two major *Mesynodites* describers, C. Bruch and A. Reichensperger, revealed one specific problem, regular inconsistent and careless use of type specimen labels and reproduction of label information, especially by the latter. Regular use of "Type", "Cotype" or "Paratype" labels on specimens collected months and years after the paper with the description of a given species was published or three different spellings for an important type locality, Inhumas in the Brazilian state of Goiás are just a couple of examples.

This circumstance presented a serious challenge during revisions of the type specimens and series. While inspecting numerous ‘type’ specimens of these authors, I have learned some helpful clues. The collecting date (if any) seems to be one of the most consistent pieces of information. Also, host records and collector’s names provided a useful tool in discovering correct type specimens. For example, all Reichensperger’s material from Costa Rica originated from 2 local collectors, F. Nevermann and H. Schmidt. All Nevermann’s specimens came from Hamburg Farm in Limon Province, while Schmidt collected in San Jose and farm La Caja near the town. Nevermann’s labels, even if incomplete, *e.g.* listing only “Costa Rica”, are often of specific teal color, allowing identity of the locality to be inferred with some confidence. All such minor details, often in combination, were used to identify type specimens. All the specific cases were addressed under particular species accounts in the systematic section.

The 4th edition of the International Code of Zoological Nomenclature (ICZN, 1999) requires (Article 74.7.3) a lectotype designation to “contain an express statement of the taxonomic purpose of the designation.” The purpose of lectotype designations in this study is to assure correct and consistent application of the names in the future. I do not repeat this statement for each lectotype designation. All specimens designated as lectotypes were supplied with the red lectotype labels. Presentation of numerous taxonomic changes below in this dissertation does not constitute formal publication. Formal publication in a separate outlet will follow.

2.5 Data Management

Character states for analysis were written into a standard matrix using MacClade 4.0 (Maddison & Maddison, 2000), and were analyzed using PAUP* 4.0b10 for Macintosh computers (Swofford, 2001). Character state evolution was examined using character mapping features of MacClade.

Data associated with every studied specimen were entered into the LSAM database supported by Biota software (Colwell, 1996). Data relevant to this project are a subset of a much larger database of Worldwide hetaeriine specimens. In total, about 150 genera, 600 species and 3500 specimens (including undescribed taxa) were documented, accounting for approximately 90% all hetaeriine specimens preserved in scientific collections. The databased information includes locality (country, province, site, coordinates), altitude if listed on the label, collector's name, date and method of collecting, host information if available, name of identification authority and identification date, deposition institution and type status if applicable. Features of Biota were used in preparation of species records and host-guest relationship data.

In a departure from traditional conventional notations for generic names, I have spelled out genera throughout Chapter 3 to avoid inevitable confusion resulting from similarity of many of the names and the need to be clear on taxonomic changes resulting from the analyses.

2.6 Choice of Exemplar Taxa

Decisions about exemplar taxon choices were confounded by the large size of the genus *Mesynodites*, containing 43 described species even in its current strict sense (Mazur, 1997), the presence of undescribed taxa fitting a loose definition of *Mesynodites*, its possible polyphyly and unclear relationships with other genera. An additional constraint was limited availability of properly identified multiple specimens of a given species, including both sexes, which would allow all necessary dissections and preparations and full character coding. I approached exemplar selection using the logic outlined below.

First, the ingroup needed to be defined. *Mesynodites* itself was not a natural choice because of apparent non-monophyly and information about phylogenetic relationships of and within Hetaeriinae is scarce. Therefore, I based my choices on Helava *et al.*'s (1985) subdivisions. In particularly, I decided to adopt their Group E as a working ingroup based on Helava *et al.*'s results and my preliminary observations combined. Most of the species included into *Mesynodites* fit within Group E. So, broad representation of the Group E genera and *Mesynodites* species comprise the ingroup. I followed Prendini (2001) in my approach to

Table 3. List of taxa used in the phylogenetic analyses.

Higher Taxon Rank	Genus/Species Group	Species
Outroup	*Phelister* Marseul	*P. subrotundus* Say
	Synoditulus Reichensperger	undescribed *sp.*
	Thaumataerius Mann	undescribed *sp.*
	Ulkeus Horn	*sp.*
	Reninus Lewis	*R. salvini* Lewis
Ingroup		
Subgroup E 1	*Hemicolonides** Reichensperger	*H. parvulus* Lewis
	Hippeutister Reichensperger	*H. solenopsidis* Reichensperger
Subgroup E 2	*Guianahister gen. n.*	*ashei sp. n.*
	Metasynodites Reichensperger	*M. legionarius* Reichensperger
	Monotonodites Reichensperger	*M. levis* Reichensperger
		M. nitidus Reichensperger
	Eurysister Helava	*E. carinatus* Helava
Subgroup E 3	*Aemulister* Reichensperger	*A. hirsuta* Helava
	Alloiodites Reichensperger	*A. plaumanni* Reichensperger
	Cyclechinus Bickhardt	*C. amphibolus* Reichensperger
	Nymphister Reichensperger	*N. simplicissimus* Reichensperger
	Paratropinus Reichensperger	*P. scalptus* Reichensperger
	Psalidister Reichensperger	*sp.* nr. *P. furcatus* Reichensperger
	Symphilister Reichensperger	*sp.* nr. *S. hamati* Reichensperger
Subgroup E 4	*Anasynodites* Reichensperger	*A. striatus costaericae* Reichensp.
	Aphanister Reichensperger	*A. fungifer* Reichensperger
	Daitrosister Helava	*D. confirmatus* Reichensperger
	Cheilister Reichensperger	*C. lucidulus* Reichensperger
	Chrysetaerius Reichensperger	*C. iheringi* Reichensperger
Mesynodites	*M. geminus* group	*M. geminus*
		M. exclamationis Reichensperger
	M. elegantulus group	*M. elegantulus*
		M. gibbidorsum Schmidt
		M. obscurus Reichensperger
	M. bifurcatus group	*M. bifurcatus* Mann
		M. amazonicus sp. n.
	M. diadochus group	*M. diadochus* Reichensperger
		Euclasea godmani Lewis
	M. s.str. group	*M. aciculatus* Schmidt
		M. affinis Reichensperger
		M. degallieri sp. n.
	M. speculum group	*M. speculum*
		M. evanescens Reichensperger
	M. schmidti group	*M. schmidti* Lewis
		M. ciliatus Bruch
	M. unassigned species	*M. attaphilus* Bruch
		M. graniformis Schmidt
		M. major Bruch
		M. novaeteutoniae
		M. praeclusus Reichensperger

Table 3 (Continued).

Higher Taxon Rank	Genus/Species Group	Species
Mesynodites Group E, *insertae cedis*	*M.* unassigned species	*M. robustus* Reichensperger
	Trichoreninus Lewis	*T. flohri* Lewis
	Voratister Helava	*V. gilli* Helava

representation of genera in phylogenetic analysis. From terminal taxa, I used either type species of genera or species apparently closely related to those type species, *i.e.*, differing only in minute diagnostic details such as shape of aedeagus and genital sclerites, development of punctures and setae *etc*.

Final selection of non-*Mesynodites* representatives of Group E was a compromise between availability of multiple specimens per species and representation of all subgroups of Group E (Table 3). Ultimately, representatives of almost of all lineages recognized by Helava *et al.* (1985) for every subgroup were included. The only exception was the (*Fistulaster* Helava – *Tubulister* Borgmeier) clade, tentatively included in Subgroup E 2. I was not able to study any males of these genera, and no specimens of *Tubulister* were studied. Two species of *Monotonodites* were included to represent observed variability within the genus and to test its monophyly. Finally, the following are a few comments on included genera, that were omitted by Helava *et al.* or placed in other Groups.

Specimens of the type species of *Euclasea* and *Trichoreninus* were inspected during this study by pure chance as I did not have any real reason to select these genera among other hetaeriines outside Group E nor question Helava *et al.*'s placement of them in the Groups D and B, respectively. But after studying the types of *E. godmani* and *T. flohri*, I realized their importance to the study. *Euclasea godmani* appeared to be very close to several *Mesynodites* species, *e.g.*, *M. splendens* Reichensperger, *M. diadochus etc*. It was eventually chosen as a representative of the *M. diadochus* group. Characters of *T. flohri* clearly suggested its potential relatedness to several Subgroup E 3 genera. Neither *Cylcechinus* nor *Voratister* were studied by Helava *et al.* (1985), so I decided to include them into the analysis because specimens were available.

Selection of *Mesynodites* exemplars had two stages. First, all *Mesynodites* and *Euclasea* Lewis (since the type species seems to be closely related to some current *Mesynodites*) species were carefully inspected, including comparison of male genitalia of all species and female genitalia of selected species. These were sorted into what I called species groups. Each group represented a number of species possessing essentially the same phylogenetically informative characters and differing in minute, species level diagnostic features, *i.e.*, small details in the shape of the aedeagus and genital sclerites, in elytral and sternal striation (length, punctures of striae, *etc.*) and in body surface punctation (size, density, distribution over body parts). Seven species groups were identified, namely *Mesynodites bifurcatus*, *Mesynodites diadochus, Mesynodites elegantulus, Mesynodites geminus, Mesynodites schmidti, Mesynodites s. str.,* and *Mesynodites speculum* groups. Also, a few *Mesynodites* and *Euclasea* species were sorted with certainty to other genera, *i.e.*, *Daitrosister* and *Monotonodites*. Finally, six species, *Mesynodites attaphilus, Mesynodites graniformis, Mesynodites major, Mesynodites novaeteutoniae, Mesynodites praeclusus* and *Mesynodites robustus*, were not included in any group. Exact compostion of the groups is presented in the systematics section.

For the second stage of *Mesynodites* exemplar selection, two representatives of each species group (Prendini, 2001) were chosen to be included in the phylogenetic analysis. For *Mesynodites elegantulus* and *Mesynodites s. str.* groups an extra species for each, *M. obscurus* and *M. aciculatus* respectively, was added for better reflection of variability within groups (Table 3). All six group-unassigned species were also included in the analysis.

2.7 Selection of Outgroup Taxa

Understanding of sister group relationships for Hetaeriinae and relationships within the subfamily is limited (Helava *et al.*, 1985; Ôhara, 1994; Ślipiński & Mazur, 1999; Caterino & Vogler, 2002). Taxon sampling in relation to Hetaeriinae and character selection in all of the cited studies is far from optimal. The paucity of phylogenetic investigations is further hampered by extreme morphological adaptation and convergence in two apparently distantly related obligate inquilinous subfamilies, Hetaeriinae and australasian Chlamydopsinae (Ôhara, 1994; Ślipiński & Mazur, 1999; Caterino & Vogler, 2002), so the results of existing studies are not strongly supported and often are not in agreement. However, sister group relationships of Hetaeriinae and some Histerinae: Exosternini, suggested by Helava *et al.* (1985), seem to be the current consensus hypothesis among active histerid researchers (Caterino & Vogler, 2002), although these authors provided some molecular data pointing towards Histerini as an alternative sister taxon for Hetaeriinae. Overall similarity of some Hetaeriinae and Exosternini, existence of intermediate forms (*Tarsilister* Bruch and *Synoditulus*, classified currently either as basal Hetaeriinae or Exosternini [Helava *et al.*, 1985; Caterino & Vogler, 2002; N.Dégallier & A.K.Tishechkin, unpublished]), and a variety of simple forms of social insect inquilinism in Exosternini (Reichensperger, 1929; Kryzhanovskij & Reichardt, 1976; Kistner, 1982) point to those taxa as prospective sister groups to Hetaeriinae.

I chose *Phelister subrotundus* as one outgroup. The species is a common North American member of a New World genus with numerous inquilinous species that are similar to the type species of the genus, *P. rouzeti* Marseul. Another outgroup selected was *Synoditulus*, an Exosternini-looking hetaeriine genus. It was one of the basal hetaeriines in Helava *et al.*'s view and the most basal of hetaeriines studied by Caterino & Vogler (2002). I also coded a single representative from Helava *et al.*'s Groups B, C and D, *Thaumataerius, Ulkeus* and *Reninus*, respectively, to test whether inclusion of more or less relatively distantly related outgroups would improve the resolution and branch support of the resulting phylogenetic tree.

2.8 Character Selection and Descriptions

Study of the broadest range of potentially phylogenetically informative morphological characters is used throughout this study. The principles and approaches of the use of morphological characters for phylogenetic studies of Histeridae were developed in papers of Helava *et al.* (1985), Ôhara (1994) and Ślipiński & Mazur (1999), and refined recently by Caterino & Vogler (2002). In my search for characters, I tried to exploit all the morphological character systems dealt with in the above mentioned sources. As discovered by Helava *et al.* (1985), male genitalia seem to be a useful source for phylogenetically informative characters in Hetaeriinae. Also, I made extensive use of female genitalia and mouthpart characters that were only occasionally incorporated by recent histerid phylogenetic studies (Ślipiński & Mazur, 1999; Caterino & Vogler, 2002).

The external morphological terminology used throughout this study generally follows that of Helava *et al.* (1985), Ôhara (1994) and Kanaar (1997). No complete agreement exists on the homology of abdominal sclerites associated with male genitalia in Histeridae and Hetaeriinae in particular (Helava *et al.*, 1985; Ôhara, 1994; Caterino & Vogler, 2002). The recent, rather radical revision (Kovarik *et al.*, 1999; Kovarik & Caterino, 2001) of the widely accepted consensus of genital sclerite nomenclature, going back to Reichardt (1941), seems to be incompletely developed. For the sake of consistency, I chose to follow male genitalia terminology of Helava *et al.* (1985), which is consistent with Caterino & Vogler's (2002) usage, with two minor modifications. First, I used the term "velae" (Kovarik *et al.*, 1999; Kovarik & Caterino, 2001) instead of "discs" of 8th sternite. Second, Helava *et al.* (1985) apply two different terms, "internal guide" and "movable armature", to structures that appear to be homologous. I used a more functionally neutral term "ventral process" as a replacement name. Nomenclature and homology of female genital sclerites follows Hansen (1997) and Dégallier (1998c). Terminology of morphological structures and character states are presented in the character list and accompanying annotations (Chapter 3.2).

2.9. Cladistic Methods

Parsimony analyses were performed using the heuristic search option of PAUP* 4.0b10 for Macintosh (Swofford, 2001) on a MacIntosh platform. Only potentially phylogenetically informative characters are included. Numerous authors (*e.g*., Farris, 1972; Meacham, 1986; Nixon & Carpenter, 1993; Swofford & Beagle, 1993) have suggested that the most efficient and logical way of polarizing characters with parsimony programs is to do a simultaneous parsimony analysis of the outgroup and ingroup. Consequently, no assumptions were made regarding polarizations of character states, and all characters were treated as unordered. All multistate characters were treated as non-additive.

Bootstrap analysis (Felsenstein, 1985), using 1,000 resampling replicates, was employed to study the level of character support in the dataset for hypothesized clades. Character distributions and alternative tree topologies were studied using MacClade v. 4.0 (Maddison & Maddison, 2000). The monophyly of each genus group taxon was tested in the context of the phylogeny of the entire set of taxa examined.

2.10. Analysis of Host-Guest Evolution

Host relationships at the host genus level were coded as a multi-state character and optimized on the consensus tree using both ACCTRAN and DELTRAN options in MacClade (Maddison & Maddison, 2000). Host information was not included in the tree search process (Brooks & McLennan, 2002).

In the analysis of impact of the level of host specificity on speciation in neotropical Hetaeriinae, I compiled all available information on host associations using the LSAM

Hetaeriinae database (see Chapter 2.5) and relevant complimentary literature (Helava *et al.* 1985; Dégallier 1998b, 1998c and some references therein). As the database information is based on actual inspection of a large number of specimens (ca. 90% of all museum specimens Worldwide) and mistakes in published host information are rather common (see Chapters 1.1 and 2.4), priority was given to specimen-originating information (label information, host specimens mounted with guest specimens).

I used the host genus level of host specificity because of a paucity of host species level data and a general pattern of genus-to-genus specificity in hetaeriine host-guest systems (Helava *et al.*, 1985). To account for the effect of sampling effort on probability of detecting alternative, potentially less preferred and rare hosts, I used only host information derived from multiple independent host records with a lower cut-off of three records. Two separate data sources for species diversity within genera were used: first, recent published information (Mazur, 1997; Dégallier, 1998b, 1998c); second, this information was supplemented with counts of all available sorted undescribed species, which could be ascribed to a particular genus with certainty, and unpublished synonymies and generic rearrangements. Host information accompanying undescribed species was also used if available. Beetle genera reported from colonies of a single host genus were considered specialists, while genera with 2+ host genera records as generalists. Differences were tested using Wilcoxon paired test.

2.11. Preparation of Illustrations

Habitus illustrations were prepared on a FEA Quanta 200 scanning electron microscope at the Veterinary School, Louisiana State University, using uncoated specimens. Line drawings were done using two methods. Most of the illustrations were prepared using digital images taken by an Olympus U-TV1 X camera attached to an Olympus SZW12 dissecting scope and edited by Image-Pro Plus software on an IBM platform. Outlines of digital images were used as templates for drawings made with reference to corresponding structures observed under a dissecting scope.

A small fraction of the illustrations, mostly of smaller genitalia structures were prepared with a *camera lucida* attached to Wild M5 dissecting scope.

In species accounts and the identification key I sometimes refer to the illustrations of external morphologies and male genitalia in Helava *et al*. (1985). Those figures are mentioned in ***bold italic***.

CHAPTER 3. PHYLOGENY OF THE *MESYNODITES* COMPLEX

3.1 Introduction

This chapter presents the results of a phylogenetic analysis of the *Mesynodites* complex undertaken to test the monophyly of *Mesynodites s. l.*, to uncover monophyletic lineages within the *Mesynodites* complex and to investigate relationships among them. These results are used to improve generic level classification within the ingroup, specifically, to assign *Mesynodites* species to corresponding genera, to update generic assignments of species in some other genera (*e.g.*, *Euclasea* and *Monotonodites*), and to describe necessary new taxa. Also, study of genera used here as outgroups allowed some conclusions on the nature of basal Hetaeriinae.

3.2 Characters and Character States

The following characters and their states were used in the phylogenetic analysis. The states were entered into a character by taxon character-state matrix (Table 4) with missing data coded with a question mark (?). Two approaches were used to code inapplicable data in multistate characters to represent both sides of the "inapplicables' coding" controversy (Forey & Kitching, 2000). These data were coded either as numbers (corresponding states underlined in the list below) or with a dash (-) as listed in Table 4. Matrices with both types of coding were run through parsimony heuristic search in PAUP separately. A few new terms are introduced in the list below. Those are verbally explained at the first mention and referred to corresponding illustrations.

List of characters and character states.

1. Antennal club, dorsal surface: (0) not sclerotized, pubescent; (1) completely sclerotized; (2) with narrow sclerotized strip.
2. Antennal club, outer lateral surface: (0) not sclerotized, pubescent; (1) sclerotized, at least partly.

3. Antennal club, inner lateral surface: (0) not sclerotized, pubescent; (1) sclerotized, at least partly.

4. Antennal club, ventral surface: (0) not sclerotized, pubescent; (1) sclerotized, at least partly.

5. First antennomere: (0) narrow, elongate; (1) expanded, angulate.

6. Mandible, face of base: (0) unmodified; (1) with shallow depression; (2) with deep funnel-like depression, almost perforated.

7. Mandible, edge of base: (0) unmodified; (1) deeply and narrowly cut.

8. Maxilla, circular sucker on galea in males: (0) absent; (1) present.

9. Maxilla, number of major setae on outer edge of 2nd palpomere: (0) two; (1) one; (2) none; (3) three.

10. Maxilla, number of major setae on outer edge of 3rd palpomere: (0) two; (1) one; (2) none; (3) three.

11. Labium, apical setiferous pore on 1st palpomere: (0) present; (1) absent.

12. Labium, number of extra setiferous pores on latero-apical area of 1st palpomere: (0) none; (1) one; (2) two; (3) four.

13. Labium, number of major setae on outer apical area of 3rd palpomere: (0) none; (1) one; (2) two; (3) three.

14. Labium, number of major setae on inner edge of 3rd palpomere: (0) none; (1) one; (2) two; (3) three.

15. Labium, transverse striation on inner edge of 4th palpomere: (0) absent; (1) present.

16. Labium, internal edge of paraglossa: (0) without major setae; (1) with a row of major setae.

17. Labium, ventral surface of paraglossa: (0) densely covered with tiny cuticular teeth; (1) tiny cuticular teeth present only along inner edge.

18. Labium, number of major setae on inner edge of palpiger: (0) eight; (1) four (2); five; (3) six; (4) twelve.

19. Mentum, apical margin: (0) shallowly concave, almost straight; (1) deeply emarginate.

20. Mentum, number of major setae on lateral area: (0) four; (1) one; (2) two.

21. Mentum, number of minor setae on lateral area: (0) none; (1) one; (2) two; (3) three; (4) four.

22. Mentum, basal major setae: (0) present; (1) absent.

23. Labrum: (0) free from clypeus; (1) fused with clypeus.

24. Labrum, apical margin: (0) simple; (1) serrate.

25. Labrum, setae along apical edge: (0) absent; (1) present.

26. Frons, frontal stria: (0) entire; (1) interrupted; (2) absent.

27. Frons, latero-marginal carina: (0) absent; (1) present.

28. Pronotum, lateral sections of marginal stria: (0) present; (1) absent.

29. Pronotum, apical section of marginal stria: (0) present; (1) absent.

30. Pronotum, outer lateral stria: (0) absent; (1) present.

31. Pronotum, anterior stria: (0) present along apical angles; (1) complete; (2) absent.

32. Pronotum, punctured/striate depression in prescutellar area: (0) present; (1) absent.

33. Pronotum, lateral sides: (0) unmodified; (1) thickened and elevated.

34. Elytron, outer subhumeral stria: (0) present as apical fragment; (1) complete.

35. Elytron, inner subhumeral stria: (0) complete; (1) absent.

36. Elytron, oblique subhumeral stria: (0) present; (1) absent.

37. Elytron, elytro-epipleural border: (0) smooth, gradually rounded; (1) sharp, angulate along subhumeral stria.

38. Elytron, dorsal striation: (0) full set of striae present; (1) greatly reduced.

39. Elytron, strial pilosity: (0) absent; (1) present, short and depressed; (2) present, long and erect.

40. Propygidium, marginal stria along basal margin: (0) absent; (1) present.

41. Propygidium, marginal stria along lateral sides: (0) absent; (1) present.

42. Propygidium, marginal stria along apical margin: (0) absent; (1) present.

43. Propygidium, apical margin in female: (0) unmodified; (1) with small obtuse central tooth.

44. Pygidium in female: (0) unmodified; (1) with glandular pubescent oculae.

45. Pygidium in female: (0) unmodified; (1) bistriate.

46. Pygidium in female: (0) unmodified; (1) with transverse striation.

47. Pygidium in female: (0) unmodified; (1) with 2 low obtuse elevations.

48. Protibia, upper margin: (0) with few robust spines; (1) with numerous delicate spines; (2) without spines.

49. Protibia, apical spur: (0) present; (1) absent.

50. Meso- and metatibia, shape: (0) elongate triangular; (1) widened, paddle-like; (2) elongate, stick-like.

51. Meso- and metatibia, spines of upper margin: (0) present; (1) absent.

52. Meso- and metatibia, apices: (0) with several spines; (1) without spines.

53. Meso- and metatibia, apices: (0) without bristles; (1) with several bristles.

54. Meso- and metatibia, upper marginal stria on outer face: (0) absent; (1) present.

55. Meso- and metatibia, central longitudinal stria on outer face: (0) absent; (1) present.

56. Meso- and metatibia, lower marginal stria on outer face: (0) present, single; (1) absent; (2) present, double.

57. Meso- and metatibia, tarsal cavities on inner face: (0) absent; (1) present.

58. Mesotibia, upper margin: (0) without central tooth; (1) with central tooth.

59. Metatibia, upper margin: (0) without central tooth; (1) with central tooth.

60. Meso- and metafemora, longitudinal striae on outer face: (0) absent; (1) present.

61. Prosternum, prosternal lobe: (0) long, prominent; (1) short, strap-like.

62. Prosternal lobe, apical portion of marginal stria: (0) present; (1) absent.

63. Prosternal lobe, lateral portions of marginal stria: (0) absent; (1) present.

64. Prosternal lobe, deep longitudinal sutures: (0) absent; (1) present. The character state 64-1 corresponds to Helava *et al.*'s (1985) state 'pronotal lobe tripartite' (character 14), which does not adequately describe observed variation and may be misleading.

65. Prosternal lobe, preapical foveae: (0) absent; (1) present. Whether foveae on the prosternal lobe of some Hetariinae called preapical here are truly homologous with preapical foveae of many Saprininae (Kryzhanovskij & Reichardt, 1976; Ôhara, 1994) is not clear. The structure and position of the prosternal foveae in both subfamilies are quite similar, so I apply the same term for hetaeriines.

66. Prosternal lobe, lateral foveae: (0) absent; (1) present (Fig. 18-B). If present, lateral foveae of prosternal lobe are more or less small deep invaginations in the basal parts of the lobe's marginal stiae.

67. Prosternal lobe, lateral notches: (0) absent; (1) present (Fig. 11-B). If present, the lateral notches of prosternal lobe form small cuts or folds in latero-basal parts of the lobe, where it meets the rest of the prothorax.

68. Prosternum, prosternal keel: (0) rather narrow, flat; (1) narrow, acute in apical half; (2) wide, flat.

69. Prosternum, carinal striae: (0) convergent, narrowly separated; (1) parallel basally, widely separated; (2) absent.

70. Prosternum, lateral prosternal striae: (0) present; (1) absent.

71. Mesosternum, anterior marginal stria: (0) present, complete; (1) present as lateral fragments; (2) absent.

72. Mesosternum, discal marginal stria: (0) present; (1) absent.

73. Mesosternum, anterior margin outline: (0) pointed as short denticle; (1) with a prominent central process; (2) straight.

74. Metasternum, meso-metasternal sutural stria: (0) present; (1) absent.

75. Metasternum, outer lateral striae: (0) present as short fragments; (1) present, complete (with long recurrent arm); (2) absent.

76. Metasternum, inner lateral striae: (0) present; (1) absent.

77. Metasternum, recurrent arms of inner lateral striae: (0) absent; (1) present, continuous with striae: (2) present, separate from striae.

78. Metasternum, longitudinal discal striae: (0) absent; (1) present.

79. Metasternum, metepisternal striae: (0) present; (1) absent.

80. Metasternum, meta-metepisternal sutures terminate at: (0) metepisterno-metepimeral sutures; (1) outer apical parts of metacoxae.

81. First abdominal sternite, postmetacoxal striae: (0) present; (1) absent.

82. First abdominal sternite, recurrent arm of postmetacoxal striae: (0) present; (1) absent.

83. First abdominal sternite, lateral striae: (0) present; (1) absent.

84. Aedeagus, basal piece: (0) short; (1) long.

85. Aedeagus, basal piece, posterior opening: (0) caudo-ventral, asymmetric; (1) caudal, circular; (2) ventral, elongate-oval .

86. Aedeagus, basal piece, posterior opening: (0) without “collar”; (1) with “collar” (Fig. 19-B).

87. Aedeagus, basal piece, dorsal apical emargination: (0) absent; (1) wide and shallow (Fig. 15-E); (2) narrow and deep (Fig. 19-E).

88. Aedeagus, parameres: (0) long; (1) short

89. Aedeagus, parameres: (0) dorsoventrally flattened; (1) cylindrical or subcylindrical; (2) laterally flattened; (3) cylindrical at base, than dorsoventrally flattened.

90. Aedeagus, parameres, dorsal fusion: (0) present, long; (1) present, very narrow basally; (2) absent.

91. Aedeagus, parameres, ventral fusion: (0) present, long; (1) present, very narrow basally; (2) absent.

92. Aedeagus, position of apical part of penis: (0) on dorsal side of parameres; (1) central, between parameres.

93. Aedeagus, penis orientation: (0) along longitudinal axis of parameres; (1) close to perpendicular to longitudinal axis of parameres.

94. Aedeagus, parameres, lateral vertical appendages: (0) absent; (1) present.

95. Male 8th sternite, halves: (0) separated; (1) fused.

96. Male 8th sternite, size of halves: (0) full; (1) substantially reduced.

97. Male 8th sternite, velae: (0) absent; (1) present.

98. Male 8th sternite, size of velae: (0) velae absent (here and below inapplicables are underlined); (1) small to medium; (2) substantially enlarged. Velae were coded as substantially enlarged when their diameters were about half of the 8th sternite width and subequal to the distance between apical parts of 8th sternite and tergite. There is a distinct difference between states 1 and 2 as diameters ‘small to medium’ velae is about no more than 1/4 of the 8th sternite width and no more than half of the distance between apical parts of 8th sternite and tergite.

99. Male 8th sternite, number of velae: (0) velae absent; (1) separate pair; (2) fused pair; (3) two pairs.

100. Male 8th sternite, apical internal transverse sclerotization: (0) absent; (1) present. Sometimes, an area on the dorsal surface of the sternite is distinctly sclerotized and darker than the surrounding cuticle.

101. Male 8th sternite, apical internal transverse process: (0) absent; (1) present. Internal transverse process sometimes present as transverse, rather thick elevated rim on the dorsal surface of the sternite.

102. Male 8th sternite, longitudinal internal folds: (0) absent; (1) present. Fold may present on the dorsal surfaces of each half of the sternite, running through a substantial part of its length.

103. Male 8th sternite, apical setae: (0) present along most of the margin; (1) absent; (2) present in single tuft in outer angles.

104. Male 8th tergite, transverse anterior stria (TAS): (0) absent; (1) present.

105. Male 8th tergite, apical ends of TAS: (0) TAS absent; (1) at/close to apical margin; (2) at lateral sides around apical third.

106. Male 8th tergite, transverse posterior suture: (0) absent; (1) present.

107. Male 8th tergite, intra-TAS plate: (0) TAS absent; (1) more or less complete; (2) greatly reduced (nearly absent). Intra-TAS is defined as a tergite part enclosed by TAS, *i.e.*, lying inward and apicad of it.

108. Male 8th tergite, intra-TAS plate: (0) TAS absent; (1) uncut along TAS; (2) partially cut along TAS; (3) completely separated from the rest of sternite along TAS.

109. Male 8th tergite, intra-TAS plate: (0) TAS absent; (1) uncut along midline; (2) partially cut along midline; (3) completely cut along midline.

110. Male 9th sternite, basal “handle”: (0) stick-shaped; (1) spoon-shaped; (2) strap-shaped.

111. Male 9th tergite, ventral apodeme: (0) absent; (1) present.

112. Male 9th tergite, ventral apodeme: (0) absent; (1) >> than basal projection; (2) << than basal projection; (3) ~ equal to basal projection.

113. Male 9th tergite, ventral process: (0) absent; (1) present.

114. Male 9th tergite, ventral process: (0) absent; (1) present, short and membranous; (2) present, large and sclerotized, fused to sternite; (3) present; heavily sclerotized, stick-shaped, movable.

115. Male 9th tergite, lateral halves: (0) separated; (1) fused.

116. Male 9th tergite, apical projections: (0) absent; (1) rudimentary; (2) long .

117. Male 9th tergite, apical projections: (0) absent; (1) simple, thin; (2) thick, sclerotized.

118. Male 9th tergite, apical projections: (0) absent; (1) with apices squared or rounded; (2) with apices pointed.

119. Male 9th tergite, apical projections: (0) absent; (1) with apices complete; (2) with apices deeply incised.

120. Male 9th tergite, apical projections: (0) absent; (1) without dorso-apical tooth; (2) with dorso-apical tooth.

121. Male 9th tergite, apical projections: (0) absent; (1) without ventro-apical tooth; (2) with ventro-apical tooth.

122. Male 9th tergite, base of apical projections (laterally): (0) no projections present; (1) without a notch; (2) with a notch.

123. Male 10th tergite: (0) present, well-developed; (1) present, rudimentary; (2) absent.

124. Male 10th tergite, halves: (0) separate; (1) fused; (2) tergite absent.

125. Male 9th tergite, apical projection of body (?or fused remnants of 10th tergite): (0) absent; (1) present.

126. Male 9th tergite, membranous extra (dorsal) ventral processes (?or fused remnants of 10th tergite): (0) absent; (1) present.

127. Female genitalia, retractable ovipositor: (0) present; (1) absent.

128. Female 8th sternite, apical setae: (0) absent; (1) present.

129. Female 8th sternite, central tooth on apical margin: (0) absent; (1) present.

130. Female 8th sternite, apical margin: (0) unmodified, continuous; (1) moderately emarginated; (2) emarginated/cut all the way to base.

131. Female 8th sternite, apical margin: (0) simple, unmodified; (1) heavily sclerotized.

132. Female 8th sternite, basal bridge: (0) not developed; (1) distinct (Fig. 7-B, C). The basal bridge of the 8th sternite in females is a narrow transverse basal plate, separated at least

basally and laterally, usually with distinct basal angles. In case of a deeply cut sternite (130-3), it represent a true bridge connecting the two halves of the sternite.

133. Female 8th sternite, basal bridge: (0) not developed; (1) much narrower than sternite base; (2) encompasses the entire width of sternite base.
134. Female 8th sternite, basal angles: (0) rounded, not prominent; (1) angulate, prominent.
135. Female 8th sternite, basal bridge: (0) not developed; (1) lateral parts continuous with reminder of sternite; (2) lateral parts shortly angulate; (3) lateral parts form long backwards “proximal apodemes.”
136. Female 8th sternite, separate median sclerite: (0) absent; (1) present (Fig. 16-B).
137. Female 8th tergite, present as: (0) single plate; (1) two lateral sclerites; (2) narrow basal membranous band; (3) absent.
138. Female 8th tergite, apical margin: (0) straight, uncut; (1) deeply emarginated; (0) no single sclerite plate present.
139. Female 8th tergite, basal apodemes: (0) present; (1) absent.
140. Female 9th sternite, coxite shape: (0) subcylindrical, robust; (1) triangular, more or less flattened, delicate.
141. Female 9th sternite, coxite connection: (0) via separate small sclerite; (1) completely separated; (2) connected by transverse bridge/plate.
142. Female 9th sternite, dorsal coxite connection: (0) absent; (1) by a dorsal bridge; (2) by two dorsal bridges; (3) by long dorsal plate
143. Female 9th sternite, ventral coxite connection: (0) absent; (1) by a ventral bridge.
144. Female 9th sternite, coxite apical setae: (0) absent; (1) present.
145. Female 9th sternite, coxite styli: (0) present; (1) absent.
146. Female 9th sternite, valvifers: (0) not fused to coxites; (1) fused to coxites.

Table 4. Character matrix. *M.* denotes *Mesynodites*, *Monot.* – *Monotonodites.*

Taxa	Characters																																						
										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Aemulister	1	1	1	1	1	1	0	1	3	0	0	0	2	3	1	1	1	3	1	1	3	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	0	2	1
Alloiodites	1	0	1	1	1	0	0	1	3	0	0	1	2	2	1	0	1	3	1	1	4	1	1	1	1	1	1	0	0	0	2	1	0	1	1	1	1	0	1	0
Anasynodites	1	0	1	1	1	0	0	1	0	0	0	2	2	2	1	0	1	3	1	1	3	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1
Aphanister	1	0	1	1	1	1	0	1	0	0	0	1	2	2	0	0	1	3	1	1	2	1	1	0	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1
Cheilister	1	1	1	1	1	0	0	1	0	0	0	0	2	2	1	1	1	1	1	1	2	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	1	0	1
Chrysetaerius	1	0	1	1	1	0	0	1	1	1	0	0	2	2	1	1	1	1	1	1	2	1	1	0	1	1	1	0	1	1	2	1	0	1	1	1	1	0	2	1
Cyclechinus	1	0	1	1	1	0	0	1	3	0	0	1	2	2	1	0	1	3	1	1	0	1	1	1	0	1	1	1	0	1	2	1	0	1	1	1	1	0	2	0
Daitrosister	1	0	1	1	1	0	0	1	0	0	0	2	2	2	1	1	1	3	1	1	4	1	1	0	1	1	1	0	0	0	1	1	0	1	1	1	1	0	2	1
Euclasea	1	0	1	1	1	0	0	1	0	0	1	0	2	2	1	1	1	0	1	2	2	1	1	0	0	1	1	0	1	0	1	1	0	1	1	1	0	1	0	1
Eurysister	1	0	1	1	1	2	1	1	0	0	0	1	2	2	0	1	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1
Guianahister	1	0	1	1	1	2	1	1	0	3	0	0	2	2	0	1	1	1	1	1	0	1	1	0	0	1	1	0	1	1	0	1	0	1	1	1	1	1	0	1
Hemicolonides	1	0	1	1	1	0	0	1	0	0	0	0	1	2	0	1	1	1	1	2	1	0	1	0	0	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0
Hippeutister	1	1	1	1	1	0	0	1	0	0	0	0	2	1	0	1	1	1	1	2	2	0	1	0	0	1	1	0	0	1	2	1	0	1	1	1	1	1	0	0
M. aciculatus	1	0	1	1	1	0	0	1	0	1	0	0	2	2	0	0	1	3	1	1	0	1	1	0	1	1	1	0	1	0	0	1	0	1	1	1	1	0	2	0
M. affinis	1	0	1	1	1	0	0	1	0	0	0	0	2	2	1	1	1	3	1	1	4	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1
M. amazonicus	1	0	1	1	1	0	0	1	0	0	0	1	2	2	1	1	1	0	1	2	4	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1
M. attaphilus	1	0	1	1	1	0	0	1	1	1	1	0	2	2	1	1	1	3	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	0	0	1
M. bifurcatus	1	0	1	1	1	0	0	1	0	0	0	1	2	2	1	1	1	0	1	2	4	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1
M. ciliatus	1	0	1	1	1	2	0	1	0	0	0	1	2	2	1	1	1	2	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	1
M. degallieri	1	0	1	1	1	0	0	1	0	0	0	0	2	2	1	1	1	3	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1
M. diadochus	1	0	1	1	1	0	0	1	0	0	1	0	2	2	1	1	1	0	1	2	2	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0
M. elegantulus	1	0	1	1	1	0	0	1	0	0	0	0	2	1	0	0	1	2	1	1	0	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0
M. evanescens	1	0	1	1	1	2	0	1	0	0	0	0	2	2	1	1	1	3	1	2	2	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	1
M. exclamationis	2	0	1	1	1	0	0	1	3	0	0	1	2	2	1	1	1	3	1	1	2	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1
M. geminus	2	0	1	1	1	0	0	1	3	0	0	1	2	2	1	1	1	3	1	2	2	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	0	0	1
M. gibbidorsum	1	0	1	1	1	0	0	1	0	0	0	0	2	2	0	0	1	2	1	1	0	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0
M. graniformis	1	0	1	1	1	2	0	1	0	0	0	1	2	2	0	0	1	3	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	1
M. major	2	0	1	1	1	0	0	1	2	2	0	0	2	2	1	1	1	2	1	2	0	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1
M. novaeteutoniae	1	1	1	1	1	0	0	1	0	0	1	0	2	2	1	1	1	0	1	2	2	1	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	0	1	0
M. obscurus	1	0	1	1	1	0	0	1	0	1	0	0	2	1	0	0	1	2	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0
M. praeclusus	1	0	1	1	1	2	0	1	3	0	0	1	2	2	1	0	1	3	1	1	3	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	0	1	1
M. robustus	1	0	1	1	1	0	0	1	1	2	0	0	2	2	1	0	1	4	1	2	0	1	1	0	0	1	1	0	0	1	0	1	0	1	1	1	0	1	0	0
M. schmidti	1	0	1	1	1	2	0	1	0	0	0	1	2	3	1	1	1	2	1	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	1	1
M. speculum	1	0	1	1	1	2	0	1	0	0	0	0	2	2	1	0	1	3	1	2	0	1	1	0	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	1
Metasynodites	1	0	1	1	1	2	1	1	0	0	0	0	2	2	0	1	1	1	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	0	1
Monot. levis	1	0	1	1	1	2	0	1	0	0	0	0	2	2	1	1	1	3	1	1	0	1	1	0	0	1	1	0	0	0	2	1	0	1	1	1	1	1	0	1
Monot. nitidus	1	0	1	1	1	2	0	1	0	0	0	0	2	2	1	1	1	3	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	1	1	1	1	1	0	1
Nymphister	1	0	1	1	1	0	0	1	3	0	0	1	2	2	1	1	1	2	1	1	2	1	1	0	0	1	1	0	1	1	0	1	0	1	1	1	1	1	0	1
Paratropinus	1	0	1	1	1	0	0	1	3	0	0	1	2	3	1	0	1	3	1	1	3	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	1	0	0	1
Phelister	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psalidister	1	0	1	1	1	0	0	1	3	0	0	1	2	2	1	0	1	1	1	1	2	1	1	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	0	1
Reninus	1	0	1	1	1	0	0	1	1	2	0	1	2	3	1	1	0	0	1	2	4	1	1	0	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	1
Synoditulus	1	0	1	1	1	0	0	1	0	0	1	0	2	2	0	0	0	0	1	2	2	1	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	1
Symphilister	1	1	1	1	1	1	0	1	3	3	0	0	2	3	1	1	1	1	1	1	3	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0
Thaumataerius	1	1	1	1	1	0	0	0	3	0	0	3	1	1	0	0	0	1	1	2	1	1	1	0	1	2	0	0	0	0	1	1	0	1	0	1	0	1	0	1
Trichoreninus	1	0	1	1	1	0	0	1	2	2	0	1	2	2	1	1	1	3	1	2	2	1	1	1	0	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1
Ulkeus	1	0	1	1	1	0	0	1	0	0	0	0	2	2	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	1	1	1	1	0	2	1
Voratister	1	0	1	1	1	0	0	1	0	0	0	0	2	2	1	0	1	2	1	1	0	1	1	0	0	1	1	0	0	0	0	1	0	1	1	1	0	0	0	0

Table 4 (continued).

Taxa	Characters
	4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Aemulister	1 0 0 0 0 0 0 0 1 1 1 1 1 1 0 0 1 1 0 0 1 0 1 0 0 1 1 2 1 0 1 0 1 0 1 0 2 1 1 0
Alloiodites	1 0 0 1 0 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 1 0 0 0 1 0 0 1 1 0 1 1 1 0 2 1 1 0
Anasynodites	1 0 0 0 0 0 0 0 1 1 1 1 0 1 1 2 1 1 0 0 0 0 1 0 0 1 1 2 1 0 1 1 1 1 1 0 2 1 1 1
Aphanister	1 0 0 1 0 0 0 0 1 1 1 1 0 1 0 2 1 0 0 0 0 0 1 0 0 1 1 2 1 0 1 1 1 1 1 0 0 1 1 1
Cheilister	1 0 0 0 0 0 0 0 1 1 1 1 0 1 1 2 1 1 0 0 0 0 1 0 0 1 1 2 1 0 1 0 1 0 1 0 2 1 1 0
Chrysetaerius	1 0 0 0 0 0 0 0 1 2 1 1 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 2 1 0 0 1 1 0 2 0 0 1 1 0
Cyclechinus	1 0 0 0 1 0 0 0 1 1 1 1 1 1 1 2 1 0 0 1 0 0 1 0 0 1 1 0 0 1 1 0 1 0 1 1 2 0 1 0
Daitrosister	1 0 0 0 0 0 0 0 1 1 1 1 0 1 1 2 1 1 0 0 0 0 1 0 0 1 1 2 1 1 1 1 1 1 1 0 1 1 1 0
Euclasea	1 0 0 1 0 0 0 0 1 1 0 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 2 1 1 0 1 1 2 0 1 0
Eurysister	1 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 1 1 0 0 0 0 0 1 1 0 1 1 0 0 2 0 1 0 1 0 1 1 1 1
Guianahister	1 0 0 0 0 0 0 1 1 1 1 1 1 1 1 0 1 0 0 0 0 0 0 1 1 0 1 1 0 1 2 0 1 0 1 0 1 1 1 1
Hemicolonides	0 1 0 0 1 0 0 2 1 1 1 1 1 0 0 2 1 1 1 0 0 1 1 0 0 1 1 0 0 1 2 0 1 2 1 1 2 1 1 0
Hippeutister	1 0 0 0 0 0 0 2 1 1 1 1 0 0 1 2 1 0 0 0 0 1 1 0 0 0 0 2 1 1 0 0 1 1 1 0 2 0 1 0
M. aciculatus	1 1 0 0 1 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 1 1 1 1 0 1 1 0 1 1 0
M. affinis	1 1 0 0 0 0 0 0 1 1 1 1 1 1 1 2 1 1 0 0 0 0 1 0 0 1 1 0 0 0 1 1 1 0 1 0 2 1 1 0
M. amazonicus	1 0 0 0 1 0 0 0 1 1 0 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1 1 0 2 1 1 0
M. attaphilus	1 0 1 0 0 0 0 0 1 1 0 1 1 1 1 2 1 1 0 0 0 0 1 0 0 0 1 0 0 1 0 1 1 0 1 0 0 1 1 0
M. bifurcatus	1 0 0 1 0 0 0 0 1 1 0 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1 1 0 2 1 1 0
M. ciliatus	1 0 0 0 1 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 0 1 1 0 1 0 0 0 1 0 1 1 1 0 2 1 1 0
M. degallieri	1 1 1 0 1 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 1 1 1 0 1 0 2 1 1 0
M. diadochus	1 0 0 0 1 1 0 0 1 1 0 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 0 1 0 0 1 1 0
M. elegantulus	1 0 0 0 1 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 1 1 0 1 0 1 0 2 1 1 0
M. evanescens	1 1 0 0 0 0 0 0 1 1 1 1 1 1 1 2 1 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 0 1 0 0 1 1 0
M. exclamationis	1 1 0 0 0 0 1 0 1 1 0 1 1 1 1 2 1 1 0 0 0 0 0 0 0 1 1 0 0 0 1 0 1 0 1 0 2 0 1 0
M. geminus	1 1 0 0 1 0 0 0 1 1 1 1 1 0 1 2 1 1 0 0 0 0 1 0 0 1 1 0 0 1 1 0 1 0 1 0 2 0 1 0
M. gibbidorsum	1 0 0 0 0 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 0 1 0 0 1 1 0
M. graniformis	1 1 0 0 0 0 0 0 1 1 1 1 1 0 0 2 1 0 1 0 0 0 0 1 1 0 1 0 0 0 0 0 1 1 1 0 0 1 1 0
M. major	1 0 1 0 0 1 0 0 1 1 1 1 1 1 1 2 1 1 0 0 0 0 1 0 0 1 1 0 0 0 1 0 1 0 1 0 2 0 1 0
M. novaeteutoniae	0 1 0 1 0 0 0 0 1 1 0 1 1 1 1 2 1 1 1 0 0 1 1 0 0 1 1 0 0 0 1 0 1 2 1 0 2 1 1 0
M. obscurus	1 0 0 0 0 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 1 0 0 0 0 1 0 0 1 1 0 1 0 1 1 2 0 1 0
M. praeclusus	1 0 0 0 0 0 0 0 0 1 1 1 1 0 0 2 1 1 1 0 0 0 0 0 1 0 1 0 0 0 1 1 1 1 1 0 0 1 1 0
M. robustus	1 0 0 0 1 0 0 0 1 1 0 1 1 0 1 2 1 1 1 0 0 0 1 0 0 0 1 0 0 1 1 0 1 1 1 0 2 0 1 0
M. schmidti	1 0 0 0 0 0 0 0 1 1 1 1 1 1 1 2 1 1 1 0 0 0 0 1 1 0 1 0 0 0 1 0 1 1 1 1 2 0 1 0
M. speculum	1 1 ? ? ? ? ? 0 1 1 1 1 1 1 1 2 1 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 0 1 0 0 1 1 0
Metasynodites	1 0 0 0 0 0 0 0 1 1 1 1 0 1 1 2 1 0 0 0 0 0 1 1 1 0 1 1 0 0 1 0 1 1 1 0 2 1 1 0
Monot. levis	1 0 0 0 0 0 0 0 1 1 1 1 0 0 0 2 1 1 0 0 0 0 0 1 1 0 1 0 2 1 2 1 1 1 1 1 0 0 1 0
Monot. nitidus	1 1 0 0 0 0 0 0 1 1 1 1 0 0 0 2 1 1 0 0 0 0 0 1 1 0 1 0 0 0 1 0 1 1 1 0 0 0 1 0
Nymphister	1 0 0 0 0 0 1 0 1 1 1 1 1 1 1 2 1 1 0 1 1 0 1 0 0 1 1 2 1 0 1 1 1 0 1 0 2 1 1 0
Paratropinus	1 0 0 0 0 0 1 0 1 1 1 1 1 1 1 2 1 1 0 1 0 0 1 0 0 1 1 0 0 0 1 1 1 0 1 0 2 1 1 0
Phelister	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Psalidister	1 0 0 0 1 1 0 0 1 1 1 1 1 1 0 2 1 1 0 0 0 0 1 0 0 1 1 2 1 0 1 1 1 1 1 0 2 1 1 0
Reninus	1 0 0 0 0 0 0 0 1 1 0 1 1 0 1 2 1 1 0 1 0 0 0 0 0 1 0 0 0 0 0 1 1 0 0 0 1 1 1 0
Synoditulus	1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0
Symphilister	0 0 0 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 1 0 1 0 0 1 1 2 1 0 0 1 1 0 2 1 0 0 1 0
Thaumataerius	1 1 0 0 0 0 0 0 1 2 1 1 0 0 0 1 0 0 0 0 1 1 0 0 0 0 0 0 1 0 0 1 2 0 2 1 0 0 1 1
Trichoreninus	1 1 0 0 1 0 0 0 1 1 1 1 1 1 1 2 1 1 0 0 0 0 1 0 0 1 1 0 0 0 1 0 1 0 1 0 2 0 1 0
Ulkeus	1 0 0 0 0 0 0 0 1 1 1 1 0 1 1 0 1 0 0 1 0 1 0 0 0 0 1 0 0 0 1 0 1 0 1 1 2 0 1 0
Voratister	1 0 0 0 1 0 1 0 1 1 0 1 1 1 1 2 1 1 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1 1 0 2 1 1 0

Table 4 (continued).

Taxa	Chatracters 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
	8 8 8 8 8 8 8 8 8 9 9 9 9 9 9 9 9 9 9 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Aemulister	0 1 0 1 1 0 1 1 1 2 0 1 0 0 0 1 1 1 1 1 0 0 1 1 1 1 2 1 3 1 1 1 0 – 1 2 2 1 1 1
Alloiodites	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 1 0 1 1 1 1 2 1 3 1 1 3 0 – 1 2 2 1 2 1
Anasynodites	0 1 0 1 1 0 1 1 1 1 2 1 0 0 0 0 1 2 2 0 0 0 1 1 1 1 1 1 1 2 1 2 1 3 0 2 1 1 1 1
Aphanister	0 0 0 1 1 0 1 1 3 1 2 1 0 0 0 0 1 2 2 0 0 0 1 1 1 1 1 1 1 2 1 2 1 3 0 2 1 1 1 1
Cheilister	0 1 0 1 1 0 1 1 3 1 2 1 0 0 0 1 1 2 1 0 0 0 1 1 2 1 1 1 2 2 1 2 1 3 0 1 1 1 1 1
Chrysetaerius	0 0 0 1 1 0 1 1 3 1 2 1 0 0 0 0 1 1 1 0 0 0 1 1 2 1 1 1 1 2 1 1 1 3 0 1 1 1 1 1
Cyclechinus	0 1 1 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 0 0 1 1 1 1 2 1 3 1 1 3 0 – 1 2 2 1 1 1
Daitrosister	0 1 0 1 1 0 1 1 3 1 2 1 0 0 0 0 1 1 3 0 0 0 1 1 1 1 1 2 2 2 1 2 1 3 0 1 1 1 1 1
Euclasea	0 1 1 1 2 0 1 0 0 0 0 1 0 1 1 0 1 1 1 1 0 0 2 1 1 1 1 1 1 1 1 2 1 2 0 1 1 1 1 1
Eurysister	0 1 1 1 1 0 1 1 1 1 2 1 0 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 3 1 1 2 1 1 1 2 1 2 1 1
Guianahister	0 1 0 1 1 0 1 1 1 1 2 1 0 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 1 1 2 1 2 1 2 1 1 1 1
Hemicolonides	0 1 0 1 2 0 1 0 0 0 0 1 0 0 1 0 1 2 1 0 0 0 2 1 2 1 1 1 1 1 1 2 1 1 0 2 1 1 1 2
Hippeutister	0 1 0 1 1 0 1 0 0 0 0 0 0 0 1 0 1 1 3 0 0 0 1 1 2 1 1 1 1 1 1 2 1 2 1 2 1 1 1 1
M. aciculatus	0 1 1 1 1 1 2 1 0 1 1 1 0 0 0 0 1 1 1 0 0 0 1 1 1 1 1 2 2 0 0 ? 1 1 1 2 1 1 1 1
M. affinis	0 1 0 1 1 1 2 1 0 1 1 1 0 0 0 0 1 1 1 0 0 1 1 1 1 1 1 1 2 0 0 – 1 1 1 2 1 1 1 1
M. amazonicus	0 1 0 1 1 0 1 1 0 1 1 1 0 0 0 0 1 2 1 0 0 0 1 1 1 1 1 2 2 1 1 2 1 2 0 2 1 2 1 1
M. attaphilus	0 1 0 1 1 1 2 1 0 1 1 1 0 0 0 0 1 1 1 2 0 1 1 1 1 1 1 1 2 0 0 ? 1 1 1 2 1 1 1 1
M. bifurcatus	0 1 0 1 1 0 1 1 0 1 1 1 0 0 0 0 1 2 1 0 0 0 1 1 1 1 1 2 2 1 1 2 1 2 0 2 1 2 1 1
M. ciliatus	0 1 0 1 1 0 1 1 2 2 2 1 0 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 1 1 2 0 – 1 2 1 1 1 1
M. degallieri	0 1 0 1 1 1 2 1 0 1 1 1 0 0 0 0 1 1 1 2 0 1 1 1 1 1 1 1 2 0 0 ? 1 1 1 2 1 1 1 1
M. diadochus	0 1 0 1 2 0 1 0 0 0 1 1 0 1 1 0 1 1 1 1 0 0 2 1 1 0 1 1 3 1 1 2 1 2 0 1 1 1 1 1
M. elegantulus	0 1 0 1 1 0 1 0 1 2 1 1 0 0 0 1 1 1 1 0 0 0 1 1 1 1 1 2 2 1 1 3 0 – 1 2 2 1 1 1
M. evanescens	0 1 0 1 1 0 1 1 2 2 2 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1
M. exclamationis	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 1 0 1 1 1 1 2 1 3 1 1 2 0 ? 1 2 1 1 1 1
M. geminus	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 1 0 1 1 1 1 2 1 3 1 1 2 0 – 1 2 2 1 1 1
M. gibbidorsum	0 1 0 1 1 0 1 0 1 2 1 1 0 0 0 1 1 1 1 0 0 0 1 1 1 1 1 2 2 1 1 3 0 – 1 2 2 1 1 1
M. graniformis	0 1 0 1 1 0 1 1 2 2 2 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 1 0 1 2 1 2 1 2 2 2 1 1
M. major	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 0 0 0 1 1 1 1 2 1 3 1 1 3 0 – 1 2 2 1 1 2
M. novaeteutoniae	0 1 0 1 2 0 1 1 0 0 0 1 0 1 1 0 1 1 1 1 0 0 2 1 1 1 1 1 1 0 1 2 1 2 0 1 1 1 1 1
M. obscurus	0 1 1 1 1 0 1 0 1 2 1 1 0 0 0 1 1 1 1 0 0 0 1 1 1 1 1 2 2 1 1 2 0 – 1 2 2 1 1 1
M. praeclusus	0 1 0 1 1 0 1 1 2 2 1 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1
M. robustus	0 1 0 1 1 1 1 1 0 1 2 1 0 0 0 0 1 1 1 0 0 0 1 1 1 1 1 2 2 0 1 2 1 1 1 2 1 1 1 1
M. schmidti	0 1 0 1 1 0 1 1 2 2 2 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 0 1 2 0 – 1 2 1 1 1 1
M. speculum	0 1 0 1 1 0 1 1 2 2 2 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 1 1 2 1 2 1 2 1 1 1 1
Metasynodites	0 1 0 1 1 0 1 1 1 1 2 1 0 0 0 1 1 1 1 0 0 0 1 1 1 1 1 3 3 1 1 2 1 1 1 2 1 1 1 1
Monot. levis	0 1 0 1 1 0 1 1 2 2 2 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 0 1 2 1 2 1 2 1 1 1 1
Monot. nitidus	0 1 0 1 1 0 1 1 2 2 2 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 1 1 2 0 1 2 1 2 1 2 1 1 1 1
Nymphister	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 0 0 1 1 1 1 1 2 3 1 1 3 0 – 1 2 2 1 1 1
Paratropinus	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 1 0 1 1 1 1 2 1 3 1 1 1 0 – 1 2 2 1 1 2
Phelister	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 – – 0 0 0 0 0 – – – – – 0 0 – 0 – 0 0 – – – –
Psalidister	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 3 1 0 0 1 1 1 1 1 3 3 1 1 3 0 – 1 2 2 1 2 1
Reninus	0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 2 1 1 0 1 1 1 1 1 2 1 2 0 1 1 2 1 1
Synoditulus	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 – – 0 0 0 0 0 – – – – – 0 0 – 1 2 1 2 1 1 1 1
Symphilister	1 0 1 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 0 0 1 1 1 1 2 1 3 1 1 3 0 – 1 2 2 1 1 2
Thaumataerius	1 0 1 1 1 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 1 1 0 2 1 1 1 1
Trichoreninus	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 1 0 1 1 1 1 2 1 3 1 1 2 0 – 1 2 2 1 1 1
Ulkeus	0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 2 1 2 0 2 1 1 1 1
Voratister	0 1 0 1 1 0 1 1 1 2 1 1 0 0 0 1 1 1 1 1 1 0 1 1 1 1 1 2 3 1 1 3 0 – 1 2 2 1 1 1

Table 4 (continued).

Taxa	Characters
	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
	2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5
	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0
Aemulister	1 1 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 3 0 0 1 1 2 1 1 0
Alloiodites	1 1 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
Anasynodites	1 1 2 – 0 0 1 1 0 2 0 1 1 1 3 0 3 – 1 1 2 3 1 1 1 1 2 1 2 0
Aphanister	1 1 2 – 0 0 1 1 0 1 0 1 1 1 3 0 3 – 1 1 2 3 1 1 1 1 1 1 2 0
Cheilister	1 1 2 – 0 0 1 1 1 1 0 1 1 1 3 0 2 – 1 1 2 3 1 1 1 1 1 1 2 0
Chrysetaerius	1 1 2 – 0 0 1 1 0 2 0 1 1 1 3 0 3 – 1 1 2 3 1 1 1 1 2 1 2 0
Cyclechinus	1 2 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 1 0
Daitrosister	1 1 2 – 0 0 1 1 1 1 0 1 1 1 3 0 2 – 1 1 2 3 1 1 1 1 1 1 2 0
Euclasea	1 1 0 1 0 0 1 0 0 0 1 1 2 0 3 0 0 0 1 1 2 2 0 1 1 1 1 1 1 0
Eurysister	1 1 2 – 0 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 1
Guianahister	1 1 2 – 0 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 1
Hemicolonides	1 1 0 1 0 0 1 1 0 2 0 1 2 0 3 0 0 0 1 1 1 0 0 1 1 1 1 1 1 0
Hippeutister	1 1 0 1 0 0 1 0 0 2 0 1 1 0 2 0 0 0 1 1 1 0 0 1 1 1 1 1 1 0
M. aciculatus	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
M. affinis	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
M. amazonicus	1 1 0 1 0 0 1 1 0 1 0 1 1 0 2 0 1 – 1 1 2 1 1 1 1 1 1 1 2 0
M. attaphilus	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
M. bifurcatus	1 1 0 1 0 0 1 1 0 1 0 1 1 0 2 0 1 – 1 1 2 1 1 1 1 1 1 1 2 0
M. ciliatus	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 1
M. degallieri	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 0 0 1 1 1 2 1 0 1 1 1 1 1 1 0
M. diadochus	1 1 0 1 0 0 1 0 0 0 1 1 2 0 3 0 0 0 1 1 2 2 0 1 1 1 1 1 1 0
M. elegantulus	1 1 2 – 0 0 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
M. evanescens	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 0
M. exclamationis	1 1 2 – 1 0 1 0 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 2 0
M. geminus	1 2 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 2 0
M. gibbidorsum	1 2 2 – 0 0 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
M. graniformis	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 0 0 1 1 1 2 1 0 1 1 1 1 1 1 1
M. major	1 2 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 2 0
M. novaeteutoniae	1 1 1 0 0 0 1 0 0 0 1 1 2 0 3 0 0 0 1 1 2 2 0 1 1 1 1 1 1 0
M. obscurus	1 1 2 – 0 0 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0
M. praeclusus	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 0
M. robustus	1 1 2 – 1 0 1 0 0 2 0 1 1 0 2 0 0 1 1 1 2 1 0 1 1 1 1 1 1 0
M. schmidti	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 1
M. speculum	1 1 2 – 1 0 ?
Metasynodites	1 1 2 – 0 0 1 0 0 2 0 1 1 0 2 1 1 – 1 1 2 1 0 1 1 1 1 1 1 1
Monot. levis	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 1
Monot. nitidus	1 1 2 – 1 0 1 1 0 2 0 1 1 0 2 1 0 1 1 1 2 1 0 1 1 1 1 1 1 1
Nymphister	2 1 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 1 0
Paratropinus	2 1 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 1 0
Phelister	– – 0 0 0 0 0 0 0 0 0 0 – 0 – 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Psalidister	1 1 2 – 0 1 1 0 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 0 1 1 1 1 1 0
Reninus	1 1 0 0 0 0 1 1 0 2 0 1 1 0 1 0 0 0 0 1 1 0 0 0 1 1 0 1 1 0
Synoditulus	1 1 1 1 0 0 1 0 0 1 0 1 1 0 1 0 0 0 0 1 1 0 0 0 1 1 0 1 1 0
Symphilister	1 1 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 3 0 0 1 1 2 1 1 0
Thaumataerius	1 1 0 1 0 0 1 0 0 0 0 1 2 0 2 0 0 0 0 1 1 0 0 1 1 1 0 1 1 0
Trichoreninus	1 2 2 – 0 1 1 0 0 2 0 1 1 0 2 0 1 – 1 1 2 3 0 0 1 1 2 1 1 0
Ulkeus	1 1 0 1 0 0 1 0 0 2 0 1 1 0 2 0 0 0 0 1 1 0 0 0 1 1 0 1 1 0
Voratister	1 1 2 – 0 1 1 1 0 2 0 1 1 0 2 0 1 – 1 1 2 1 0 1 1 1 1 1 1 0

147. Female 9th tergite, present as: (0) pair of plates; (1) single plate.

148. Female 9th tergite, connection to 9th sternite: (0) connected by apex; (1) connected by base; (2) fused laterally to form intercoxite bridge.

149. Female genital sclerites, present as: (0) very long straps; (1) elongate sclerites; (2) comma-shaped sclerites subdivided into "head" and tail" (Fig. 13-A).

150. Female genital sclerites, present as: (0) separate pair; (1) fused V/U-shaped pair.

3.3 Results of Parsimony Analysis

Cladistic analysis of the above characters with unapplicables coded as dashes using PAUP* produced 6 most parsimonious cladograms with a length of 614 steps, CI=0.33, RI=0.60, RC=0.20. Their strict consensus is shown on Fig. 1. Analysis of alternatively coded inapplicables (see 3.2), yielded 3 most parsimonious cladograms with almost the same statistics (length 638, CI=0.34, RI=0.61, RC=0.21) and topology. The only difference in the strict consensus tree topology in that analyses was some resolution introduced into the (*Mesynodites attaphilus - Mesynodites affinis*) clade as ((*Mesynodites attaphilus - Mesynodites aciculatus*) + (*Mesynodites degallieri - Mesynodites affinis*)).

Analyses with additional outgroups (*Thaumataerius, Ulkeus, Reninus*, in all possible compositions and 2 types of inapplicable coding, 12 in total) revealed the same major lineages within the ingroup as the above analyses (Fig. 1), namely (*Hemicolonides – Mesynodites diadochus*), (*Eurysister – Metasynodites*), (*Eurysister – Mesynodites evanescens*), (*Mesynodites attaphilus – Mesynodites affinis*), (*Mesynodites bifurcatus - Mesynodites amazonicus),* (*Anasynodites – Cheilister*), (*Alloiodites – Psalidister*) and (*Mesynodites geminus – Mesynodites major*) nested within it and (*M. elegantulus – M. gibbidorsum*) as well as sister relationships of *Euclasea* and *M. novaeteutoniae*, *Eurysister* and *Guianahister*, *Monotonodites nitidus*

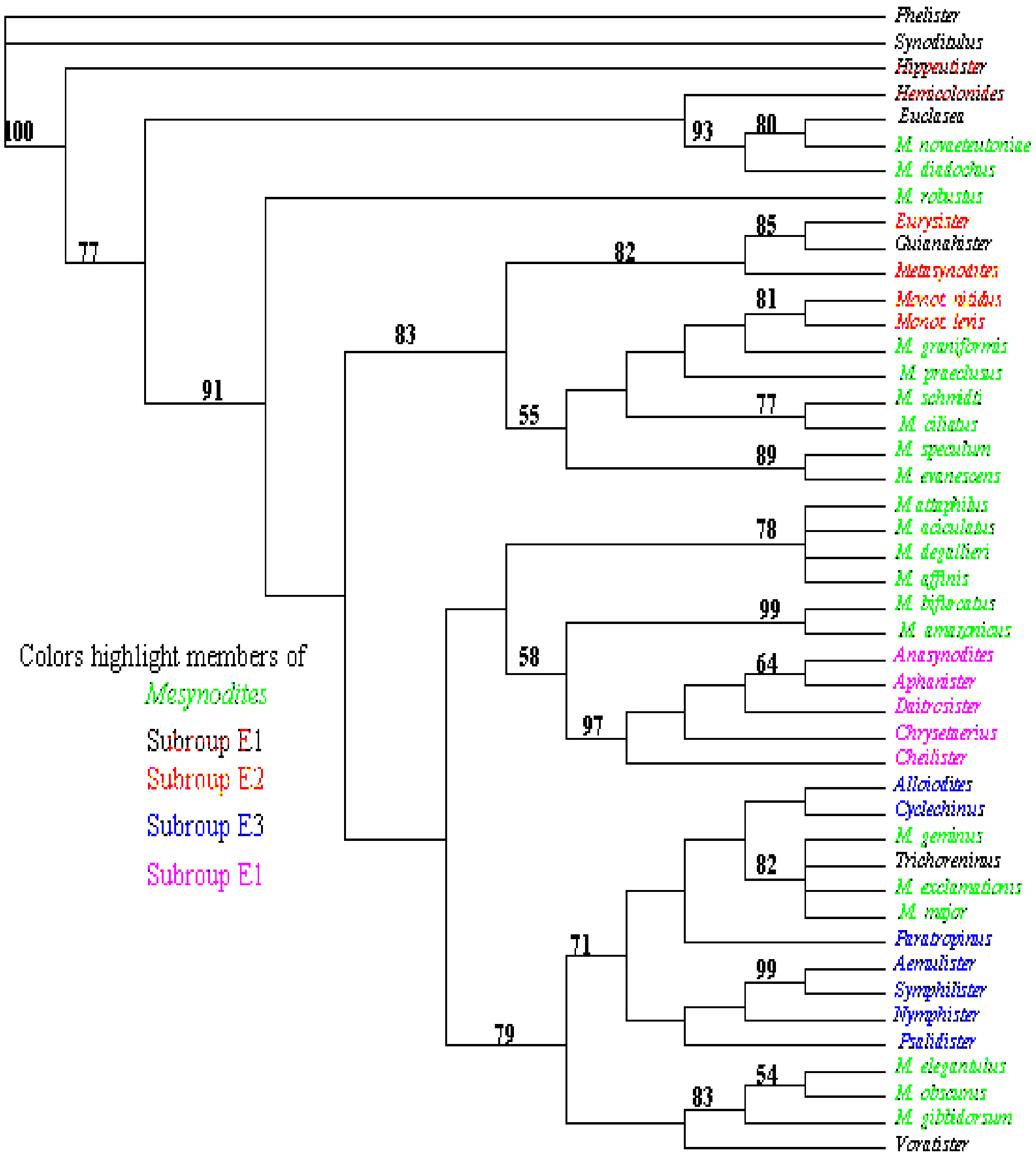


Fig. 1. Strict consensus of six most parsimonious trees for *Mesynodites* and allies obtained by heuristic search in PAUP (unapplicables coded as missing) with bootstrap values above 50% (1,000 replicates) shown. Species of *Mesynodites* and members of subgroups of Group E *sensu* Helava *et al*. (1985) are highlighted in colors. Terminal taxa with names shown in black represent outgroups and genera with doubtful affinities.

and *Monotonodites levis*, *Mesynodites schmidti* and *Mesynodites ciliatus*, *Mesynodites speculum* and *Mesynodites evanescens*, *Anasynodites* and *Aphanister*, *Aemulister* and *Symphilister, Mesynodites graniformis* and *Mesynodites praeclusus* within (*Monotonodites – Mesynodites evanescens*) clade/grade. Four of these 12 trees have essentially the same topology as depicted on Fig. 1, two of them differing by minor details in the clade (*Eurysister – Mesynodites evanescens*) exclusive of (*Eurysister – Metasynodites*).

The remaining eight of these alternative trees represented several differences with respect to relative positions of major clades (Fig. 2). First, the position of *Mesynodites robustus* varies from sister taxon of (*Eurysister – Mesynodites evanescens*) or (*Mesynodites attaphilus – Mesynodites affinis*) to basal to (*Eurysister – Voratister*). Second, if *Mesynodites robustus* was not basal to this group, this position was occupied either by (*Mesynodites bifurcatus* + *Mesynodites amazonicus*) or (*Mesynodites bifurcatus - Cheilister*). Third, if (*Mesynodites bifurcatus* + *Mesynodites amazonicus*) was not a sister to (*Anasynodites – Cheilister*), or unresolved near it, it was a sister to (*Mesynodites attaphilus – Mesynodites affinis*) in one of analyses. Fourth, *Voratister* alternatively was found on two occasions to be a sister of (*Aemulister – Psalidister*) or on one occasion unresolved within (*Alloiodites – Psalidister*). Fifth, (*Mesynodites schmidti* + *Mesynodites ciliatus*) were recovered twice outside (*Monotonodites – M. evanescens*) as a sister to (*Eurysister – Metasynodites*).

Statistics of alternative trees were similar to that revealed by the analysis with *Phelister* and *Synoditulus* as the only outgroups within the following ranges: CI=0.31-0.35, RI=0.59-0.62, RC=0.18-0.21. Almost all the bootstrap support values above 50% reported on Fig. 1 were recovered for the corresponding nodes in the analysis using additional outgrops within ±5% of respective values in Fig. 1. However, bootstrap support >50% was never found for nodes leading to (*Mesynodites bifurcatus - Cheilister*) and (*Monotonodites – Mesynodites evanescens*). So, because alternative

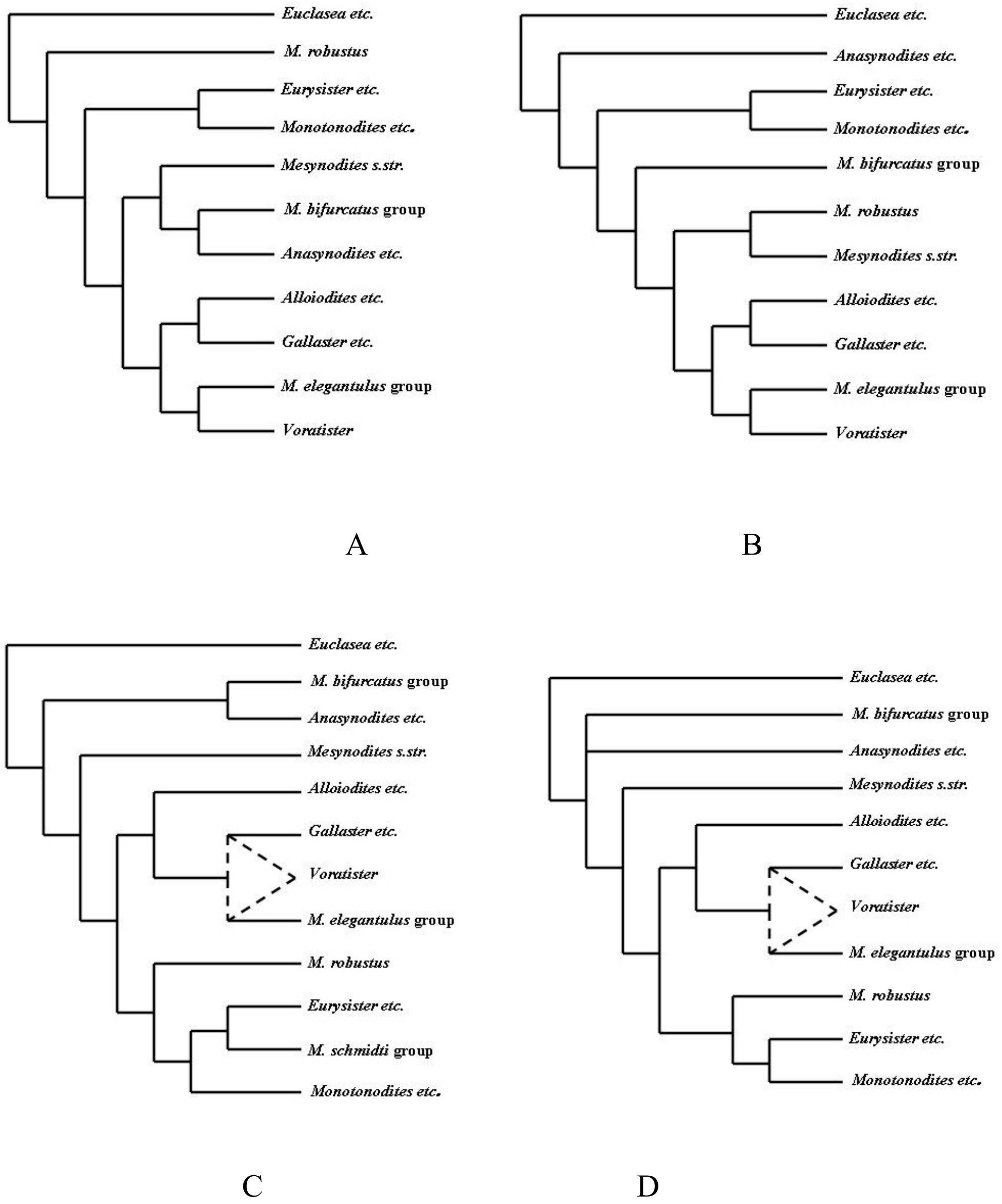


Fig. 2. Summary of alternative topologies of the relationships within Group E obtained with alternative coding of unapplicables and variable numbers/combinations of outgroups. A. Topology depicted on Fig. 1, B-D. Condensed variants of alternative topologies. Broken lines indicated alternative nodes. Major clades are abbreviated after Fig. 1 as follows: *Euclasea etc.* = (*Hemicolonides – Mesynodites diadochus*), *Eurysister etc.* = (*Eurysister – Metasynodites*), *Monotonodites etc.* = (*M. nitidus – Mesynodites evanescens*), *Mesynodites s.str.* = (*M. attaphilus – A. affinis*), *M. bifurcatus* group = (*M. bifurcatus – M. amazonicus*), *Anasynodites etc.* (*Anasynodites – Cheilister*), *Alloiodites etc.* = (*Alloiodites – Paratropinus*), *Gallaster etc.* = (*Gallaster – Psalidister*), *Mesynodites elegantulus* group = (*M. elegantulus – M. gibbidorsum*), *M. schmidti* group = (*M. schmidti – M. ciliatus*).

analyses with extra outgroups recovered the same major clades, provided the same or less support and resolution and the discovery of the phylogeny for the entire Group E is beyond the scope of this study, I will follow with a discussion of the parsimony results depicted on Fig. 1 and will address alternative topologies only in a context of host-guest relationships.

The resulting phylogenetic tree (Fig. 1) is in general congruence with the subgroup relationships of Helava *et al.*'s (1985) Group E, with all *Mesynodites* representatives included within it. Subgroup E 1 members, *Hemicolonides* and *Hippeutister*, along with some *Mesynodites* and *Euclasea* are basal, while the remaining Subgroups are united in a monophyletic clade. Within this large clade Subgroups E 2-4 are evident as monophyletic groups, with *Mesynodites* species embedded within and between subgroups of Helava *et al.*'s in one or another way. The node of an expanded Group E in the cladogram has 100% bootstrap support.

Under closer scrutiny, recognition of Subgroup E 1 within Group E seems to be problematic. The only Group E synapomorphy (and diagnostic character) is the character state 31-2 of Helava *et al.* (1985: 145): "Basal piece long, parameres short." Careful inspection of Helava *et al.*'s illustrations of *Hemicolonides* and *Hippeutister* aedeagi and their comparison with the genitalia illustrations of the Group D members (synapomorphic in having both parameres and basal piece long) reveals that both of the Subgroup E 1 members should be classified within Group D. Their aedeagus lengths are 72-78% of paramere length, the ratio that fits a definition of long parameres and aedeagus quite naturally. Dégallier's (1998b) redescription of *Plagioscelis* (= *Poneralister sensu* Helava *et al.* [1985], the third member of the Subgroup E 1, see Dégallier [1998b] for synonymy and details) confirms both tentative placement of it into Subgroup E 1 by Helava *et al*. based on female specimens only and necessity of its formal classification within Group D.

High support of the Group E node (*Hippeutister – Voratister*) in my analysis seems to be misleading as most probably it reflects relatively more distant relationships between outgroup members on one side and ingroup members on the other. *Hemicolonides, Hippeutister* and members of (*Euclasea – M. diadochus*) lack many synapomorphies of the (*Eurysister – Voratister*) clade (see below), while sharing several character states (*e.g*., 95-0, fused halves of male 8th sternite; 103-0, 2, presence of male 8th sternite apical setae; 123-0, 1, presence of male 10th tergite) with some members of Group D (*e.g*., *Reninus, Hetaeriobius, Nevermannister*; Helava *et al*., 1985, personal observations). So, I consider *Hemicolonides, Hippeutister* and (*Euclasea – Mesynodites diadochus*) as belonging to Group D, but not Group E, and will refer to the (*Eurysister – Voratister*) clade as "revised Group E."

The results of the analysis (Fig. 1) show strong support for the monophyly of revised Group E, based on numerous unambiguous synapomorphies (Fig. 3). Unique synapomorphies are genitalia characters and include characters 88-1, short parameres, and 84-1, long basal piece, Helava *et al.*'s original diagnostic feature for Group E. The remaining three include characters 103-1, absence of apical setae on male 8th sternite; 105-1, position of the TAS ends on apical margin of male 8th sternite; 123-2, absence of male 10th tergite; 142-1, dorsal connection of coxites by a single bridge. The bootstrap support for this clade is 91%.

Within revised Group E, the consensus of shortest trees provides evidence for the existence of four major lineages, one of them represented by a single species, *Mesynodites robustus*, and positioned as a sister to the rest. Among these three clades, (*Eurysister – Mesynodites evanescens*) is a sister of two others and its monopyly is

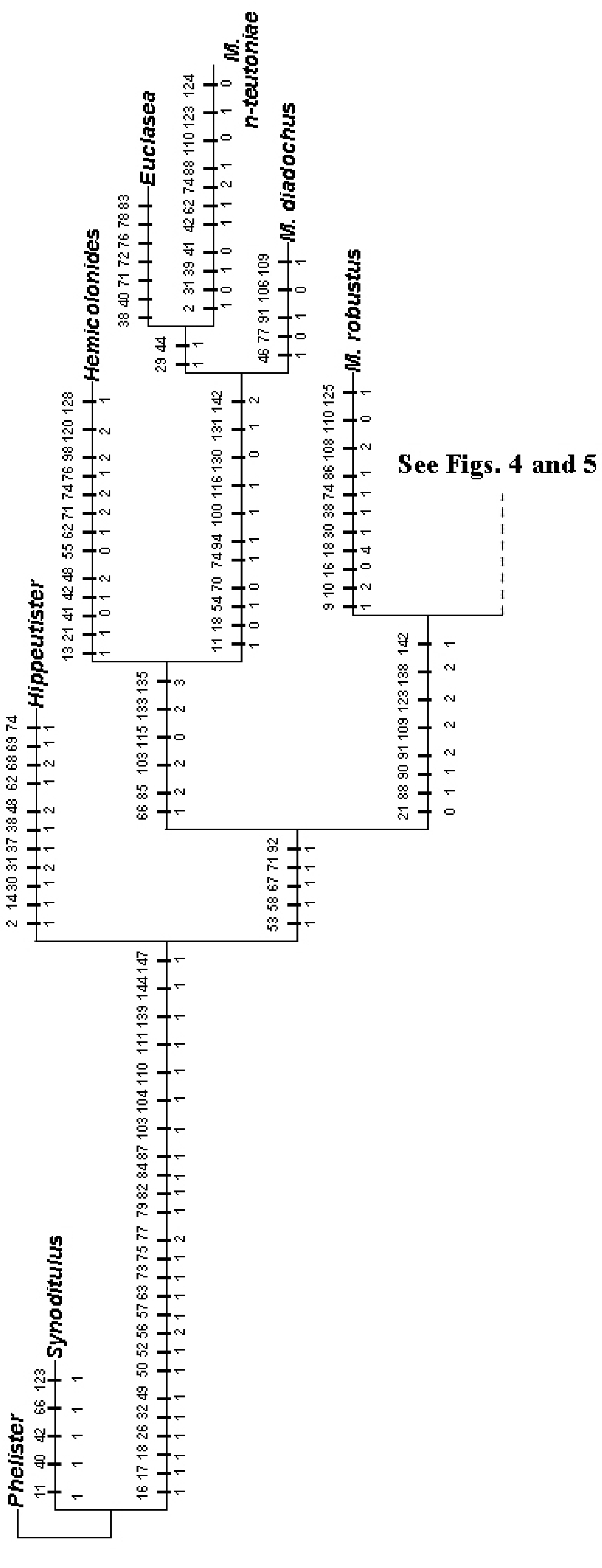


Fig. 3. Part of strict consensus cladogram of most parsimonious trees for *Mesynodites* and allies featuring unambiguous characters supporting each clade (character number on top of each branch, character number below). See Figs. 4 and 5 for the rest of the cladogram and Fig. 1 for the entire topology.

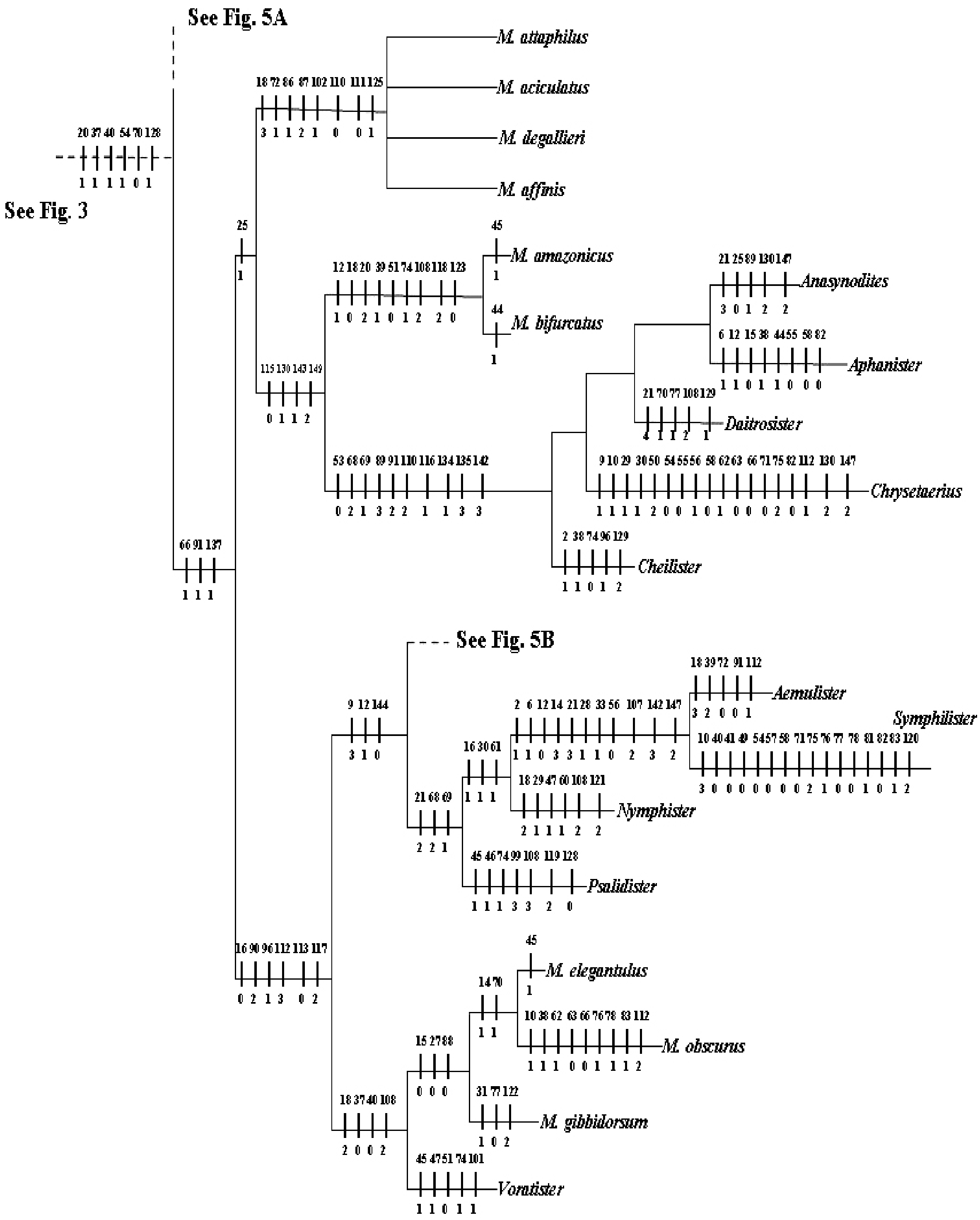


Fig. 4. Part of strict consensus cladogram of most parsimonious trees for *Mesynodites* and allies featuring unambiguous characters supporting each clade. See Figs. 3 and 5 for the rest of the cladogram and Fig. 1 for the entire topology.

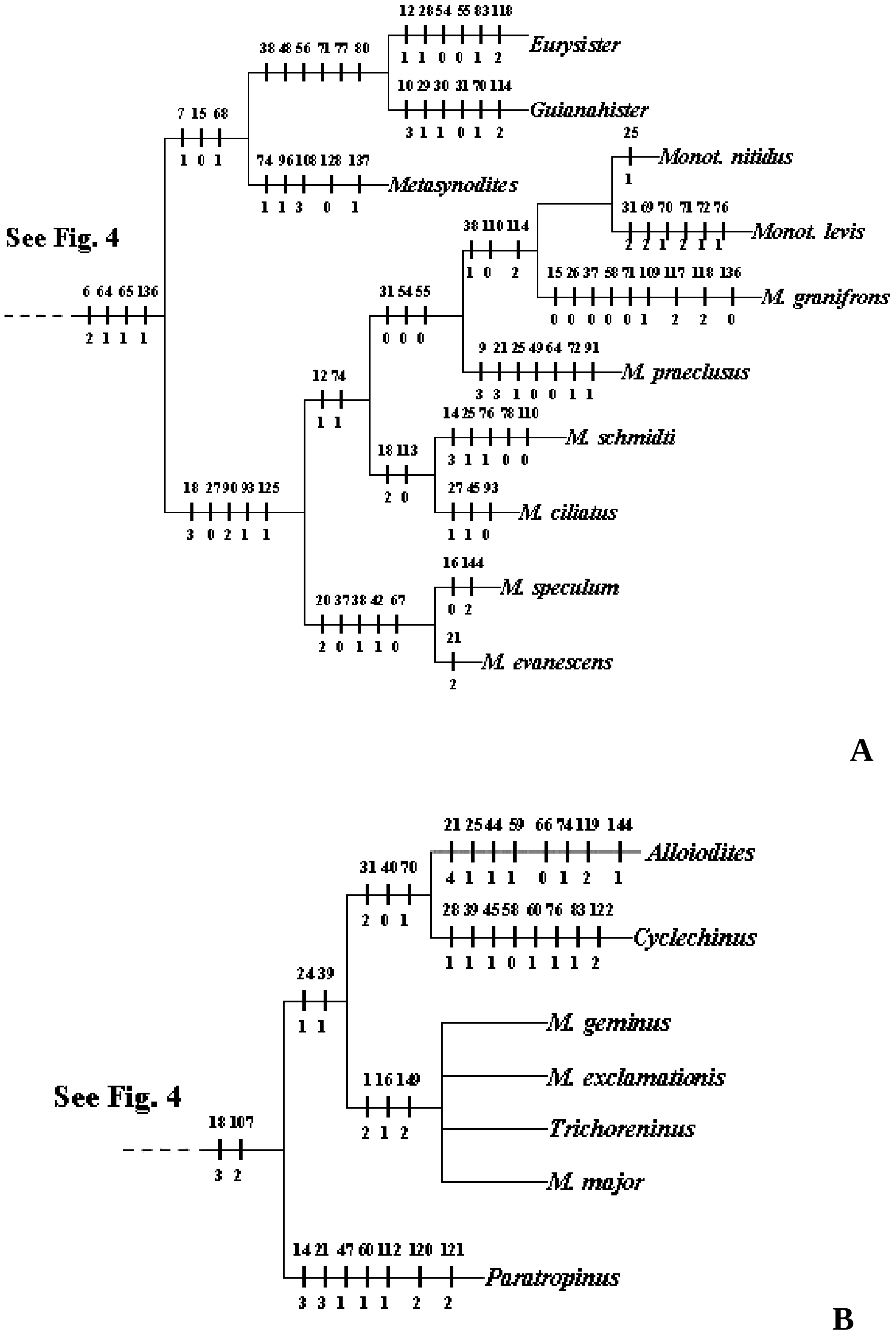


Fig. 5. Parts of strict consensus cladogram of most parsimonious trees for *Mesynodites* and allies featuring unambiguous characters supporting each clade (character number on top of each branch, character number below). See Figs. 3 and 4 for the rest of the cladogram and Fig. 1 for the entire topology.

supported by four unambiguous synapomorphies (Fig. 5) and high bootstrap value (83%).

Relationships of the other two major clades, (*Mesynodites attaphilus – Cheilister*) and (*Alloiodites – Voratister*), as well is their relations to the (*Eurysister – Mesynodites evanescens*) clade and even their exact compositions are less well supported. Nodes connecting (*Mesynodites attaphilus – Voratister*), (*Mesynodites attaphilus – Cheilister*) and (*Mesynodites bifurcatus – Cheilister*), have low bootstrap values. The (*Mesynodites attaphilus – Voratister*) clade is supported by six synapomorphies (Fig. 4), but all of them represent several reversals. Clade (*M. bifurcatus – Cheilister*) is supported by four unambiguous synapomorphies (Fig. 4) aincluding three unique ones. Clade (*M. attaphilus – Cheilister*) is less well supported among them with only one synapomorphy, including a reversal within the group (25-1).

This study was not designed originally to uncover relationships within Group E in its entirety. This problem will require a phylogenetic analysis with much denser taxon sampling. At the current level of knowledge, revised Group E consists of at least three major lineages more or less corresponding to Helava *et al.*'s Subgroups E 2-4 and enriched with *Mesynodites* representatives. However, it is important to keep in mind that the number of important clades within Group E may eventually increase with inclusion of unstudied/undiscovered genera into new clades and a possibility for increased resolution of at least two *Mesynodites s.l.* clades, (*Mesynodites attaphilus – Mesynodites affinius*) and (*Mesynodites bifurcatus – Mesynodites amazonicus*).

3.4 Test of the *Mesynodites* Complex Monophyly

The results of this phylogenetic analysis clearly show that *Mesynodites* is a polyphyletic group. Its representatives are spread widely across the entire phylogeny of the revised Group E as well as outside it. They are included within seven highly supported (77-99% bootstrap values) clades, and three species represent single taxon lineages.

Two *Mesynodites* species included into the analysis, *Mesynodites novaeteutoniae* and *Mesynodites diadochus*, were placed outside revised Group E, along with *Euclasea*, into a well supported (93%) clade with 11 unambiguous synapomorphies (Fig. 3), including six unique ones. Another group of *Mesynodites* species that formed a well-supported (82%) clade unresolved with a representative of *Trichoreninus* includes *Mesynodites exclamationis, Mesynodites geminus* and *Mesynodites major*. This clade (*Mesynodites geminus - Mesynodites exclamationis*) is characterized by three unambiguous synapomorphies (Fig. 5). The fact that the type species of named genera (*Euclasea* and *Trichoreninus*) were nested with (*Euclasea-Mesynodites diadochus*) and (*Mesynodites geminus - Mesynodites exclamationis*) clades, respectively, along with high bootstrap support for both of them is the basis of a taxonomic decision on the limits of these corresponding genera and *Mesynodites* species transferred to them (Chapter 4).

The clade (*M. attaphilus - M. affinis*) represents *Mesynodites s.str*. The type species of *Mesynodites*, *M. schuppii* Schmidt, is hardly distinguishable from *Mesynodites affinis*. Although somewhat variable in external morphology (25 characters are polymorphic within the clade, only four of them genitalic), the lineage is characterized by numerous synapomorphies in genital characters (Fig. 4). Observed variability of external morphologies apparently reflects diversity of host relationships within the group, which is the highest known for hetaeriine genera with three ecitonine ant genera and one myrmycine ant genus recorded (Chapters 4 and 6).

The remaining *Mesynodites* species in the analysis were mostly grouped away from any other named genera. This requires taxonomic decisions on generic assignments/descriptions. Well supported clades (*Mesynodites schmidti* – *Mesynodites ciliatus*), (*Mesynodites speculum* – *Mesynodites evanescens*), (*Mesynodites bifurcatus* – *Mesynodites amazonicus*) and (*Mesynodites elegantulus* – *Mesynodites gibbidorsum*) present minor problems in that respect (Fig. 1), although their relationship with more or less closely related taxa are not always well resolved. *Mesynodites robustus* was a sister taxon to the remainder of revised Group E (or, in alternative analyses, as a sister to large clades within it, Fig. 2). In all analyses it was an isolated lineage, based on a peculiar combination of characters (retention/independent evolution of characters 9-1, 10-2, 30-1, 74-1, 86-1, 108-2, 125-1, some autapomorphies not included into character matrix, see Fig. 3 and Chapter 4).

The situation with the remaining two species, *Mesynodites praeclusus* and *Mesynodites granifrons*, is somewhat more complicated. They fit into a poorly resolved part of the tree between *Monotonodites* and clades (*Mesynodites schmidti* – *Mesynodites ciliatus*), or sometimes the (*Mesynodites speculum* – *Mesynodites evanescens*) clade (Figs. 1 and 2). In general, the clade (*Monotonodites* - *Mesynodites evanescens*) was poorly resolved, with low support for many nodes and a mosaic distribution of many characters. *Monotonodites* as well as the (*Mesynodites schmidti* – *Mesynodites ciliatus*) and (*Mesynodites speculum* – *Mesynodites evanescens*) clades are well-supported and clearly defined lineages. However, affinities of *Mesynodites praeclusus* and *Mesynodites granifrons* within the (*Monotonodites* - *Mesynodites evanescens*) group are unclear. They never emerged as sisters in any of the analyses, nor could they be naturally associated with any of the subclades mentioned because both possess a unique combination of character states autapomorphic within the

(*Monotonodites - Mesynodites evanescens*) clade (characters 26-0, 37-0, 109-1, 117-1, 118-2, 136-0 for *Mesynodites granifrons*; 21-3, 25-1, 39-1, 64-0, 72-1 for *Mesynodites praeclusus*, Fig. 5), as well as some autapomorphies not included into the character matrix (see Chapter 4).

To summarize the above discussion, the following taxonomic actions will be formally undertaken below (Fig. 6, Chapter 4). The genera *Euclasea, Mesynodites* and *Trichoreninus* will be treated based on the concepts of the (*Euclasea – Mesynodites diadochus*), (*Mesynodites attaphilus - Mesynodites affinis*) and (*Mesynodites geminus – Mesynodites exclamationis*) clades, respectively. Seven new genera will be described to accommodate species in the (*Mesynodites schmidti – Mesynodites ciliatus*), (*Mesynodites speculum – Mesynodites evanescens*), (*Mesynodites bifurcatus – Mesynodites amazonicus*) and (*Mesynodites elegantulus – Mesynodites gibbidorsum*) clades and monotypic lineages of *Mesynodites granifrons, Mesynodites praeclusus* and *Mesynodites robustus*.

3.5 Comments on Basal Hetaeriinae

Helava *et al*. (1985) put their Group A, comprising a single genus *Tarsilister* Bruch, as the most basal hetaeriine lineage. Recent critical investigation of *Tarsilister* specimens has revealed some important problems with this assessment. First, it is apparently a synonym of another hetaeriine genus, *Mecistostethus* Marseul, and, second, neither of these genera belong in Hetaeriinae, but in Histerinae: Exosternini (Dégallier & Tishechkin, unpublished). This conclusion leaves an important question of which taxon is basal within Hetaeriinae unanswered.

According to the phylogeny of Helava *et al*. (1985), the removal of *Tarsilister* from Hetaeriinae puts *Synoditulus* as a next candidate for a basal genus. In fact, this seems to be both a convention among active histerid systematists and a suggestion by

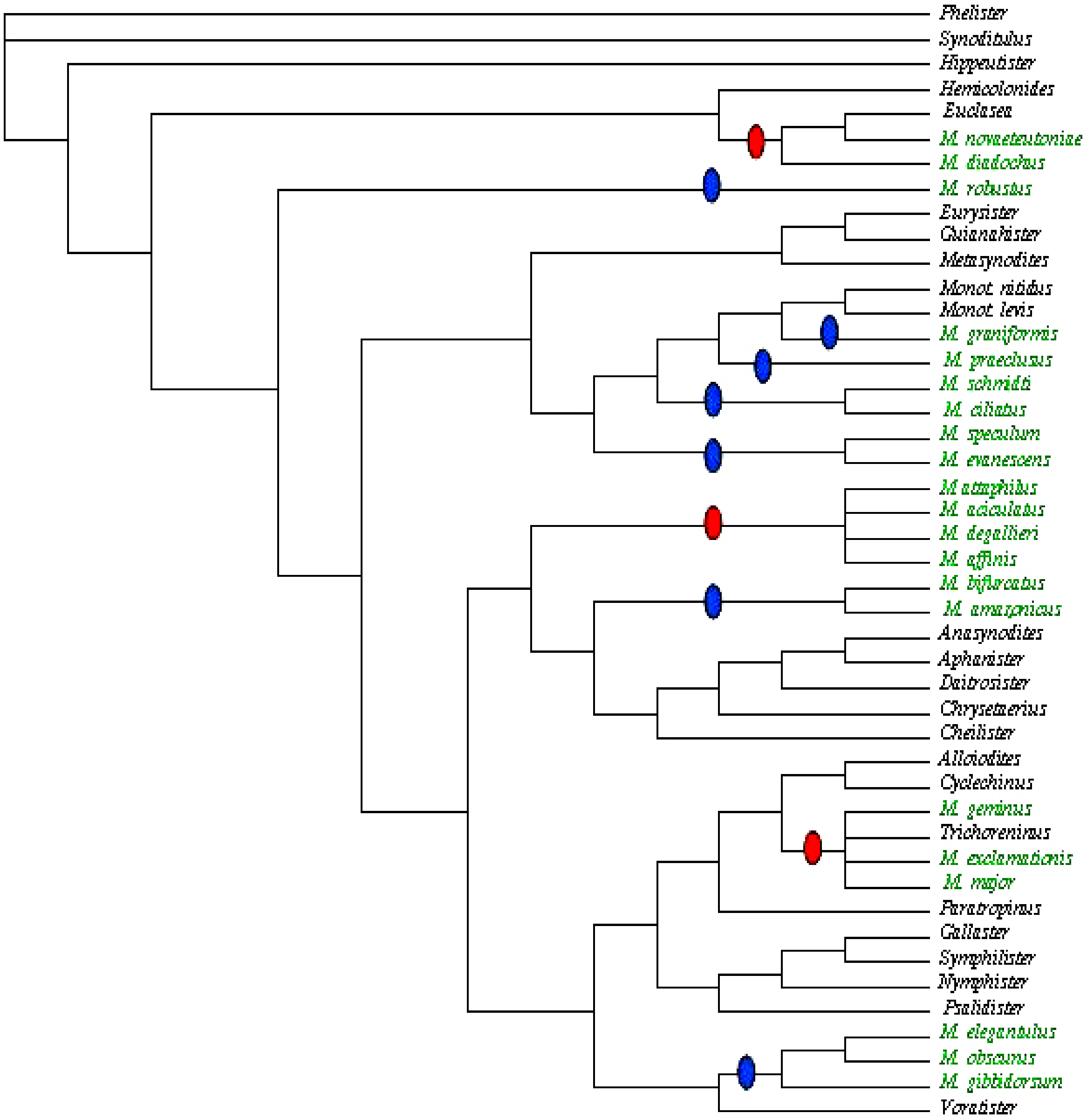


Fig. 6. Summary of taxonomic changes in *Mesynodites* and allies. Phylogenetic tree is from Fig.1 with *Mesynodites* species highlighted. Nodes marked with red ovals represent described genera, where *Mesynodites* are placed (*Euclasea*, *Mesynodites* and *Trichoreninus*, top to bottom). Blue ovals mark lineages described below as new genera (*Reichenspergerites*, *Nicolasites*, *Bruchodites*, *Microsynodites*, *Mutodites*, *Alienodites*, and *Helavadites*, top to bottom).

limited formal data available (Caterino & Vogler, 2002). In Caterino and Vogler's(2002) analyses, *Synoditulus* is placed as the most basal Hetaeriinae in phylogenies based on morphological, molecular and combined datasets. As their hetaeriine representation was low, I scored characters of *Synoditulus* and another outgroup genus, *Phelister*, to investigate evidence regarding the basal position of *Synoditulus*. *Phelister* is a representative of a tentative hetaeriine sister taxon, Histerinae: Exosternini. Mypreliminary hypothesis was that *Synoditulus* would be found to belong to Exosternini along with *Tarsilister*. Superficially it is similar in appearance to an exosternine possessing a few hetaeriine synapomorphies, *i.e.*, fused labrum and clypeus, triangularly enlarged basal antennomere and sclerotized antennal club surface (Helava *et al*., 1985). These characters could have evolved convergently with hetaeriines as a result of *Synoditulus*' ecitophilous habits.

In all my phylogenies, *Synoditulus* was basal to all hetaeriine taxa, but never as a sister to *Phelister* (except in the case where it was the only extra Group E hetaeriine taxon included, Fig. 1). Analysis of the character distribution revealed that *Synoditulus* possesses a mixture of exosternine and hetaeriine characters. The former character system includes numerous characters shared in this analysis only between *Synoditulus* and *Phelister* (Fig. 3), including mouth part (character 17-0), pronotum (32-0), leg (49-0, 50-0, 52-0, 57-0) and sternal (73-0, 75-0, 79-0, 82-0) morphologies. But a substantial number of hetaeriine external synapomorphies found in *Synoditulus* were absent in *Phelister* (characters 1-1, 3-1, 4-1, 5-1, 8-1, 19-1, 22-1, 23-1, 34-1, 35-1, 36-1, 41-1).

Genitalia characters portray *Synoditulus* as a distinct member of Hetaeriinae. A few male genitalia characters shared between *Synoditulus* and *Phelister* (characters 84-0, 87-0, 92-0, 97-0, 103-0, 104-0) are widespread in Hetaeriinae outside revised Group E (Table 4, Helava *et al*. 1985). *Synoditulus* possesses male genitalia similar to numerous genera, indisputably belonging to Groups B and C of Hetaeriinae (Helava *et al*., 1985). Futhermore, female genitalia of *Synoditulus* are of a distinctly hetaeriine

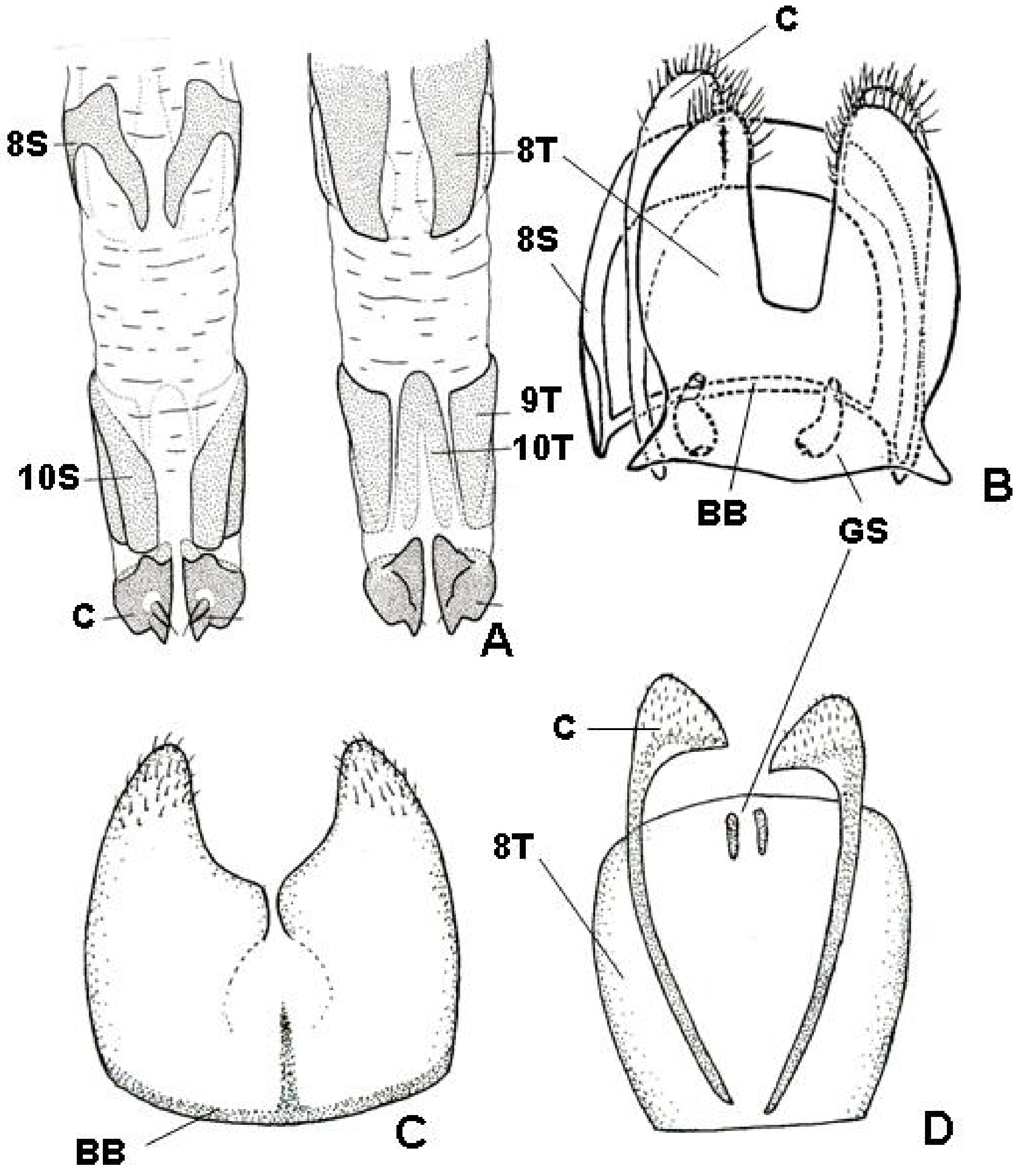


Fig. 7. Female genitalia. A. *Sphaerites glabratus* (F.). Basal type characteristic of most Histeroidea (after Hansen, 1987); B. *Troglosternus ecitonis* Mann. Homology and terminology of typical hetaeriine female genitalia (after Dégallier, 1998c). C. *Synoditulus sp*. Female genitalia, 8th sternite. D. *Synoditulus sp*. Female genitalia with 8th sternite omitted. Abbreviations: 8S – 8th sternite, 8T – 8th tergite, 9S – 9th sternite, 9T – 9th tergite, B – basal bridge, C – coxite, G – gonocoxite, GS – genital sclerite, ST – stylus.

type (Fig. 7, characters 127-1, 132-1, 140-1, 145-1, 146-1, 148-1) that is fundamentally different from genitalia of all other histerid subfamilies as well as the basic histeroidean plan (see Kryzhanovkij & Reichardt, 1976; Vienna, 1980; Hansen, 1997; Caterino & Vogler, 2002 and Fig. 7). In conclusion, *Synoditulus* seems to be a hetaeriine missing link to Histerinae, Exosternini in particular, a hetaeriine genus retaining multiple exosternine external characters and possessing tentatively basal hetaeriine male genitalia and typical hetaeriine female genitalia. As far as available morphological information stands, *Synoditulus* is the best candidate for a basal hetaeriine suggesting potential sister relationships between Hetaeriinae and Exosternini. However, this conclusion needs additional testing with more taxa, and morphological and molecular data. In contrast with this preliminary conclusion, limited molecular data available points towards Histerinae: Histerini as a sister group of hetaeriines (Caterino & Vogler, 2002). If this alternative hypothesis is supported by future study, *Synoditulus*' exosternine-like external morphology will represent another amazing case of convergent evolution.

Finally, this analysis of *Synoditulus* and *Phelister* characters allows me to add to the list of hetaeriine synapomorphies. In addition to three characters of labrum, clypeus and antennae cited previously (Helava *et al*., 1985: 141), the presence of a circular sucker on the galea of males (character 8-1), deeply emarginate apical margin of mentum (19-1), and a complex of female genitalia characters (127-1, 132-1, 140-1, 145-1, 146-1, 148-1) may be added to the list of hetaeriine synapomorphies.

CHAPTER 4. SYSTEMATIC TREATMENT OF TRIBES AND SELECTED GENERA

4.1. Introduction

The following is the treatment of all genera dealt with taxonomically during the course of this study. The generic treatment is embedded into the tribal classification that includes descriptions of two new tribes and is preceded by a review of tribal history within Hetaeriinae.

Genera treated include *Mesynodites s. str.*, new genera described to accomodate species of *Mesynodites s.l.* and all genera involved with intergeneric species transfers. This also includes reexamination of *Alloiodites* and *Metasynodites*, the status and composition of which has remained unchanged since their original description (Helava *et al.*, 1985). Generic and specific accounts follow standard format, with 'Synonymy', 'Citations', 'Description', 'Types', 'Material', 'Distribution' and 'Remarks' sections. Genera with previous detailed descriptions available are supplemented with additional descriptive information, dealing mainly with the morphology of the genitalia. Finally, an identification key to all genera of Nymphestirini is provided.

4.2. Tribal Classification of Hetaeriinae

The history of tribal subdivisions of Hetaeriinae began when Bickhardt (1914) introduced Hetaeriomorphini. Although based on a single character (shape of antennal club), this subdivision apparently was appropriate for the known diversity of the subfamily during this time. Since Bickhard's time, progress on the hetaeriine tribal classification has been minimal. In the 1920-30s, the period of the most active description of genera and species, neither Bruch nor Reichensperger addressed supra-generic classification. Wenzel (Wenzel, 1939, 1944; Wenzel & Dybas, 1941) mentioned Hetaeriomorphini specifically several times but did not provide any comments on hetaeriine tribes. Subsequently, subdivision of Hetaeriinae into Hetaeriini and Hetaeriomorphini was accepted in monographs by Kryzhanovskij and Reichardt (1976) and Mazur (1984).

The next and the only taxonomic action on tribal level classification for the subfamily since Bickhardt (1914) was undertaken by Helava *et al.* (1985). After their study of substantial material, they realized that separation of Hetaeriinae into tribes based exclusively on the shape of the antennal club is artificial and abandoned tribal subdivisions completely. This decision was adopted in the next edition of the World catalogue of Histeridae (Mazur 1997). By contrast, Helava *et al.* (1985) employed some hierarchical subdivisions of Hetaeriinae as a result of their phylogenetic analysis and introduced supra-generic "Groups" and "Subgroups" "that [were] not intended to have any taxonomic status" (Helava *et al.*, 1985: 130). This reluctance was caused by the prematurity of their analysis and incomplete taxon sampling. Although tentative and preliminary, these subdivisions appeared to be useful in subsequent hetaeriine research and were mentioned multiple times in several publications (Dégallier, 1998a, b, c; present study).

After conducting this study, I feel confident in contributing to the tribal classification of Hetaeriinae. I follow Helava *et al.* (1985) in relying heavily on genitalic characters in tribal diagnoses. The following classification contains descriptions of two new tribes, one for the genus *Synoditulus*, the most basal hetaeriine (Caterino & Vogler 2002, Chapter 3.3) and another for revised Group E. Lower taxa are either included within appropriate tribes or listed as *insertae cedis* based on publications of Dégallier (1998a, b, c), results of this study and my inspection of authentic material of some other genera, not dealt with here specifically.

4.3. Systematic Treatment

Tribe Synoditulini, new tribe (Figs. 7, ***14-17***)

Diagnosis. Body shiny, without setae or trichomes. Elytra with full set of dorsal striae. Legs of exosternine type, protibia with apical spurs, meso- and metatibia elongate triangular in shape, with numerous spines on upper margins and apices. Aedeagus with short basal piece and long parameres. Parameres mostly fused, flattened dorsoventrally, apical part of penis situated on ventral side of parameres. Male 8th sternite with separate halves, lacking velae. Male 8th tergite without transverse apical stria. Male 8th tergite without ventral process. Male 10th tergite absent. Female 8th sternite with deeply emarginated apical margin, narrow basal bridge without projecting lateral parts. Female 8th tergite present as single plate. Coxites completely separated. Female 9th tergite present as single plate connected to coxites at base. Female genital sclerites simple, separate.

Type genus: *Synoditulus* Reichensperger.

Remarks. Phylogenetic analyses place this tribe at the base of the Hetaeriinae (Helava *et al.*, 1985; Caterino & Vogler, 2002; Chapter 3.3). The tribe is monotypic. Detailed descriptive and diagnostic characters may be extracted from Helava *et al.* (1985) and Chapter 3.3.

List of genera. *Synoditulus* Reichensperger.

Tribe Nymphisterini, new tribe

Diagnosis. Aedeagus with long basal piece and short parameres. Parameres narrowly fused basally or completely free, apical part of penis situated between parameres. Male 10th tergite absent. Coxites connected by dorsal bridge.

Type genus: *Nymphister* Reichensperger.

Remarks. This tribe corresponds to 'revised Group E' of this study (see Chapter 3.1). At the present level of knowledge, diagnostic characters include only some male genitalia features. Use of other male or female genitalia and external characters is impossible before a complete revision of the tribe Hetaeriini is undertaken.

List of genera. *Aemulister* Reichensperger, *Alienodites* Tishechkin (described herein), *Alloiodites* Reichensperger, *Anasynodites* Reichensperger, *Aphanister* Reichensperger, *Aristonister* Dégallier, *Bruchodites* Tishechkin (described herein), *Cheilister* Reichensperger, *Chrysetaerius* Reichensperger, *Clientister* Reichensperger, *Cyclechinus* Bickhardt, *Daitrosister* Reichensperger, *Daptesister* Helava, *Ecclisister* Reichensperger, *Eurysister* Helava, *Latronister* Reichensperger, *Leptosister* Helava, *Mesynodites* Schmidt, *Metasynodites* Reichensperger, *Microsynodites* Tishechkin (described herein), *Monotonodites* Reichensperger, *Mutodites* Tishechkin (described herein), *Nicolasites* Tishechkin (described herein), *Nymphister* Reichensperger, *Oaristes* Helava, *Panoplitellus* Hedicke, *Psalidister* Reichensperger, *Pulvinister* Reichensperger, *Reichenspergerites* Tishechkin (described herein), *Trichoreninus* Lewis, *Sternocoelopsis* Reichensperger, *Symphilister* Reichensperger, *Voratister* Helava.

***Aemulister* Reichensperger, 1938**

Type species: *Aemulister borgmeieri* Reichensperger

Reichensperger, 1938: 75. Mazur, 1984: 321. Helava *et al.*, 1985: 337-338. Mazur, 1997: 159. Dégallier, 1998c: 347.

Synonym: *Gallaster* Helava in Helava *et al.*, 1985: 292, new synonymy.

Helava *et al.*, 1985: 292-295. Mazur, 1997: 156.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985, as *Gallaster*) and Dégallier (1998c). The following is additional descriptive information. Setose patch on proepisternum either present, or absent. Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present as 2 lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite completely fused to coxites to form intercoxite bridge. Female genital sclerites separate, simple, elongate.

Remarks. In describing *Gallaster*, Helava (Helava *et al.*, 1985) compared it only with two genera that emerged as its closest relatives in the phylogenetic analysis, *Daptesister* and *Latronister*. However, they did not examine *Aemulister*. Reading through the Reichensperger's (1938) paper, careful comparison of the *Aemulister borgmeieri* illustration with Dégallier's (1998c) redescription of *A. borgmeieri* and specimens (including a paratype) of *Gallaster hirsuta* led me to conclude that these two genera are synonyms. The presence of a setose patch on the proepisternum was an important character in Helava *et al.*'s (1985) phylogenetic analysis, but that character is polymorphic within the genus. *Aemulister borgmeieri* (along with a specimen from southern Peruvian Amazonia in the SEC that corresponds to the *A. borgmeieri* description) has the patch, while *A. hirsuta* does not. This difference correlates with the difference in host ants between species, *Eciton* spp. for *A. hirsuta* and *Nomamyrmex esenbecki* Westwood for *A. borgmeieri*.

List of Species

***Aemulister borgmeieri* Reichensperger, 1938**

Reichensperger, 1938: 76. Mazur, 1984: 321. Helava *et al.*, 1985: 338. Mazur, 1997: 159. Dégallier, 1998c: 347.

Remarks. This species was revised recently by Dégallier (1998c). It is known only from the holotype (not studied), originating from Campinas, Goiás State, Brazil. The above mentioned Peruvian specimen could not be assigned to this species with certainty without a comparison with the holotype.

***Aemulister hirsuta* (Helava in Helava *et al.*, 1985)** new combination

Helava *et al.* 1985: 295 (as *Gallaster*). Mazur, 1997: 156 (as *Gallaster*). Tishechkin, 2003: 677(as *Gallaster*).

Remarks. One of the paratypes of this species (from Cerro Campana, Panama, in the collection of C.W. Rettenmeyer; Helava *et al.*, 1985: 294) was studied as background for the recent review of distribution and host records for the species (Tishechkin, 2003).

***Alienodites,* new genus** (Figs. 8-10)

Description. Body oval, convex dorsally, large (PPL 3-4 mm). Body surface smooth and shiny, setose, with abundant, deep and coarse punctures throughout. Head with frons and vertex deeply and densely punctate, prominent latero-marginal frontal carina and interrupted frontal stria. Mandibles with dense rugose punctures, and faces of bases unmodified. Antennal clubs with dense pubescence except on large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral stria complete, anterior stria interrupted medially and represented by fragments along anterior pronotal angles. Lateral sides of pronotum slightly raised and thickened as low costate elevations. Pronotal disc with dense large shallow punctures and abundant erect yellow setae. Elytron with complete set of dorsal striae, complete outer subhumeral, 1st-5th dorsal and sutural, and abbreviated extra stria between 5th dorsal and sutural. Dorsal striae represented by single or multiple rows of dense deep punctures bearing short erect setae. Elytro-epipleural border sharp, angulate along subhumeral stria. Propygidium with marginal stria along basal and lateral margins, densely punctate and setose. Pygidium with dense punctures, especially basally, short erect setae, in females with longitudinal elevations or furrows. Prosternal lobe with complete marginal stria, lateral foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, with few punctures and short setae, its anterior margin produced medially as prominent triangular process. Marginal lateral stria of mesosternum present as indistinct lateral fragments, discal marginal stria complete. Metasternal disc with numerous large punctures and sparse short setae, in males with slight transverse depression in the middle and tiny acute medial tooth near posterior margin. Both outer and inner lateral striae of metasternum present, with long recurrent arms; recurrent arm of inner lateral stria separate. Longitudinal discal stria of metasternum present, complete. First abdominal sternite with dense punctures and sparse short setae, distinct and long lateral and postmetacoxal striae. Legs relatively short, tibia paddle-like. Protibia with 7-9 short spines, meso- and metatibia without teeth and spines on outer margins. Aedeagus with parameres dorso-ventrally flattened, with narrow basal fusion ventrally and dorsally. Penis aligned along the longitudinal paramere axis. Basal piece with shallow and wide dorsal apical emargination. Male 8th sternite with separate full-sized halves and enlarged pair of velae. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male 9th sternite with spoon-shaped “handle”. Male 9th tergite with small ventral apodeme, long basal projection, long thin pointed apical projections and large sclerotized fused ventral process. Halves of male 9th tergite separate, 10th tergite present. Female 8th sternite with moderately emarginated apical margin, distinct basal bridge with shortly

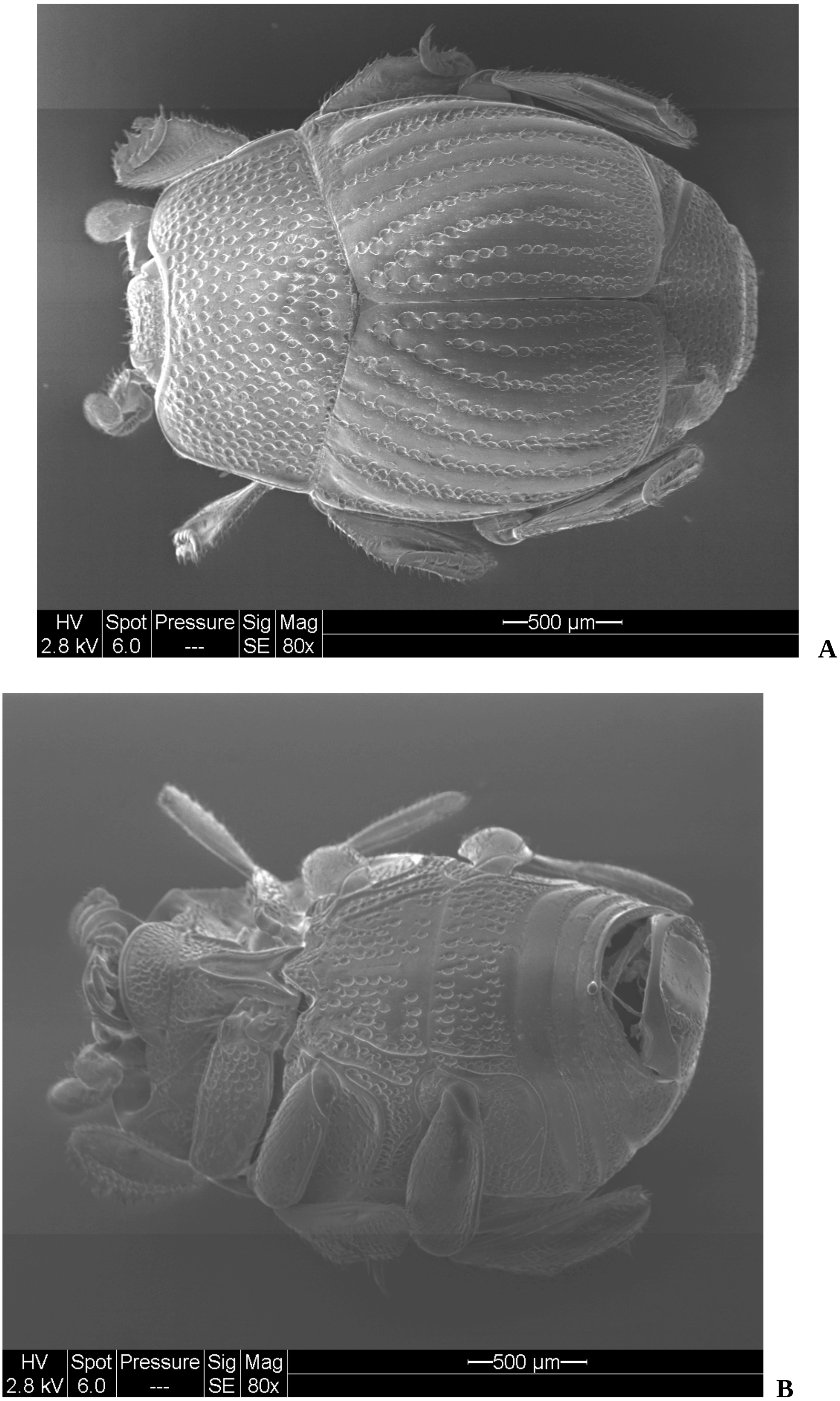


Fig. 8. Habitus of *Alienodites amazonicus*. A. Dorsal aspect; B. Ventral aspect.

angulate lateral parts and rounded basal angles. Female 8th tergite present as 2 lateral sclerites. Coxites connected both by dorsal and ventral bridges. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, comma-shaped.

Type species. *Mesynodites bifurcatus* Mann.

Etymology. The genus name represents a combination of Latin word “alienus” meaning “foreign, strange, alien” and a part of the generic name *Mesynodites*, reflecting distant relationships of the new genus and superficial similarity to *Mesynodites*. The gender is masculine.

Remarks. The genus *Alienodites* is superficially similar to large representatives of *Mesynodites* and also some other genera with generalized appearance (*e.g.*, *Daitrosister, Trichoreninus*). The combination of large size, shiny body surfaces with abundant dense punctures, erect setae, full set of punctate dorsal striae, and keeled metasternal lateral striae are diagnostic. Also, the male and/or female genitalia are unique (discussed above) and allow confirmation of identification.

List of Species.

***Alienodites amazonicus,* new species** (Fig. 8-10)

Description. Body dark reddish brown, PPL 3.2-3.4 mm, width 2.0-2.2 mm. Head with frons and vertex deeply and densely (0.3-1) punctate, with prominent smooth and shiny latero-marginal frontal carina and interrupted frontal stria. Labrum with dense rugose punctures and several long erect seate. Mandibles with a row of long erect setae on outer faces. First antennomere with rugose surface and numerous long erect setae. Pronotum with anterior stria represented by fragments along anterior pronotal angles, interrupted behind eyes. Pronotal punctures drop-shaped, relatively shallow, longer and denser laterally (0.3-0.8) than medially on disc (0.5-1.2). Pronotal setae scattered and short. Elytron with complete outer subhumeral stria, 1st-5th dorsal and sutural striae, and extra stria between 5th and dorsal; sutural stria abbreviated in basal fourth. Fifth dorsal and sutural striae united basally. Dorsal striae represented by rows of dense deep elongate punctures, one, occasionally two punctures wide, each bearing short erect seta or pair of setae. Apical 1/5-1/6 of elytra between 1st dorsal and sutural striae with dense (0.2-0.8) small punctures. Propygidium with dense (0.5-1.2), more or less circular punctures. Pygidium with dense (1-2) punctures in approximately basal half, occupying more area in males. In females, apical half of pygidium with two pairs of more or less longitudinal furrows or pits, variable in length, width and spacing. Prosternal lobe with dense (0.3-0.5) rugose punctures, lateral foveae deep and conspicuous. Prosternal keel punctate, space between carinal striae flat, smooth and shiny. Mesosternum with several elongate punctures anterior to discal marginal stria, area between the latter and very fine meso-metasternal suture smooth. Metasternal disc with numerous large, mainly elongate punctures, aligned in two loose groups laterad of midline, median part of the disc smooth. In males, metasternum with slight transverse depression medially and tiny acute medial tooth near posterior margin. Lateral metasternal striae raised as low keels, area between inner lateral and longitudinal discal striae with dense (0.2-0.7) irregular punctures. Longitudinal discal stria with inward hook anteriorly, length of the hooked part 1/5-1/3 of the strial length. First abdominal sternite with dense (0.7-1.2) irregular elongate punctures, somewhat obscuring lateral and postmetacoxal striae. Tibia and femora with numerous long erect setae on lower surfaces and along edges. Male genitalia as figured (Fig. 7). Female genitalia as figured (Fig. 8).

Holotype: male mounted on point and labeled: “BRESIL: Pará, Tucurui

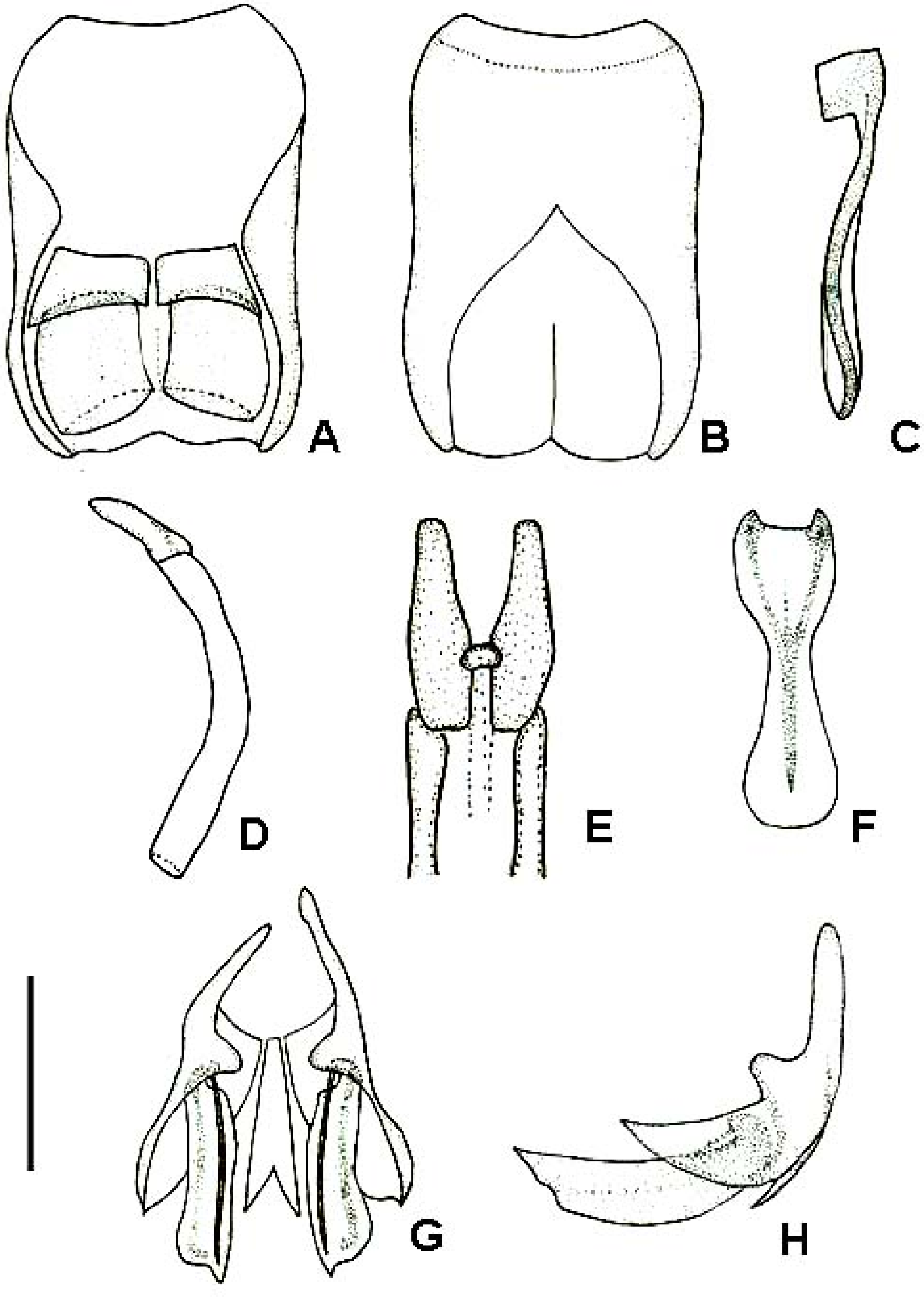


Fig. 9. Male genitalia of *Alienodites amazonicus*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

3º45'S 49º40'W Piege d'Interception N.Dégallier leg. 5-17.XII.1985 / LSAM 0042262 / HOLOTYPE *Alienodites amazonicus* sp. n. A.Tishechkin des. 2003" (MZSP). Paratypes (all collected in flight intercept traps by N.Dégallier): 7 specimens from the same locality and date as holotype (AKT, HUB, MHNG, MZSP, ND); 3 specimens collected at the same locality, but on 16-29.VII.1985 (MZSP, ND); 2 specimens collected at the same locality, but in VI.1985 (ND); 1 specimen collected at the same locality, but on 27.X.-9.XI.1985; 2 specimens collected at the same locality, but on 19.VI.-7.VII.1986 (ND); 1 specimen collected at "BRESIL: Pará**,** Melgaço Distr., Rio Marinau" on 27.X.-3.XI.1993 (ND); 1 specimen collected at "BRESIL: Pará**,** Utinga (I.P.E.A.N.), Belem, 1º27'S 48º26'W" on IX.1985 (ND); 3 specimens collected at "BRESIL: Pará**,** Carajas (Serra Norte) , 6º04'S 50º12'W" on XI.1984 (AKT, ND); 1 specimen collected at the same location on 16.IX.-6.X.1986 (ND).

Etymology. The specific epithet reflects the species' wide distribution in the basin of the lower Amazon River.

Remarks. Differs from the only described congener, *A. bifurcatus* Mann from Central America, by less dense pronotal punctures (especially on the disc), lack of deep pygydial furrows in females, much stronger development of punctures on the metasternum and 1st abdominal sternite and structure of the male genitalia, especially 8th sternite.

Distribution. Known from several localities in eastern Amazonia, in the Brazilian state Pará.

Alienodites bifurcatus (Mann, 1925) new combination

Mann, 1925: 170 (as *Synodites*). Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

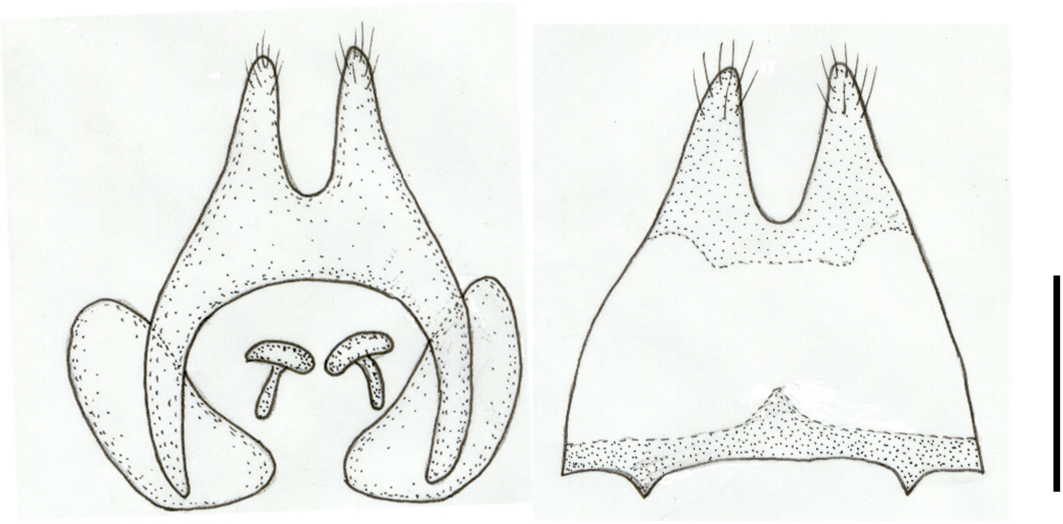


Fig. 10. Female genitalia of *Alienodites amazonicus*. A. Genitalia with 8th sternite omitted, dorsally. B. 8th sternite, ventrally. Scale bar – 0.5 mm.

Holotype: male mounted on point and labeled “Barro Colorado Isl CZ Aug 1 / Type No. 53182 U.S.N.M. / *Synodites bifurcatus* type Mann” (USNM).

Other material. **PANAMA: Panama:** Barro Colorado Island, 26.VII.1956, C.W.Rettenmeyer (1, FMNH).

Distribution. Known from a single locality in the lowlands of central Panama.

***Alloiodites* Helava, 1985**

Type species: *Alloiodites plaumanni* Reichensperger

Reichensperger, 1939: 99 (as *Mesynodites* [*Alloiodites*]). Mazur, 1984: 309 (as *Mesynodites* [*Alloiodites*]). Helava *et al.*, 1985: 309-312. Mazur, 1997: 157.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985). The following is additional descriptive information. Female pygidium with variable sculptural modifications. Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with short lateral angles and rounded basal angles. Female 8th tergite present as 2 lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, simple, elongate.

List of Species.

Alloiodites dispar (Reichensperger, 1939)

Reichensperger, 1939: 104 (as *Mesynodites*). Mazur, 1984: 309 (as *Mesynodites*). Helava *et al.*, 1985: 312. Mazur, 1997: 157.

Lectotype: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Type ! Reichensperger / n.g. *Alloiodites* / *Mesynodites Alloiodites* n.subg. Reichensp. / *Alloiodites Mesynodites dispar* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites dispar* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Paratype ! Reichensperger / *Mesynodites dispar* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites dispar* Reichen. A.Tishechkin des. 2002" (FIMAK); male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Paratypus / *Mesynodites dispar* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites dispar* Reichen. A.Tishechkin des. 2002" (FMNH).

Other material. **ARGENTINA: Chaco:** Chaco N.P., 100 km NW Resistencia, flight intercept trap, 12-17.XII.1990, S. & J.Peck (1, CMN). **BRAZIL: Santa Catarina**: Nova Teutonia, V.1953, F.Plaumann (2, FMNH and USNM); with *Labidus praedator* F.Smith, F.Plaumann (2, FMNH and FIMAK); with *Eciton* prey, II.1959, F.Plaumann (10, FMNH and SM).

Distribution. Known from two localities in northern Argentina (Chaco Province) and southern Brazil (Santa Catarina State).

Alloiodites plaumanni (Reichensperger, 1939)

Reichensperger, 1939: 99 (as *Mesynodites*). Mazur, 1984: 309 (as *Mesynodites*). Helava *et al*., 1985: 312. Mazur, 1997: 157.

Lectotype: female mounted on point and labeled “F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Type ! Reichensperger / n.g. *Alloiodites* / *Mesynodites Alloiodites* n.subg. Reichensp. / Genotyp. / *Mesynodites (All. Plaumanni* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites plaumanni* Reich. A.Tishechkin des. 2002” (FIMAK). Paralectotypes: female mounted on point and labeled “F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Type ! Reichensperger / *Mesynodites Plaumanni*. Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites plaumanni* Reichen. A.Tishechkin des. 2002” (FIMAK); female mounted on point and labeled “F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / Paratypus / *Mesynodites Plaumanni*. Reichensp. / PARALECTOTYPE *Mesynodites plaumanni* Reichen. A.Tishechkin des. 2002” (FMNH).

Other material. **ARGENTINA: Misiones:** P.N. Iguazu, Empalme 101, 206 m, flight intercept trap, 8.XII.1990-6.I.1991, S. & J.Peck (1, CMN). **BRAZIL: Rio de Janeiro:** km 47 – Itaguai, 7.II.1961, W. Zikán (1, AKT; 2, ND). **Santa Catarina**: Nova Teutonia, 11.II.1936, F.Plaumann (2, USNM); II.-V.1941, F.Plaumann (1, FMNH); 1953, F.Plaumann (2, FMNH; 1 SM; 2, ZIN); V.1953, F.Plaumann (2, FMNH); with *Labidus praedator*, F.Plaumann (1, FIMAK); with *L. praedator*, 1951, F.Plaumann (2, FMNH); with *L. praedator*, 26.I.1951, F.Plaumann (2, FMNH; 1, USNM); with *L. praedator*, 30.I.1951, F.Plaumann (1, SM; 1, USNM); with *L.*

praedator, III.1952, F.Plaumann (1, FMNH; 2, SM); with *L. praedator*, IV.1952, F.Plaumann (5, FMNH); with *L. praedator*, 1-6.VI.1952, F.Plaumann (5, FMNH).

Distribution. Norhtern Argentina (Misiones Province) and southern Brazil (Rio de Janeiro and Santa Catarina States).

***Alloiodites regulus* Reichensperger (1939)**

Lectotype: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / Paratype ! Reichensperger / *Mesynodites regulus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites regulus* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotype: female mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / Type ! Reichensperger / n.g. *Alloiodites* / *Mesynodites Alloiodites regulus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites regulus* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other material. **BRAZIL: Santa Catarina**: Nova Teutonia, V.1953, F.Plaumann (2, FMNH; 1 ZIN); with *Labidus praedator*, II.1936, F.Plaumann (1, FIMAK); with *L. praedator*, IV.1952, F.Plaumann (1, FMNH); with *Eciton* prey, II.1959, F.Plaumann (2, FMNH; 3, SM).

Distribution. Known from a single locality in the Brazilian state Santa Catarina.

***Bruchodites,* new genus** (Fig. 11-12)

Description. Body elongate oval, small (PPL 2 mm). Body surface smooth and shiny, with sparse punctures and sparse short erect setae, pygidia with very fine transverse microsculpture. Head without latero-marginal frontal carinae, frontal stria complete. Faces of mandible bases with deep funnel-like depression and uncut edge. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral stria complete, anterior stria interrupted medially and represented by fragments along anterior pronotal angles. Pronotal disc with sparse elongate drop-shaped punctures. Elytron with complete set of dorsal striae, complete outer subhumeral, 1st-5th dorsal and sutural. Dorsal striae with large elongate punctures. Elytro-epipleural border smooth, gradually rounded. Propygidium with few circular punctures and marginal stria along basal and lateral margins. Pygidium impunctuate, without modifications in females. Prosternal lobe with complete marginal stria, deep longitudinal sutures, preapical foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triagular process. Marginal lateral stria of mesosternum present as indistinct lateral fragments, discal marginal stria complete. Metasternal disc flat, with few scattered punctures, unmodified in males. Outer lateral and inner lateral and longitudinal discal metasternal striae present, inner lateral stria without recurrent arm, longitudinal discal stria double. First abdominal sternite with irregular dense punctures and distinct long postmetacoxal and lateral striae. Legs relatively short, tibia paddle-like. Protibia with 6-7 short spines, meso- and metatibia with few spines on outer margins, metatibia with central tooth. Aedeagus with parameres short, laterally flattened, but robust, drop-shaped in profile, with no fusion present. Penis alinged perpendicularly to the longitudinal paramere axis. Basal piece long, with shallow and wide dorsal apical emargination. Male 8th sternite with separate, normal-sized halves and a pair of normal-sized velae. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male 9th sternite with spoon-shaped “handle”. Male 9th tergite with small ventral apodeme and

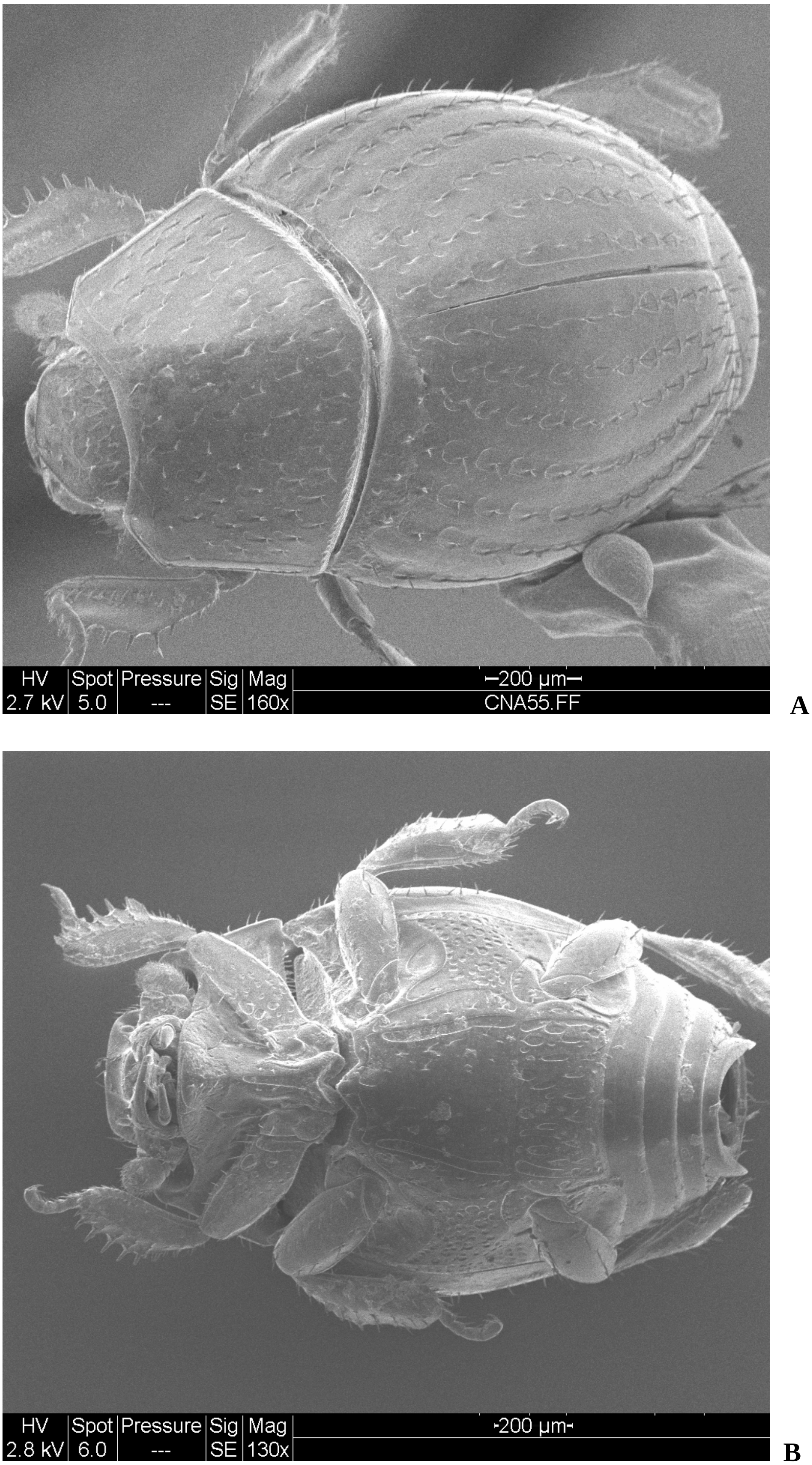


Fig. 11. Habitus of *Bruchodites praeclusus*. A. Dorsal aspect; B. Ventral aspect.

long basal projection, long thin apical projections with angulate apices bent inwards and with short thin sclerotized ventral process. Halves of male 9th tergite fused, tergite body with small square projection on posterior margin, 10th tergite absent (or incorporated into mentioned projection). Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with shortly angulate lateral sides and rounded basal angles and separate median sclerite. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, fused into U/V-shaped figure.

Type species. *Mesynodites praeclusus* Reichensperger, 1939.

Etymology. The genus name represents a combination of the generic name *Mesynodites* and part of Carlos Bruch's name, honoring his remarkable contribution to the studies of inquilinous beetles. The gender is masculine.

Remarks. Externally, the genus is similar to several representatives of *Mesynodites s. str.*, down to many small details including specific elongate drop-shaped pronotal punctures. However, phylogenetic analysis confidently puts *Bruchodites* outside *Mesynodites s. str.* and confirms its close relationships with the genera of the (*Monotonodites – Mesynodites evanescens*) clade. The structure of the the mandible bases and prosternal lobe in *Bruchodites* are distinct from all members of *Mesynodites s. str*. In addition to *Mesynodites s. str.*-like appearance, the following combination of characters allows separation of *Bruchodites* from other genera in the (*Monotonodites – Mesynodites evanescens*) clade: double longitudinal metasternal stria, robust parameres, 9th tergite with thin short sclerotized ventral processes, inwardly bent apices of apical projections, wide fusion of halves and short rectangular process of tergite body.

List of Species.

***Bruchodites praeclusus* (Reichensperger, 1939) new combination**

Reichensperger, 1939: 112 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al*., 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*). Lectotype: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Type ! Reichensperger / *Mesynodites praeclusus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites praeclusus* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotype: female mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Paratype ! Reichensperger / *Mesynodites praeclusus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites praeclusus* Reichen. A.Tishechkin des. 2002" (FIMAK); female mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / Type ! Reichensperger / *Mesynodites praeclusus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites praeclusus* Reichen. A.Tishechkin des. 2002" (FIMAK); female mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton Lab. praedator* / *Mesynodites praeclusus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites praeclusus* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other material. **BRAZIL: Santa Catarina**, Nova Teutonia, V.1953, F.Plaumann (4, FMNH and USNM); with *Labidus praedator*, F.Plaumann (1, FIMAK); with *Eciton* prey, F.Plaumann (2, FMNH and SM).

Distribution. Known only from the type locality in the Brazilian state Santa Catarina.

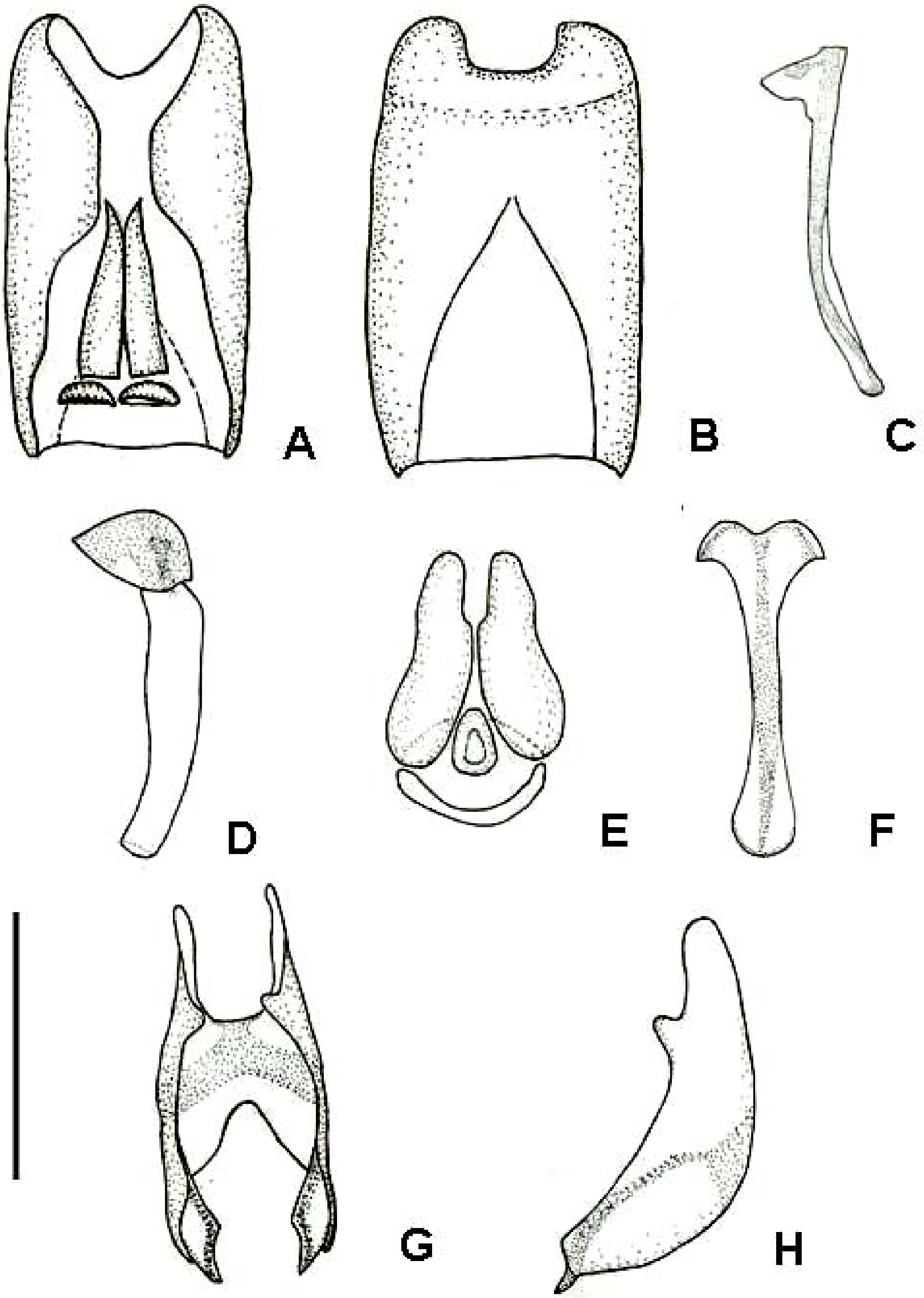


Fig. 12. Male genitalia of *Bruchodites praeclusus*. A. 8th sternite-tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

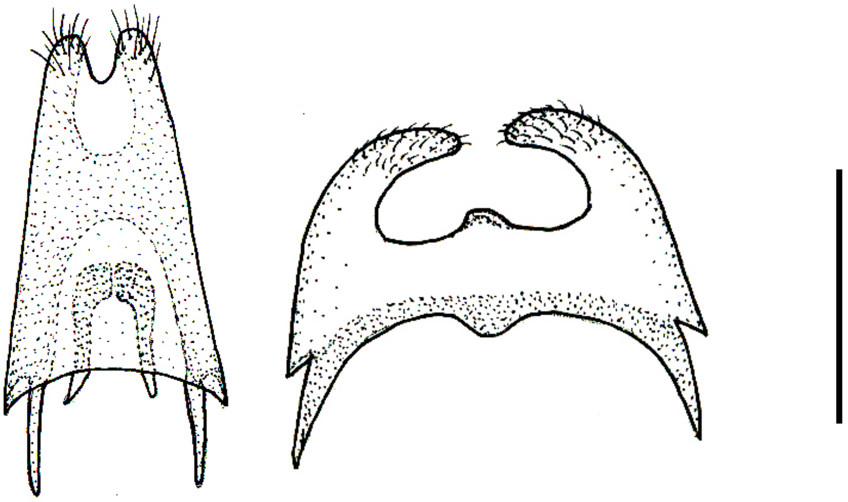


Fig. 13. Female genitalia of *Cheilister lucidulus*. A. Genitalia with 8th sternite omitted, dorsally. B. 8th sternite, ventrally. Scale bar – 0.5 mm.

***Cheilister* Reichensperger, 1924** (Fig. 13)

Type species: *Cheilister lucidulus* Reichensperger, 1924

Reichensperger, 1924b: 147. Mazur, 1984: 300. Helava *et al.* 1985: 319-321. Mazur, 1997: 158.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985). The following is additional descriptive information. Female 8th sternite with moderately emarginated apical margin and central tooth, distinct basal bridge with rounded basal angles, lateral parts forming long posteriorly proximal apodemes.

Female 8th tergite absent. Coxites connected both by dorsal and ventral bridges. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, comma-shaped.

Remarks. As a result of the present species re-arrangement in *Mesynodites* and allies, *Cheilister* in its currents status includes only one species.

List of Species.

Cheilister lucidulus Reichensperger, 1924

Reichensperger, 1924b: 148. Mazur, 1984: 300. Helava *et al.*, 1985: 321. Mazur, 1997: 158.

Lectotype: male mounted on point and labeled “Blumenau Bras. P.Witte / *Eciton burchelli /* A.Reichensperger desc. 1923 / TYPUS / *Cheilister lucidulus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Cheilister lucidulus* Reichen. A.Tishechkin des. 2003” (FIMAK). Paralectotype: female mounted on points and labeled “Blumenau Bras. P.Witte / *Eciton burchelli /* Paratype! Reichensperger/ *Cheilister lucidulus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Cheilister lucidulus* Reichen. A.Tishechkin des. 2003” (FIMAK).

Other material. **COSTA RICA: Limon:** Hamburg Farm, all collected with *Eciton burchelli* Westwood by F.Nevermann, 29.IX.1933 (2, FMNH and FIMAK), 2.VII.1934 (1, FIMAK), 2.XII.1937 (1, FMNH). **Puntarenas:** Las Cruces Biol. Station, with *Eciton burchelli,* 10.IV.2002, A.Tishechkin (1, LSAM). **ECUADOR: Napo:** Yasuní Res. Station, with *Eciton burchelli,* 26.VI.1999, A.Tishechkin (4, AKT and LSAM). **MEXICO: San Luis Potosi:** 6.5 mi S Cuidad Valles, with *Eciton burchelli,* 25.XII.1973, J.Watkins (1, FMNH); El Naranjo, 1200m, with *Eciton burchelli,* 24.IV.1974, A.Newton (1, FMNH); **Veracruz:** canyon SW Rio Metlac, 950 m, with *Eciton burchelli,* 31.VI.1973, A.Newton (1, FMNH). **PANAMA: Panama:** Barro Colorado Island, all with *Eciton burchelli*, 17.III.1955, C.Rettenmeyer (1, FMNH); 7.III.1956, C.Rettenmeyer (1, FMNH); 3.V.1956, C.Rettenmeyer (1, FMNH); 7.II.1976, A.Newton (2, FMNH); 16.II.1976, A.Newton (2, FMNH). **PERU: Loreto:** Campamento San Jasinto, 2°18.75’S 75°51.77’W, with *Eciton*, 8.VII.1993, R.Leschen (2, SEC); 160 km NE Iquitos, 2 km from Rio Napo on Rio Sucusari, with *Eciton burchelli,* 27-31.VII.1992, P.Skelley (3, PWK). **TRINIDAD:** Tunapuna, Mt. St.Benedict, 500 m, flight intercept trap, 5-21.VI.1993, S. & J. Peck (1, BDG)

Distribution. The species is probably distributed throughout almost the entire Neotropical Region, from central Mexico to southern Brazil, in lowland to low montane forests. However, its distribution in South America is poorly documented, with records only from the western Amazonia, Trinidad and southern Brazilian forests (Santa Catarina State).

Remarks. External and male genitalia morphology is conservative throughout the entire huge range with a single exception. A female from “San Jose, Costa Rica” (FIMAK, the only specimen from that locality) has a pair of shallow longitudinal oval pygidial oculae, but otherwise is in complete agreement with other specimens. Neither existence of a cryptic species or polymorphism in female pygidium structure (observed in some other genera, *e.g.*, *Alienodites* and *Psalidister*, this publication and unpublished) can not be ruled out in this case.

***Daitrosister* Helava in Helava *et al.*, 1985**

Type species: *Mesynodites confirmatus* Reichensperger, 1935

Helava *et al.*, 1985: 317-319. Mazur, 1997: 158.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985). The following is additional descriptive information. Punctures of dorsal surface variable, with a gradient from moderate development characteristic of the type species to very dense punctures obscuring dorsal striae almost entirely. Male 8th sternite with 2-4 normal sized velae. Female 8th sternite with moderately emarginate apical margin and central tooth, distinct basal bridge with rounded basal angles, lateral sides with long posteriorly directed proximal apodemes. Female 8th tergite absent. Coxites connected both by dorsal and ventral bridges. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, comma-shaped.

List of Species.

Daitrosister confirmatus **(Reichensperger, 1935)**

Reichensperger, 1935b: 194 (as *Mesynodites*). Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 319. Mazur, 1997: 158.

Lectotype: female mounted on point and labeled "San Jose Costa Rica H.Schmidt 11.34 / *Eciton burchelli* / Type ! Reichensperger / *Mesynodites confirmatus* Reichensp. / *Daitrosister* Helava, 1985 N.DEGALLIER / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites confirmatus* Reich. A.Tishechkin des. 2002" (FIMAK). Paralectotype: female mounted on point and labeled "HAMBURGFARM REVENTAZON EBENE LIMON / *Eciton burchelli* 7.34 / *Mesynodites confirmatus* Reichensp / Paratype ! Reichensperger / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites confirmatus* Reich. A.Tishechkin des. 2002" (FIMAK).

Other Material. **COSTA RICA: San Jose:** San Jose, H.Schmidt (1, FIMAK); with *Eciton burchelli*, H.Schmidt (1, FIMAK); with *E. burchelli*, XI.1934, H.Schmidt (1, USNM); with *E. burchelli*, VI.1936, H.Schmidt (1, FMNH); with *E. burchelli*, VII.1936, H.Schmidt (1, FIMAK); with *E. burchelli*, X.1936, H.Schmidt (1, FIMAK). **PANAMA: Panama:** Barro Colorado Island, with *E. burchelli*, 21.II.1955, C.W.Rettenmeyer (1, FMNH); with *E. burchelli*, 22.II.1955, C.W.Rettenmeyer (1, FMNH); with *E. burchelli*, 23.II.1955, C.W.Rettenmeyer (1, ZIN). with *E. burchelli*, 5.III.1955, C.W.Rettenmeyer (1, FMNH); with *E. burchelli*, 16.II.1976, A.Newton (2, FMNH).

Distribution. Known from two localities, premontane and lowland, in central Costa Rica and central Panama.

Daitrosister ecitonis (Bruch, 1923)

Bruch, 1923: 190 (as *Synodites*). Reichensperger, 1938: 90 (as *Mesynodites*). Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 158.

Lectotype: male mounted on point and labeled "Alta Gracia La Granja Sierras de Córdoba 4.XII.21 C.Bruch leg. / *Eciton dulcius jujuensis* For. / Cotypus / Reichensperger v. Autor 1924 / *Synodites ecitonis* Bruch / MUSEUM KOENIG BONN / LECTOTYPE S*ynodites ecitonis* Bruch A.Tishechkin des. 2002" (FIMAK). Paralectotype: female mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled "Alta Gracia Córdoba 4.I.22 Bruch / Typus / *Synodites ecitonis* Bruch / *Synodites ecitonis* Bruch C.BRUCH DETERM. / PICHADO / Mus. Arg. Cs. Nat. / PARALECTOTYPE S*ynodites ecitonis* Bruch A.Tishechkin des. 2002" (MACN).

Other Material. **ARGENTINA: Córdoba:** Alta Gracia, C.Bruch (1, FMNH); 4.XII.1921, C.Bruch (1, MACN); with *Eciton dulcius* Forel, 21.I.1924, C. Bruch (1, MACN); with *E. dulcius*, XII.1925, C.Bruch (2, USNM); with *E. dulcius*, I.1926, C.Bruch (1, FMNH). Cabana (Unquillo), with *E. dulcius*, I.1926, C.Bruch (5, FMNH, MACN and ZIN). **Jujuy:** Calilegua Nat.Park, El Cortaderal, 800 m, flight intercept trap, 18-28.XII.1987, S. & J.Peck (1, CMN). **BRAZIL: Goiás:** Campinas, with *E. mexicanum* Roger, 28.XII.1935, P.Schwarzmaier (1, FIMAK).

Distribution. Known from northern Argentina (Córdoba and Jujuy Provinces) and southern Brazil (Goiás State).

Daitrosister irregularis **(Reichensperger, 1938) new combination**

Reichensperger, 1938: 88 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point and labeled “Campinas Goyaz, Brasil. 27.X.33 / *Eciton dulcius* / Type ! 2 Reichensperger / *Mesynodites irregularis* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites irregularis* Reichen. A.Tishechkin des. 2002” (FIMAK). Paralectotype: female mounted on point and labeled “Campinas Goyaz, Brasil. 27.X.33 / *Eciton dulcius* / Type ! Reichensperger / *Mesynodites irregularis* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites irregularis* Reichen. A.Tishechkin des. 2002” (FIMAK).

Other Material. **BRAZIL: Goiás:** Campinas, with *Eciton dulcius*, 27.X.1933, P.Schwarzmaier (1, FIMAK); with *E. dulcius*, XII.1937, P.Schwarzmaier (1, FIMAK).

Distribution. Known from a single locality in the Brazilian state Goiás.

Daitrosister longipilus **(Reichensperger, 1931) new combination**

Reichensperger, 1931: 270 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1984: 152 (as *Mesynodites*).

Holotype: female mounted on point and labeled “15.I.30 *Eciton dulcius* [on the other side of the label] Campinas Goyaz Schwarzmaier / *Eciton dulcius* For. / Type ! Reichensperger / *Mesynodites longipilus* Reichensp. / MUSEUM KOENIG BONN” (FIMAK).

Other Material. **BRAZIL: Goiás:** Campinas, with *Eciton dulcius*, 27.X.1933, T.Borgmeier (1, FIMAK); with *E. dulcius*, 4.XII.1933, T.Borgmeier (2, FIMAK and FMNH); with *E. dulcius*, XII.1937, P.Schwarzmaier (2, AKT and FIMAK); with *E. dulcius*, 15.XII.1937, P.Schwarzmaier (1, FIMAK).

Distribution. Known from a single locality in the Brazilian state Goiás.

Daitrosister reticulatus **(Bruch, 1926) new combination**

Bruch, 1926a: 8 (as S*ynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled "Cabana Unquillo Córdoba I.926 / Cotypus / *Synodites reticulatus* Bruch C.BRUCH DETERM. / ARGENTINA 1968 Colln. J.Daguerre / LECTOTYPE S*ynodites reticulatus* Bruch A.Tishechkin des. 2002" (USMN). Paralectotypes: female mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled "Cabana (Unquillo) Córdoba I.1926 C.Bruch leg. / Typus / Foto / *Synodites reticulatus* Bruch C.BRUCH DETERM / PICHADO / Mus. Arg. Cs. Nat. / PARALECTOTYPE S*ynodites reticulatus* Bruch A.Tishechkin des. 2002" (MACN); female mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled as previous specimen, but without the label "Foto" (MACN); female mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled as previous specimen, but with the label "Cotypus" instead of "Typus" (MACN); 3 females mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled as previous specimen, but with the extra label "*Synodites reticulatus* Bruch 1926 Syntypus" (MACN); female mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled as previous specimen, but with the label "Typus" instead of "Cotypus" (MACN); male and female mounted on the same cartboard and labeled "Cabana (Unquillo) Córdoba I.1926 C.Bruch leg. / *Eciton dulcius jujuensis* / C.TYPUS / Collectio Reichensperger / *Synod. reticulatus* Bruch / MUSEUM KOENIG BONN // PARALECTOTYPE S*ynodites reticulatus* Bruch A.Tishechkin des. 2002" (FIMAK); male mounted on point with a worker of *Eciton dulcius* next to it and labelled as previous two specimens (FIMAK); female mounted on cardboard, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled "Cabana Unquillo Córdoba, I.926 / Cotypus / *Synodites reticulatus* Bruch C.BRUCH DETERM. / PARALECTOTYPE S*ynodites reticulatus* Bruch A.Tishechkin des. 2002" (FMNH).

Other Material. **ARGENTINA: Córdoba:** Cabano (Unquillo), with *Eciton dulcius*, XII.1925, C.Bruch (2, MACN). **Jujuy:** Calilegua Nat. Park, Aguas Negras, 550 m, flight intercept trap, 18-28.XII.1987, S. & J.Peck (1, CMN).

Distribution. Northern Argentina (Córdoba and Jujuy Provinces).

***Daitrosister setulosus* (Reichensperger, 1923) new combination**

Reichensperger, 1923: 243 (as *Synodites*). Mazur, 1984: 309 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "Rio Negro Paraná P.Witte / *Eciton 4glumme* 1.II.23 / *Synodites setulosus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted on point with a worker of *Eciton quadriglumme* and labeled "Rio Negro Paraná 8.XI.23 coll. Reichensperger / *Eciton 4glumme* / Paratype 1923 / Reichensperger Paratype ! / *Synodites setulosus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (FIMAK); female mounted on point and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton 4glumme* / P.TYPUS / *Synodites setulosus* Reichensp. / WMMann Coll. 1954 / PARALECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (USNM); male mounted on point and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton 4glumme* / *Synodites* *setulosus* Reichensp. / coll. DEI Eberswalde / PARALECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (DEI); male mounted on point and labeled "Rio Negro Paraná P.W. / *Eciton 4glumme* / Collectio Reichensperger / *Synodites setulosus* Reichensp. / PARALECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (NMM); female mounted on point and labeled "Rio Negro Paraná coll. Reichensperger / coll. Reichensperger Paratyp. / *Synodites setulosus* Reichensp. / PARALECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (NMM); 2 females mounted on point and labeled "[golden circle] /Rio Negro Paraná coll. Reichensperger / *ex nido Ecitonis quadriglumis* / *Synodites setulosus* Reichensp. Paratype / PARALECTOTYPE *Synodites setulosus* Reichen. A.Tishechkin des. 2002" (ZIN).

Other Material. **BRAZIL: Rio Grande do Sul:** São Fransisco do Paula, with *Eciton quadriglumme* Haliday, 25.VII.1925, P.Buck (1, FMNH). **Santa Catarina:** Nova Teutonia, X.1954, F.Plaumann (2, AKT and FIMAK); with *E. quadriglumme*, F.Plaumann (1, FIMAK). **COSTA RICA: San Jose:** San Jose, with *Labidus coecus*, H.Schmidt (4, AKT and FIMAK).

Distribution. Known from two widely separated areas, central Costa Rica and southern Brazil (Rio Grade do Sul and Santa Catarina States). Specimens from these disparate localities completely agree in all morphological characters.

***Guianahister*, new genus** (Fig. 14-16)

Description. Body rectangular oval, medium sized (PPL ca. 2.5 mm), flattened dorsally and ventrally. Body surface smooth and shiny, with very dense alucaceous microsculpture on parts of elytra, propygidium, pygidim and sterna, asetose; rows/groups of long erect setae preset on 1st antennomeres and along edges of tibia and femora. Head with separate latero-marginal frontal carinae, incomplete frontal stria and complete supraorbital stria. Faces of mandible bases with deep funnel-like depression and cut edge. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal and ventral surfaces. Pronotum with marginal stria abbreviated along basal halves of lateral sides, outer and inner lateral striae long, located distant from lateral margin, connected with long anterior stria. Pronotal disc smooth and shiny. Elytron with complete set of abbreviated dorsal striae. Dorsal striae impunctate, represented as rather wide shallow furrows. Elytro-epipleural border sharp, angulate along subhumeral striae. Most of elytral surface, except basal areas, with alutaceous microsculpture. Propygidium completely alutaceous, with marginal stria along basal and lateral margins. Pygidium impunctate, with basal half alutaceous and without modifications in females. Prosternal lobe with marginal stria present only apically, with deep longitudinal sutures, preapical foveae and lateral notches. Prosternal keel rather narrow, flat basally and angular in apical half, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Meso- and metasternal discs with surfaces mainly alutaceous and numerous excavations, mostly along and between striae; surfaces of excavated areas smooth and glossy. All meso- and metasternal striae thin and indistinct along margins of excavations. Mesosternum narrow, its anterior margin produced medially as prominent triangular process. Marginal lateral stria of mesosternum present as indistinct lateral fragments, discal marginal stria complete, area between it and meso-metasternal suture excavated. Metasternal disc flat, impunctate, with elongate inverted B-shaped excavation in each half, unmodified in males. Outer lateral and inner lateral and longitudinal discal metasternal striae present, complete, inner lateral stria with recurrent arm. First abdominal sternite alutaceous, with distinct thin long postmetacoxal and lateral striae, separated by

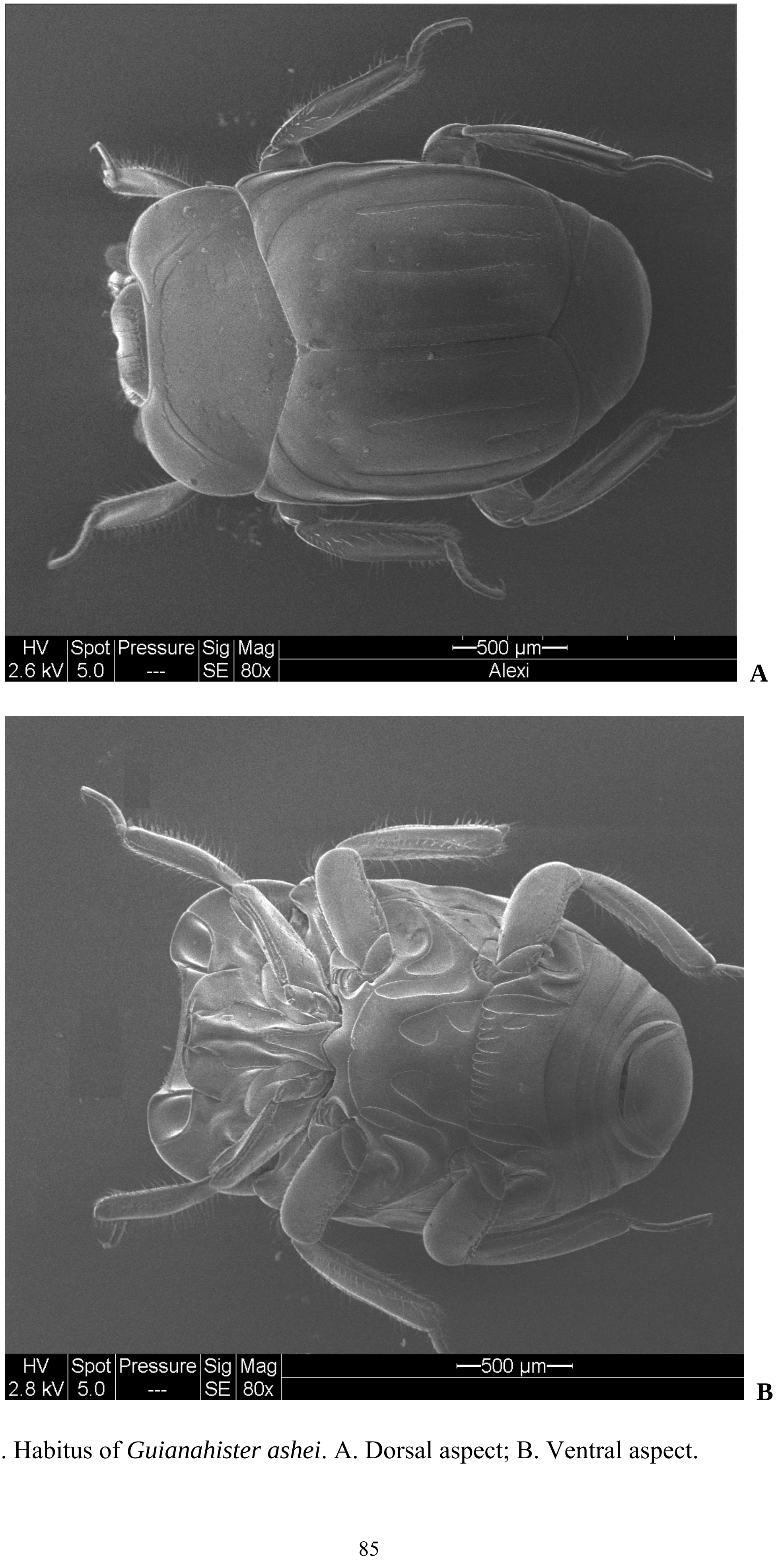


Fig. 14. Habitus of *Guianahister ashei*. A. Dorsal aspect; B. Ventral aspect.

elongate excavation. Legs relatively long, tibia paddle-like. All femora and tibia with a row of long erect setae on each margin on both sides. Protibia with 15-18 long spines, mesotibia with two short spines on outer margins, meso- and metatibia without central tooth. Aedeagus with parameres short, subcylindrical, with narrow basal fusion dorsally and ventrally. Penis alinged along longitudinal paramere axis. Basal piece long, with shallow and wide dorsal apical emargination. Male 8th sternite with separate, normal-sized halves and pair of normal-sized velae. Male 8th tergite with TAS and transverse posterior suture present, somewhat reduced intra-TAS plate and produced latero-apical areas. Male 9th sternite with spoon-shaped "handle." Male 9th tergite with small ventral apodeme and long basal projection, long thin apical projections with rounded apices bent inwards and with relatively short sclerotized ventral processes. Halves of male 9th tergite narrowly fused, 10th tergite absent. Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with briefly angulate lateral parts and rounded basal angles and separate median sclerite. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, fused into U/V-shaped figure.

Type species. *Guianahister ashei* new species.

Etymology. The genus name represents a combination of the generic name of *Hister* and a word "Guiana," reflecting its occurrence in and apparent endemicity to all three 'Guianas', French Guiana, Guyana and Suriname. The gender is masculine.

Remarks. *Guianahister* is closely related to the genus *Eurysister*, sharing with it, along with numerous synapomorphies of the (*Eurysister-Metasynodites*) clade, the general body shape, pattern of setae distribution, structure of protibia and presence of metasternal excavations. However, it possesses several autapomorphic features,

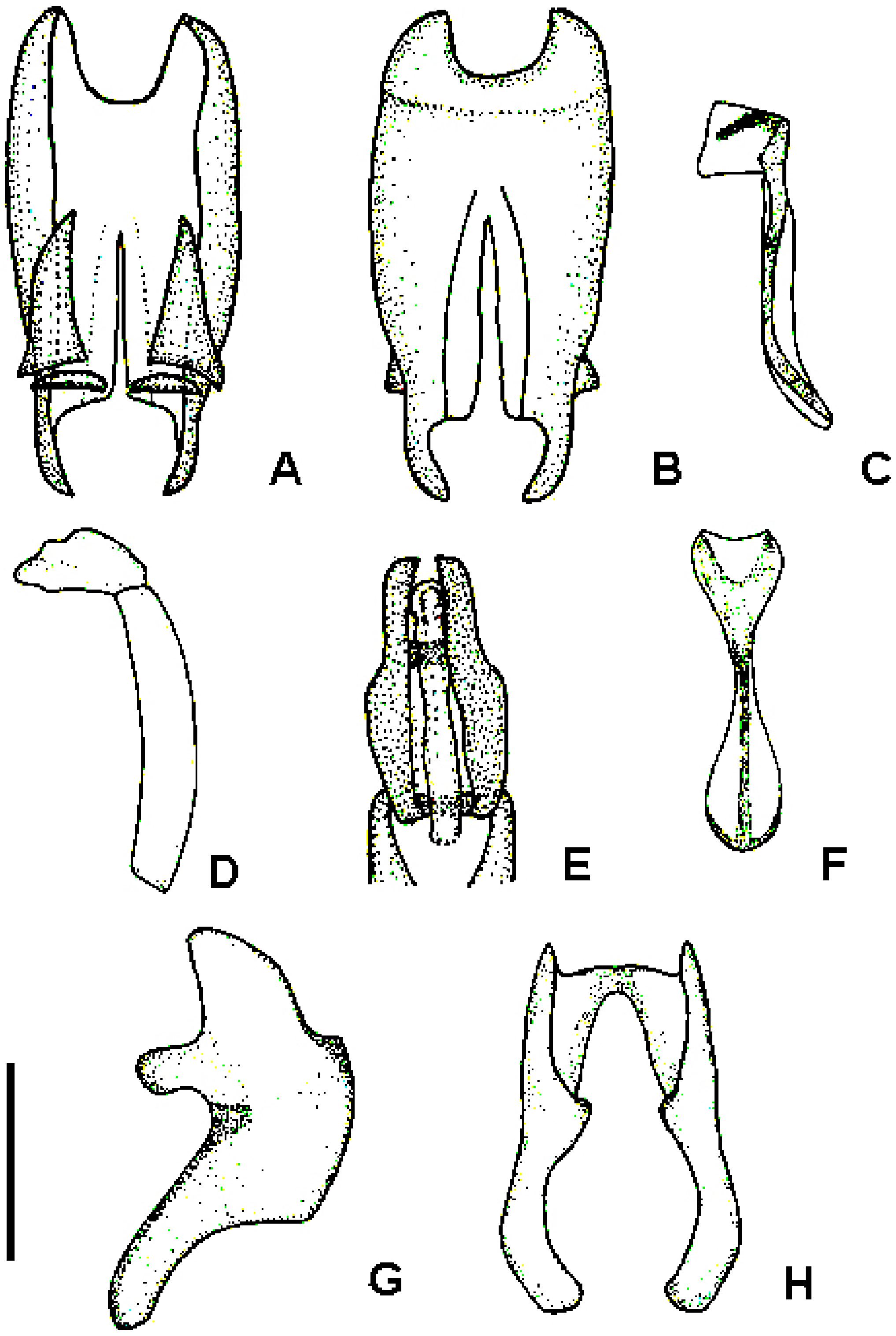


Fig. 15. Male genitalia of *Guianahister ashei*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

warranting its generic status and allowing separation from *Eurysister*, including abbreviated marginal stria of pronotum, presence and interior position of both lateral pronotal striae, characteristic elytral striae, lack of elytral costae, shape of metasternal discal excavations, widespread alutaceous microsculpture, produced latero-apical areas of male 8th tergite and paramere shape.

***Guianahister ashei*, new species** (Fig. 14-16)

Description. Body reddish-brown, PPL 2.4-2.7 mm, width 1.7-1.9 mm. Head with shiny and smooth frons and vertex, punctate supraorbital stria with a row of long erect setae. Labrum with a small acute median tooth on apical margin and a tuft of long erect setae on each side. Mandibles impunctate, with several long erect setae on outer face. First antennomere with numerous long erect setae. Pubescence of antennal clubs rather long and sparse. Pronotal disc slightly convex, with shallow longitudinal depressions approximately halfway between midline and lateral margin. Outer and inner lateral striae thin, long, impunctate, parallel, abbreviated in basal fourth, both connected or nearly connected with thin, impunctate, variably irregular anterior stria. Elytron long and parallel-sided. Outer subhumeral and 1st dorsal stria complete, their lateral edges somewhat keeled. Second, 4th and sutural striae long, slightly abbreviated both basally and apically, occasionally with variable fragments/punctures in the areas of abbreviation. Third and 5th striae short, present as series of short apical fragments. Prosternal profile nearly straight. Preapical foveae elongate and shallow, longitudinal sutures of prosternal lobe with continuous with lateral prosternal striae. Metasternal excavations present on each side of disc, between longitudinal discal and inner metasternal, inner and outer metasternal striae, outer metasternal striae and mesocoxae. First abdominal sternite with row of large, triangular, shallow, postobsolete (puncture rims broken and excavations level posteriorly) punctures along

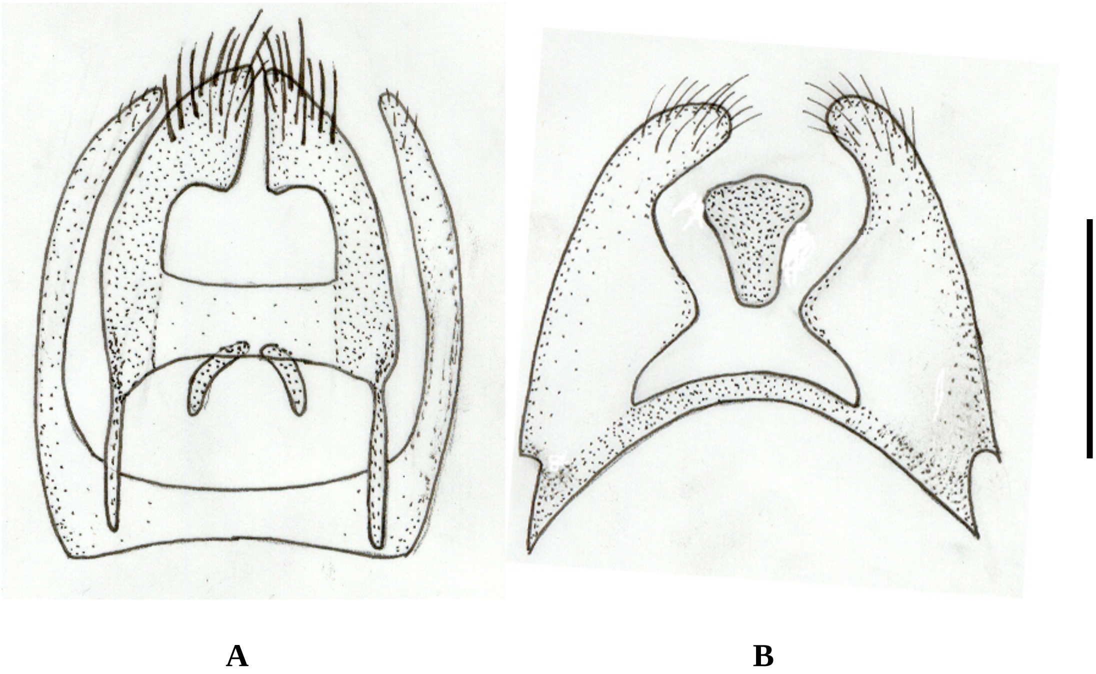


Fig. 16. Female genitalia of *Guianahister ashei*. A. Genitalia with 8th sternite omitted, dorsally. B. 8th sternite, ventrally. Scale bar – 0.5 mm.

anterior margin. Male genitalia as figured (Fig. 13). Female genitalia as figured (Fig. 14).

Holotype: male mounted on point and labeled: "FRENCH GUIANA Roura, 18.4 km SSE, 240 m 4º36'38"N 52º13'25"W 29 MAY – 10 JUNE 1997 J.Ashe, R.Brooks FG 1AB97 180 ex: flight intercept trap / SM0100694 KUNHM-ENT [bar code label] / LSAM 0043971 / HOLOTYPE *Guianahister ashei* sp. n. A.Tishechkin des. 2003" (SEM). Paratypes (all collected by flight intercept traps): **FRENCH GUIANA** (all collected by J.Ashe and R.Brooks): 3 specimens collected at the same locality and date as the holotype (3, AKT, PWK and SEM); 2 specimens collected at the same locality as the holotype, but on 22-24.V.1997 (2, AKT and PWK); 1 specimen from "Roura, 8.4 km SSE, 200 m, 4º40'41"N 52º13'25"W, 25-29.V.1997" (SEM); 2 specimens from "Roura, 27.4 km SSE, 280 m, 4º44'20"N 52º13'25"W, 10.VI.1997" (SEM); 2 specimens from "Saül, 7 km N, Les Eaux Claires, 200-300 m, 3º39'46"N 53º13'19"W, 30.V.-4.VI.1997" (1, AKT and SEM); 2 specimens collected at the same locality, but on 4-8.VI.1997 (SEM); 1 specimen from “Cayenne, 33.5 km S and 8.4 km NW of N2 on Hwy D5, 30 m, 4º48’18”N 52º28’41”W, 29.V.-9.VI.1997” (SEM); **GUYANA:** 3 specimens from “Region 8, Iwokrama Forest, Kabocalli Field Stn., 4º17’4”N 58º50’36”W, 3-5.VI.2001, R.Brooks, Z.Falin” (3, AKT and SEM); **SURINAME:** 1 specimen from “Marowijne, Palumeu, ca. 160 m, 3º20’56”N 55º26’18”W, 5-7.VII.1999, Z.Falin, D.Konoe” (SEM); 1 specimen from “Commewijne, Akintosoela, CELOS Camp, 39 km SE Suriname River bridge, road to Redi Doti, 40 m, 5º16’17”N 54º55’15”W, 29.VI.-3.VII.1999, Z.Falin” (SEM).

Etymology. Named after James S. Ashe, one of the species’ collectors, in appreciation of his outstanding collecting efforts in the Neotropics that have lead to discoveries of many rare and new hetaeriines.

Distribution. French Guiana, Guyana and Suriname.

Helavadites,* new genus** (Fig. 17, ***298)

Description. Body oval or elongate oval, sometimes teardrop-shaped, convex dorsally, small (PPL 1-2 mm). Body surface mostly covered with dense small punctures, sometimes with shiny alutaceous microsculpture (may be almost smooth in smallest species), asetose or with dense tiny setae on dorsal surface. Head with prominent latero-marginal frontal carina united medially, with complete frontal stria. Mandibles with faces of bases unmodified. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral striae complete, anterior stria interrupted medially and represented by fragments along anterior pronotal angles or absent entirely. Pronotal disc mostly with dense small punctures. Elytron with variable set of dorsal striae, only outer subhumeral present consistently. Dorsal striae, if present, thin and impunctate. Elytro-epipleural border smooth, gradually rounded. Propygidium

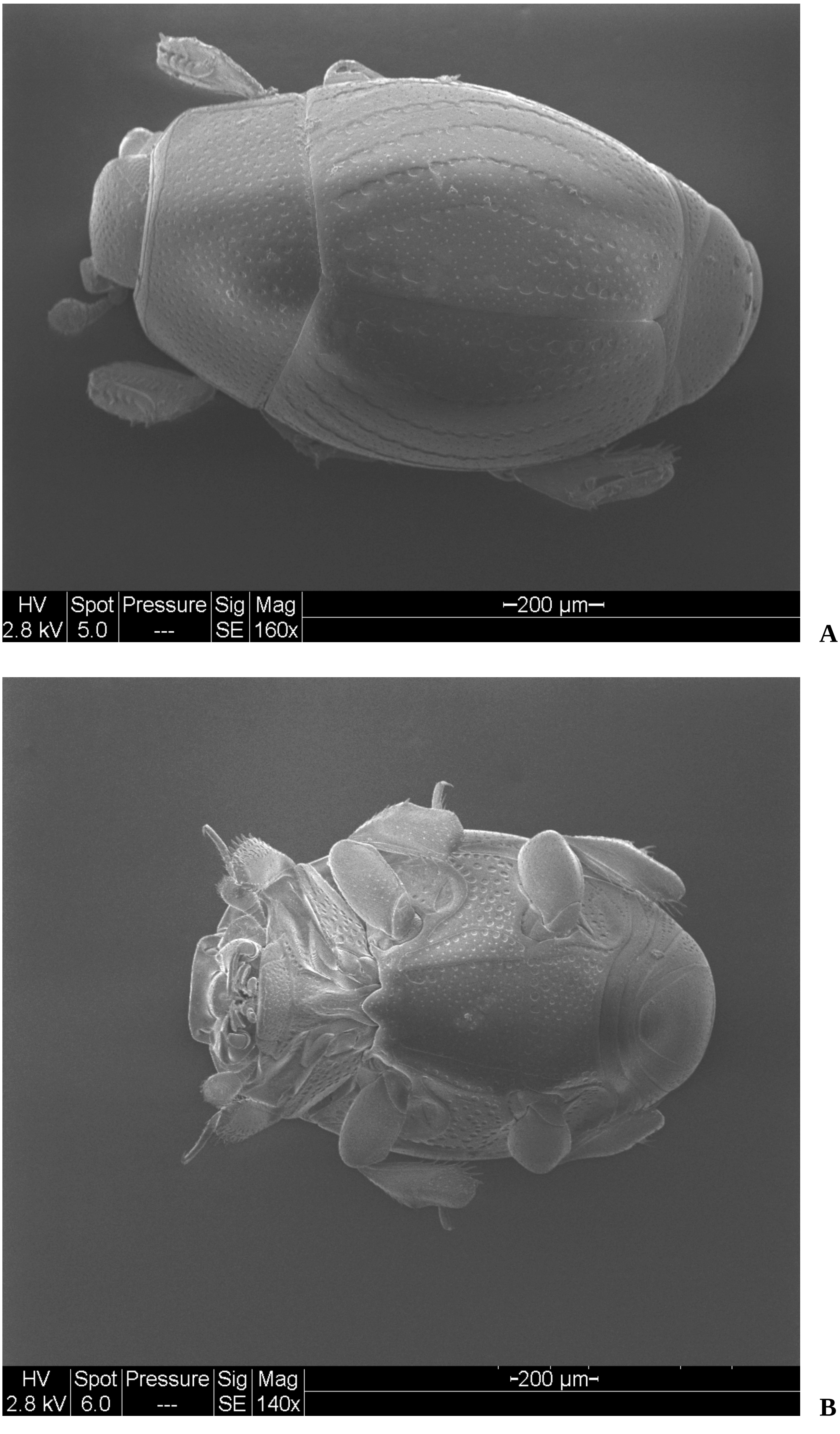


Fig. 17. Habitus of *Helavadites gibbidorsum*. A. Dorsal aspect; B. Ventral aspect.

with marginal stria along basal and lateral margins. Pygidium mostly without punctures, often with transverse linear microsculpture, without modifications in females. Prosternal lobe with complete marginal stria, lateral foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triangular process. Marginal lateral stria of mesoternum present as indistinct lateral fragments, discal marginal stria complete. Metasternal disc flat or convex, sometimes in males with weak median longitudinal depression. Lateral and longitudinal discal striae of metasternum variable, only outer lateral striae present consistently. First abdominal sternite with distinct and long lateral and postmetacoxal striae. Legs relatively short, tibia paddle-like. Protibia with 7-9 short spines, meso- and metatibia with central tooth and spines on outer margins. Aedeagus with parameres long, subcylindrical, with narrow basal fusion ventrally. Penis aligned along the longitudinal paramere axis. Basal piece with shallow and wide dorsal apical emargination. Male 8th sternite with separate, reduced halves and pair of regular-sized velae. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male 9th sternite with spoon-shaped “handle.” Male 9th tergite with small ventral apodeme and long basal projection, long sclerotized pointed apical projections and without ventral process. Halves of male 9th tergite fused, 10th tergite absent. Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present as 2 lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, simple, elongate.

Type species. *Mesynodites gibbidorsum* Schmidt.

Etymology. The genus name represents a combination of a part of the generic name *Mesynodites* and Jussi Helava's name, honoring his remarkable contribution to the studies of Hetaeriinae. The gender is masculine.

Remarks. The genus is defined largely by male genitalic characters, elongate subcylindric parameres in combination with very long acute scerotized apical projections of 9th tergite, lacking ventral processes. Species of the genus represent two relatively distinct ground plans, reflected in the identification key. First, there are larger elongate beetles with well developed dorsal and metasternal striae and background punctures. Another group is represented by tiny, around 1 mm long, teardrop-shaped beetles with reduced punctures and striation (*H. nanus, H. obscurus*). While representatives of the first group are distinct, mainly through abundant background punctures, correct identification of small *Helavadites* requires inspection of genitalia as these beetles often look extremely similar to some other small generalized hetaeriines, especially small *Euclasea* species.

List of Species

Helavadites elegantulus **(Reichensperger, 1939) new combination**

Reichensperger, 1939: 115 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al*., 1985: 335 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Paratype ! Reichensperger / *Mesynodites elegantulus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites elegantulus* Reich. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Paratype ! Reichensperger / A.Reichensperger / *Mesynodites* *elegantulus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites elegantulus* Reich. A.Tishechkin des. 2002" (FIMAK); male mounted on cardboard and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / *Mesynodites elegantulus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites elegantulus* Reich. A.Tishechkin des. 2002" (FIMAK); male mounted on point and labeled as previous specimen (FIMAK); male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / Type ! Reichensperger / *Mesynodites elegantulus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites elegantulus* Reich. A.Tishechkin des. 2002" (FIMAK).

Other Material. **ARGENTINA: Misiones:** P. N. Iguazu, Empalme 101, flight intercept trap, 8.XII.1990-6.I.1991, S. & J.Peck (2, CMN and FMNH). **BRAZIL: Santa Catarina:** Nova Teutonia, 1953, F.Plaumann (1, SM); V.1953, F.Plaumann (5, SM and ZIN); with *Labidus praedator*, F.Plaumann (1, FIMAK); with *L. praedator*, III.1952, F.Plaumann (1, SM); with *L. praedator*, 7.III.1952, F.Plaumann (2, FMNH); with *L. praedator*, 10.III.1952, F.Plaumann (1, FMNH); with *L. praedator*, 15.III.1952, F.Plaumann (6, FMNH, SM and USNM); with *L. praedator*, 5.IV.1952, F.Plaumann (1, FMNH); 7.IV.1952, F.Plaumann (1, FMNH); 10.IV.1952, F.Plaumann (1, FMNH); 13.IV.1952, F.Plaumann (2, FMNH); with *L. praedator*, 1-6.VI.1952, F.Plaumann (6, FMNH and USNM); with *L. praedator*, I.1954, F.Plaumann (3, CMN).

Distribution. Known from two localities in northern Argentina (Misiones Province) and southern Brazil (Santa Ctarina State).

***Helavadites gibbidorsum* (Schmidt, 1893) new combination** (Fig. 17). Schmidt, 1893: 180 (as *Synodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "Type / *Synodites gibbidorsum* Bahia / coll. J.Schmidt / *gibbidorsum* Schm / *Synodites* Schm" (HUB).

Other Material. **BRAZIL: Amapá:** Serra do Navio, 0º59'N 52º00'W, flight intercept trap, 1-14.V.1991, N.Dégallier (1, ND); **Pará:** Tucurui, 3º45'S 49º40'W, flight intercept trap, VI.1985, N.Dégallier (1, ND); flight intercept trap, 20.V.-5.VI.1986, N.Dégallier (1, ND); flight intercept trap, 19.VI.-7.VII.1986, N.Dégallier (1, ND); Utinga (I.P.E.A.N.), Belem, 1º27'S 48º26'W, flight intercept trap, VIII.1984, N.Dégallier (15, AKT, FMNH, FIMAK, MZSP, ND); flight intercept trap, IX.1984, N.Dégallier (1, ND). **SURINAME: Commewijne:** Akinto Soela, 5º16'17"N 54º55'15"W, 40 m flight intercept trap, 29.VI.-3.VII.1999, Z.Falin (1, PWK).

Distribution. Lowlands of eastern South America, known from the Brazilian states Amapá, Bahia and Pará and Suriname.

***Helavadites manicus* (Reichensperger, 1939) new combination**

Reichensperger, 1939: 121 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "San Jose Costa Rica H.Schmidt *L. coec.* / *Eciton coecum* / Type ! Reichensperger / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites manicus* Reich. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: male and female mounted on the same cardboard and labeled "San Jose Costa Rica H.Schmidt / *Eciton coecum* r. 1937 / Paratype ! Reichensperger / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites manicus* Reich. A.Tishechkin des. 2002” (FIMAK); male and female mounted on the same cardboard and labeled “San Jose Costa Rica H.Schmidt / *Eciton coecum* Kol.3 37 / Paratype ! Reichensperger / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites manicus* Reich. A.Tishechkin des. 2002” (FIMAK); male and female mounted on the same cardboard and labeled as previous specimens, but lacking the paratype label (FIMAK); male and mounted on cardboard with minor worker of *Labidus coecus* Latreille and labeled “San Jose Costa Rica H.Schmidt *L. coecum* / A.Reichensperger / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites manicus* Reich. A.Tishechkin des. 2002” (FIMAK); male and female mounted on points and labeled “San Jose Costa Rica H.Schmidt / *Eciton coecum* Kol.4 37 / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites manicus* Reich. A.Tishechkin des. 2002” (FIMAK); male mounted on point, two females and female on two cardboards, each with minor worker of *Labidus coecus*, female mounted on point, with cardboard-mounted major worker of *Labidus coecus* under it, all labeled “San Jose Costa Rica H.Schmidt / *Lab. coecus* / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites manicus* Reich. A.Tishechkin des. 2002” (FIMAK).

Other material. **COSTA RICA:** Limon: Hamburg Farm, with *Labidus coecus*, 1937, F.Nevermann (1, FIMAK); with *L. coecus*, X.1937, F.Nevermann (1, FIMAK). **San Jose:** San Jose, H.Schmidt (2, FIMAK); with *L. coecus*, H.Schmidt (5, AKT and FIMAK).

Distribution. Known from two localities in the Costa Rican provinces San Jose and Limon.

Helavadites nanus **(Reichensperger, 1939) new combination**

Reichensperger, 1939: 118 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Holotype: female mounted on point and labeled “Hamburg-Farm Costa Rica Nevermann / *Eciton praedator* Nr. 45 3.12.36 / Type ! Reichensperger / 2 / *Mesynodites manicus* Reichensp. / MUSEUM KOENIG BONN” (FIMAK).

Distribution. Known from the single locality in the Costa Rican province Limon.

Helavadites obscurus **(Reichensperger, 1939) new combination**

Reichensperger, 1939: 119 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on cardboard and labeled “Hamburg-Farm Costa Rica Nevermann / *Eciton praedator* XI.36 / Type ! Reichensperger / *Mesynodites obscurus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites obscurus* Reichen. A.Tishechkin des. 2002” (FIMAK). Paralectotypes: female mounted on the same cardboard as the lectotype, label “PARALECTOTYPE *Mesynodites obscurus* Reichen. A.Tishechkin des. 2002” placed under the lectotype label (FIMAK); female mounted on point and labeled “Hamburg-Farm Costa Rica Nevermann / *Eciton praedator* XI.36 / *Mesynodites obscurus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites obscurus* Reichen. A.Tishechkin des. 2002” (FIMAK).

Other Material. **PANAMA: Panama:** Barro Colorado Island, 30.V.1956, C.W. & M.E.Rettenmeyer (1, FMNH).

Distribution. Known from two localities in lowlands of central Costa Rica and central Panama.

Mesynodites **Reichardt, 1924** (Fig. 18-20, ***299*****)**

Type species: *Synodites schuppii* Schmidt

Reichardt, 1924: 166. Mazur 1984: 307. Helava *et al.*, 1985: 331-337. Mazur 1997: 151. Dégallier, 1998b: 137-138.

Synonym: *Synodites* Schmidt 1893: 175. - Reichardt 1924: 166.

Description. The genus was described in detail, diagnosed and illustrated by Dégallier (1998b). The following is additional descriptive information. Development of surface setae, pronotal and pygidial punctures and elytral striae variable. The type species represents the most common *gestalt*. Sometimes setae absent almost entirely, and punctures of dorsal surface, including punctures of dorsal striae, are small and sparse. Apical margin of pygidium in females sometimes with short obtuse tooth. Pygidium in females often with variable sculptural modifications. Female 8th sternite with deeply emarginated apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present either a single plate as with deeply emarginated apical margin or as 2 lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, simple, elongate.

List of Species

Mesynodites aciculatus **(Schmidt, 1893)**

Schmidt, 1893: 179 (as *Synodites*). Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 335. Mazur, 1997: 151 (as *Mesynodites*).

Synonym: *Mesynodites collaris* Reichensperger, 1939: 110, new synonym.

Reichensperger, 1939: 110. Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 335. Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "Brasil / Type / coll. J.Schmidt / *Synod aciculatus*" (HUB). Lectotype of *Mesynodites collaris*: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* 12.II.37 / Paratype ! Reichensperger / *Mesynodites collaris* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites collaris* Reichen. A.Tishechkin des. 2002" (FIMAK). Pralectotypes of *Mesynodites collaris*: female mounted on point, with the same labels as the lectotype, but with paralectorype instead of lectotype label (FIMAK); female mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Paratype ! Reichensperger / *Mesynodites collaris* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites collaris* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other Material. **BRAZIL: Santa Catarina**, Nova Teutonia, F.Plaumann (1, ZIN); 1953, F.Plaumann (4, FMNH); V.1953, F.Plaumann (5, FMNH, SM and USNM); with *Labidus praedator*, F.Plaumann (1, FIMAK); with *L. praedator*, 7.IV.1952, F.Plaumann (1, FMNH); with *Eciton* prey, III.1959, F.Plaumann (2, FMNH and SM).

Distribution. Known only from type locality in southern Brazil (Santa Catarina State).

***Mesynodites affinis* Reichensperger, 1931**

Reichensperger, 1931: 283. Bruch, 1937: 131. Mazur, 1984: 307. Helava *et al.*, 1985: 335. Mazur, 1997: 151.

Lectotype: male mounted on point and labeled "Campinas Goyaz Schwarzmaier / *Eciton crassicorne* 27.8.28 / Paratype ! Reichensperger / *Mesynodites affinis* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites affinis* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted on

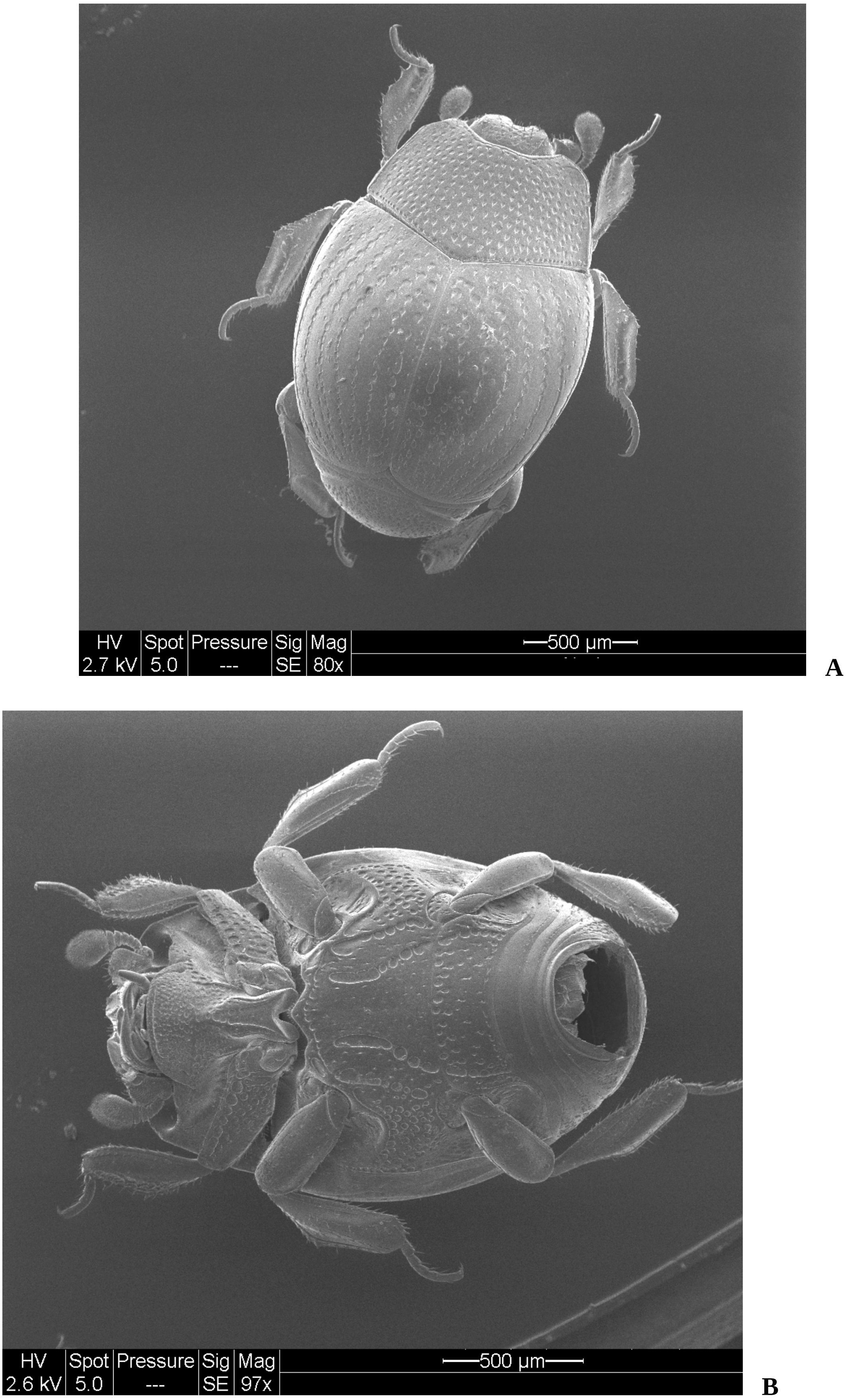


Fig. 18. Habitus of *Mesynodites degallieri*. A. Dorsal aspect; B. Ventral aspect.

point and labeled “Campinas Goyaz Schwarzmaier / *Eciton crassicorne* 27.8.28 / Paratype ! Reichensperger / *Mesynodites affinis* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites affinis* Reichen. A.Tishechkin des. 2002” (FIMAK); female mounted on point and labeled “Campinas Goyaz Schwarzmaier / *Eciton crassicorne* 27.8.28 / Type ! Reichensperger / *Mesynodites affinis* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites affinis* Reichen. A.Tishechkin des. 2002” (FIMAK); female mounted on point and labeled “Campinas Goyaz Schwarzmaier / *Eciton crassicorne* 27.8.28 / *Mesynodites affinis* Reichensp. / coll. DEI Eberswalde / PARALECTOTYPE *Mesynodites affinis* Reichen. A.Tishechkin des. 2002” (DEI); female mounted on point and labeled “Campinas Goyaz Schwarzmaier ! / *Eciton crassicorne* 29.I.29 / Paratype ! Reichensperger // *Mesynodites affinis* Reichensp. / Purchase ex colln. Tomaz Borgmeier Pres. By C.C.Gregg / PARALECTOTYPE *Mesynodites affinis* Reichen. A.Tishechkin des. 2002” (FMNH); female mounted on point and labeled “27.XII.28 Inhacimas *E. crassicorne* [on the other side of the label] Goiaz Schwarzmaier / Type ! Reichensperger / *Mesynodites affinis* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites affinis* Reichen. A.Tishechkin des. 2002” (FIMAK).

Other Material. **BRAZIL: Goiás:** Bella Vista, with *Nomamyrmex esenbecki*, 14.III.1934, P.Schwarzmaier (1, FIMAK). Campinas, with *N. esenbecki*, P.Schwarzmaier (2, AKT and FIMAK); with *N. esenbecki*, 26.IV.1929, P.Schwarzmaier (1, MACN); with *N. esenbecki*, 21.II.1933, P.Schwarzmaier (1, FIMAK); with *N. esenbecki*, 28.X.1935, P.Schwarzmaier (1, FIMAK); with *N. esenbecki*, 8.XI.1936, P.Schwarzmaier (3, AKT and FIMAK).

Distribution. Known from two localities in the Brazilian state Goiás. I could not confirm the report from Misiones Province, Argentina (Bruch, 1937; Mazur, 1984, 1997), as no specimens of *Mesynodites* close to *M. affinis* were found in any collection studied.

***Mesynodites attaphilus* Bruch, 1933**

Bruch, 1933: 32. Mazur, 1984: 307. Helava *et al.*, 1985: 335. Mazur, 1997: 151.

Holotype: male mounted on point and labeled "Est. Exp. Loreto (Misiones-Arg.) Dr. A.A.Ogloblin / Typus / con *Atta sexdens* / *Mesynodites atticola* typus C. BRUCH DETERM. / *Mesynodites attaphilus* Bruch 1933 Holotypus / PICHADO / Mus. Arg. Cs. Nat." (MACN).

Other Material. **BRAZIL: Rio de Janeiro:** Mendes, 4-15.X.1933, Eidmann (3, AKT and NHMB).

Distribution. Known from two localities in northern Argentina (Misiones Province) and southern Brazil (Rio de Janeiro State).

***Mesynodites degallieri,* new species** (Fig. 18-20)

Description. Body dark reddish brown, PPL 2.1-2.4 mm, width 1.3-1.5 mm. Head with frons and vertex shallowly and densely (0.5-1) punctate, each puncture bearing a short erect seta, with prominent smooth and shiny latero-marginal frontal carina and interrupted frontal stria. Clypeus and labrum smooth and shiny, the latter with several short erect seate along apical margin. Mandibles with scattered sparse punctures and short erect setae on outer faces. First antennomere with finely rugose surface and numerous short erect setae. Pronotum with complete anterior stria continuous with complete lateral marginal striae. Pronotal disc evenly convex, its punctures small, drop shaped, shallow, each bearing a short erect seta, dense (0.5-1)

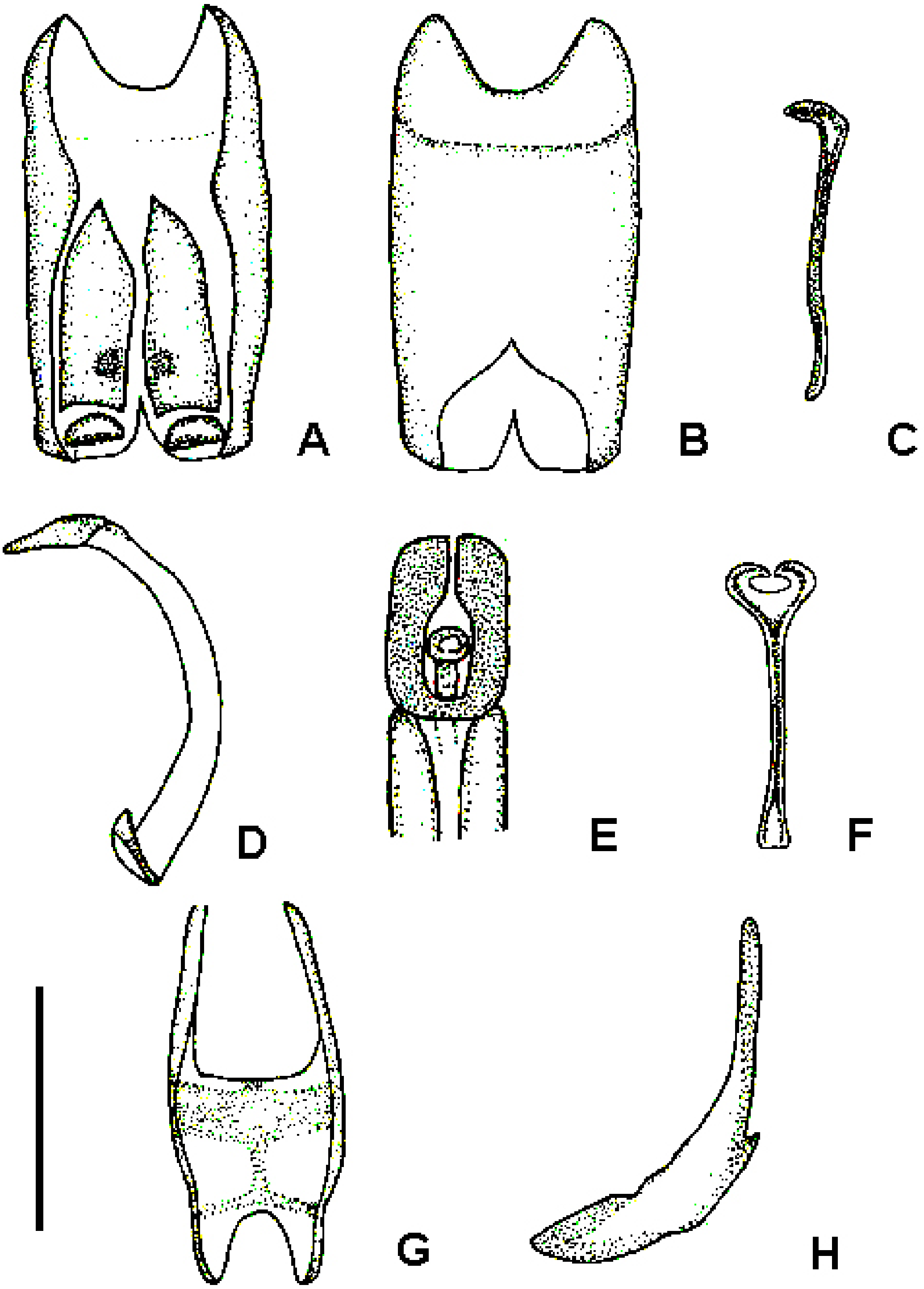


Fig. 19. Male genitalia of *Mesynodites degallieri*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

and evenly distributed over the entire disc. Elytron with complete outer subhumeral stria, 1st-5th dorsal and sutural striae, and extra stria between 5th and dorsal. Outer subhumeral and 1st dorsal striae almost contact at apical third of the elytral length. Bases of 5th dorsal, extra presutural and sutural approximate. Dorsal striae represented by rows of small, dense, shallow elongate punctures, one puncture wide, each bearing short erect seta. Sizes of punctures increase basally, strial arrangement less regular along apical and basal elytral margins, especially in prescutellar area. A few punctures arranged in two short irregular rows present between outer subhumeral and 1st dorsal striae in elytral basal thirds. Propygidium with dense (0.5-1.2), more or less circular punctures in basal third. Punctures sparser and smaller apically, and apical third of pygidium almost smooth. In females, apical margin of propygidium with dorsoventrally flattened short obtuse projection medially. Pygidium with tiny, sparse (4-6) punctures in approximately basal half, occupying more area in males. In females, apical third of pygidium with a pair of slightly arched, longitudinal, impunctate striae. Surfaces of both propygidium and pygidium with scattered sparse short erect setae. Entire ventral surface with scattered sparse short setae. Prosternal lobe with dense (0.3-0.5) shallow punctures, lateral foveae elongate-oval, shallow and conspicuous. Prosternal keel punctate, space between carinal striae flat, smooth and shiny, with a few small irregular punctures apically. Mesosternum smooth and shiny, discal marginal stria represented by dense deep circular punctures, meso-metasternal suture very fine and inconspicuous. Metasternal disc smooth and shiny, with very few small elongate punctures or thin short strioles, especially in anterior part. These strioles consistently present between inner lateral and longitudinal discal striae. In males, metasternum with slight longitudinal depression medially.

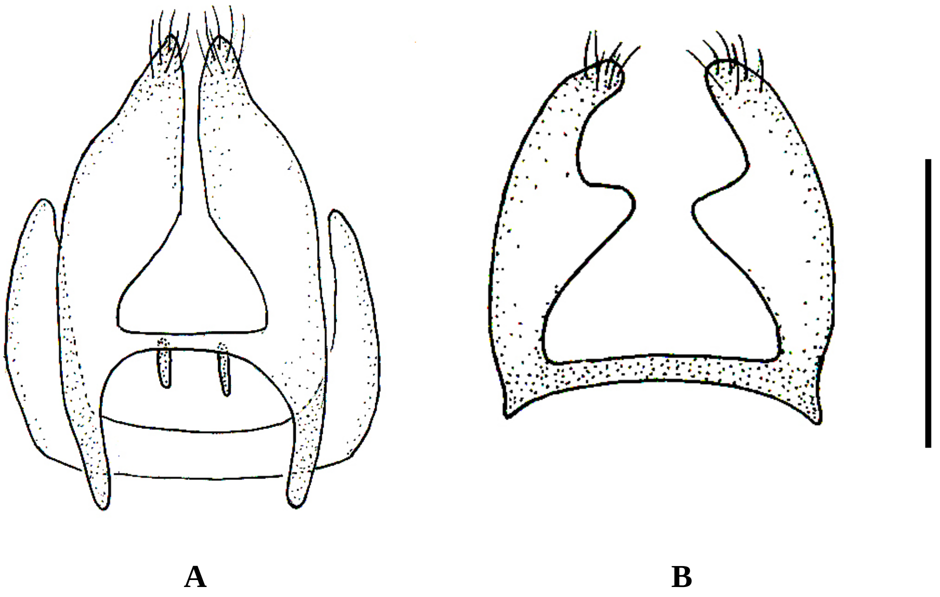


Fig. 20. Female genitalia of *Mesynodites degallieri*. A. Genitalia with 8th sternite omitted, dorsally. B. 8th sternite, ventrally. Scale bar – 0.5 mm.

Lateral discs of metasternum with large, dense (0.3-0.5), circular punctures. Outer and inner lateral and longitudinal discal metasternal striae complete, represented by dense, large, circular or elongate punctures, often with borders between them becoming obsolete. Recurrent arms of inner lateral striae absent. First abdominal sternite with dense (0.7-1.2) irregular elongate punctures, their numbers and density decreasing apically. Tibia and femora with numerous short erect setae on lower surfaces and along edges. Male genitalia as figured (Fig. 17). Female genitalia as figured (Fig. 18).

Holotype: male mounted on point and labeled: “Carajas (Serra Norte) PARA BRESIL 50º12’W; 6º04’S / piege d’Interception 11.1984 N.Dégallier / LSAM 0041900 / HOLOTYPE *Mesynodites degallieri* sp. n. A.Tishechkin des. 2003” (MZSP). Paratypes (all collected in flight intercept traps by N.Dégallier): 14 specimens from the same locality and date as holotype (AKT, ND, MZSP); 9 specimens collected at the same locality, but in X.1984 (AKT, FIMAK, ND); 2 specimens collected at the same locality, but in III.1985 (ND); 14 specimens collected at the same locality, but in V.1985 (FMNH, NHML, ND); 1 specimen collected at the same locality, but in 16.IX.-16.X.1986 (ND); 59 specimens collected at the same locality, but on 26.IX.-6.X.1986 (AKT, HUB, MNHG, MZSP, ND); 1 specimen collected at the same locality, but on 13.XI.-2.XII.1987 (ND); 1 specimen collected at "BRESIL: Pará**,** Bargança, 1º03'S 46º46'W" on 8-18.VI.1987 (ND); 1 specimen collected at "BRESIL: Pará**,** Tucurui, 3º45'S 49º40'W" in III.1985 (ND); 1 specimen collected at the same locality, but on 16-19.VII.1985 (ND); 8 specimens collected at the same locality, but on 27.X.-3.XI.1985 (FMNH, ND); 1 specimen collected at the same locality, but on 19.VI.-7.VII.1986 (ND); 1 specimen collected at the same locality, but on 23.XI.-7.XII.1986 (ND); 2 specimens collected at "BRESIL: Amapá, Serra do Navio, 0º59'N 52º00'W" in II.1989 (MZSP, ND); 3 specimens collected at "BRESIL: Amapá, Serra do Navio, Mariry, 1º10'N 52º56'W" in IX.1984 (MZSP, ND); 1 specimen labeled "French Guiana, Kouru" collected with flight intercept trap by M.Duranton in 1987 (ND); 2 specimen labeled "French Guiana, Roura, 27.4 km SSE, 280 m, 4º44'20"N 52º13'26"W" collected with flight intercept trap by S.Ashe and R.Brooks on 10.VI.1997 (SEM).

Etymology. The specific epithet honors my friend Nicolas Dégallier, the collector of most of the type series, in recognition of our long term collaboration and his outstanding contribution to the studies of neotropical Hetaeriinae.

Remarks. This species belongs to the group of relatively large *Mesynodites s. str*. possessing abundant setae on the dorsal surface and lacking pronotal background microsculpture. The group also includes *M. affinis*, *M intermedius* Reichensperger, *M. schuppii* and *M. virgatus* Reichensperger. Two of these species, *M intermedius* and *M. virgatus*, could be easily distinguished from the rest by characteristic scale-like body surface setae and consistently large body size, respectively. *M. degallieri* is the only

Mesynodites species known from Amazonia and it differs from both *M. affinis* and *M. schuppii* by the lack of deep metasternal depression in males and presence of propygidial projection in females.

Distribution. Known from French Guiana and several localities in the Brazilian states Amapá and Pará.

Mesynodites intermedius Reichensperger, 1933

Reichensperger, 1933: 190. Mazur, 1984: 308. Helava *et al.*, 1985: 336. Mazur, 1997: 151.

Holotype: male mounted on point and labeled "Campinas Goyaz, Brasil. 9.II.33 / *Eciton coecum* / *Mesynodites intermedius* Reichensp. / MUSEUM KOENIG BONN / HOLOTYPE *Mesynodites intermedius* Reichensp." (FIMAK).

Other Material. **BRAZIL: Goias:** Campinas, with *Labidus coecus*, 12.XI.1935, P.Schwarzmaier (1, FIMAK); with *Labidus coecus*, 22.XII.1935, P.Schwarzmaier (1, FIMAK); with *L. coecus*, XII.1936, P.Schwarzmaier (2, AKT and FIMAK). **PARAGUAY:** San Bernardino, K.Fiebrig (1, USNM).

Distribution. Known from two localities, in the Brazilian state Goiás and in Paraguay.

Mesynodites schuppii (Schmidt, 1893)

Schmidt, 1893: 173 (as *Synodites*). Reichensperger, 1931: 284. Mazur, 1984: 308. Helava *et al.*, 1985: 336. Mazur, 1997: 152. Dégallier, 1998b: 138.

Lectotype (designated by Dégallier 1998b): male mounted on point and labeled " Saõ Leopoldo / Type / coll. J.Schmidt / *Synodites schuppii* typ. Schm." (HUB).

Other Material. **BRAZIL: Rio de Janeiro:** Campo Bello, with *Labidus praedator* (1, FIMAK). **Santa Catarina**, Nova Teutonia, forest floor litter, 28.XII.1962, F.Plaumann (1, FMNH).

Distribution. Southern Brazil: three localities in Rio de Janeiro and Santa Catarina States.

Mesynodites virgatus Reichensperger, 1931

Reichensperger, 1931: 272. Mazur, 1984: 309. Helava *et al.*, 1985: 337. Mazur, 1997: 152.

Lectotype: male mounted on point and labeled "Campinas. Goyaz Schwarzm. 19.XI.28 / bei *Eciton coecum* / 17 / Mus. Arg. Cs. Nat. / LECTOTYPE *Mesynodites virgatus* Reich. A.Tishechkin des. 2002" (MACN). Paralectotypes: male mounted on point and labeled " Histeridae Camp. Schw. 19.XI.28 *E. coecum* 4612 / *Eciton coecum* 19.XI.28 / Type ! Reichensperger / *Metasynodites virgatus* Reichensp. / Purchase ex colln. Tomaz Borgmeier Pres. By C.C.Gregg / PARALECTOTYPE *Mesynodites virgatus* Reich. A.Tishechkin des. 2002" (FMNH); female mounted on point and labeled "Campinas Goyaz Schwarzmaier / *Eciton coecum* 19.XI.28 / Type ! Reichensperger / *Metasynodites virgatus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites virgatus* Reich. A.Tishechkin des. 2002" (FIMAK). Other Material. **BRAZIL: Goiás:** Campinas, with *Labidus coecus*, 19.XI.1928, P.Schwarzmaier (1, FIMAK); with *L. coecus*, 18.I.1929, P.Schwarzmaier (1, MACN); with *L. coecus*, 12.XI.1935, P.Schwarzmaier (1, FIMAK); with *L. coecus*, 22.XII.1935, P.Schwarzmaier (1, FIMAK); with *L. coecus*, 18.IV.1937, P.Schwarzmaier (2, CMN).

Distribution. Known only from type locality in the Brazilian state Goiás.

Mesynodites* species *insertae cedis.

***Mesynodites drakei* (Schmidt, 1893)**

Schmidt 1893, 178: (as *Synodites*). Mazur, 1984: 307. Helava *et al.* 1985: 335. Mazur, 1997: 151.

Type locality: “Bolivien” (Bolivia).

Remarks. Type material of this species seems to have been lost for many years. While studying specimens in the HUB collection, where the remainder of Schmidt’s hetaeriine types are housed, I found no representatives of the species, nor mention of it in an old log book, presumably last filled by Bickhardt in the 1910s or 1920s. Also, neither Dégallier, nor the HUB curatorial staff were able to found it during separate searches. The original description is not detailed enough to get even a vague idea about the species’ generic affinities.

***Mesynodites sodalis* Reichensperger, 1924**

Reichensperger, 1924a: 209 (as *Synodites*). Mazur, 1984: 309. Helava *et al.*, 1985: 336. Mazur, 1997: 152.

Type locality: “Rio Negro, Paraná”

Remarks. The fate and depository of the syntypes (Reichensperger, 1924a) of this species are long unknown (Dégallier, 1993, personal communication). My searches and inquiries to find them in several collections also failed. The original description is relatively detailed and provides some clues to the species’ affinities. Reichensperger affiliated it with large *Mesynodites s. str.* species comparable to *M. schuppii*. However, my impression from the illustration of the dorsal habitus and some details in the description (*e.g.*, basal abbreviation of 4th and sutural dorsal striae, mention of ‘wide and short’ prosternum) is that *M. sodalis* is a species of *Daitrosister* close to or conspecific with *D. ecitonis*. This opinion will remain nothing more than an educated guess until type material is discovered.

Metasynodites **Reichensperger, 1930**

Type species: *Mesynodites legionarius* Reichensperger, 1929

Reichensperger, 1930: 85 (as *Mesynodites* [*Metasynodites*]). Mazur, 1984: 309 (as *Mesynodites* [*Metasynodites*]). Helava *et al.*, 1985: 277-279. Mazur, 1997: 154.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985). The following is additional descriptive information. Female 8th sternite with deeply emarginated apical margin, distinct basal bridge with shortly angulate lateral parts, rounded basal angles and separate median sclerite. Female 8th tergite present as two lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, fused into U/V-shaped figure.

Metasynodites legionarius **(Reichensperger, 1929)**

Reichensperger, 1929: 133 (as *Synodites*). Mazur, 1984: 310 (as *Mesynodites*). Helava *et al.*, 1985: 279. Mazur, 1997: 154.

Lectotype: male mounted on point with a worker of *Neivamyrmex legionis* F.Smith and labeled “Rio Negro Paraná coll. Reichensperger / *Eciton legionis* 23.3.28 / Paratypus / Subg. n. *Metasynodites* Reichensp. / *Synodites legionarius* n. sp. Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Synodites legionarius* Reichen. A.Tishechkin des. 2002” (FIMAK). Paralectotype: female (head and pronotum missing) mounted on cardboard with a worker of *Neivamyrmex legionis* and labeled “Rio Negro Paraná coll. Reichensperger 8.9.27 / *Eciton legionis* / Paratype ! Reichensperger / *Synodites legionarius* n. sp. Reichensp. / MUSEUM KOENIG

BONN / PARALECTOTYPE *Synodites legionarius* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other Material. **BRAZIL: Paraná:** Rio Negro, with *Neivamyrmex legionis* (1, FIMAK); with *N. legionis,* 8.IX.1927 (1, FIMAK); with *N. legionis,* 14.I.1929 (2, MACN and FIMAK).

Distribution. Known only from the type locality in the Brazilian state Paraná.

***Metasynodites minor* Reichensperger, 1931**

Reichensperger, 1931: 269. Mazur, 1984: 310 (as *Mesynodites*). Helava *et al.*, 1985: 279. Mazur, 1997: 154

Lectotype: male mounted on point with a worker of *Neivamyrmex legionis* and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton legionis* / Type ! Reichensperger / *Metasynodites minor* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Metasynodites minor* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted on the same point as the lectotype, label "PARALECTOTYPE *Metasynodites minor* Reichen. A.Tishechkin des. 2002" placed under the lectotype label (FIMAK); female mounted on point with a cardboard-mounted worker of *Neivamyrmex legionis* under it and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton legionis* / Paratype ! Reichensperger / *Metasynodites minor* n. Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Metasynodites minor* Reichen. A.Tishechkin des. 2002" (FIMAK); female mounted on point with a cardboard-mounted worker of *Neivamyrmex legionis* under it and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton legionis* / *Metasynodites minor* n. Reichensp. / MUSEUM KOENIG BONN PARALECTOTYPE *Metasynodites minor* Reichen. A.Tishechkin des. 2002" (FIMAK); female mounted on cardboard and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton legionis*

14.I.29 / Paratype ! Reichensperger / *Metasynodites minor* n. Reichensp. / Purchase ex colln. Tomaz Borgmeier Pres. By C.C.Gregg / PARALECTOTYPE *Metasynodites minor* Reichen. A.Tishechkin des. 2002" (FMNH).

Other Material. **BRAZIL: Paraná:** Rio Negro, with *Neivamyrmex legionis* (3, FIMAK and ZIN).

Distribution. Known only from the type locality in the Brazilian state Paraná.

Metasynodites paschalis (Reichensperger, 1930)

Reichensperger, 1930: 84 (as *Mesynodites*). Mazur, 1984: 310 (as *Mesynodites*). Helava *et al.*, 1985: 279. Mazur, 1997: 154.

Lectotype: male mounted on point with a worker of *Neivamyrmex legionis* and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton legionis* / Paratypus / *Metasynodites paschalis* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE Mesy*nodites paschalis* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotype: female male mounted on point with a worker of *Neivamyrmex legionis* and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton legionis* / Type ! Reichensperger / Mesy*nodites (Metasynodites* n. subg. Reichensp. / *M. paschalis* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE Mesy*nodites paschalis* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other Material. **BRAZIL: Paraná:** Rio Azul, 25º42'S 50º46'W, 1000 m, X.1959, F.Plaumann (1, FMNH); Rio Negro, with *Neivamyrmex legionis* (3, CMN and FIMAK); with *N. legionis,* 14.I.1929 (2, MACN). **Santa Catarina:** Nova Teutonia, V.1960, F.Plaumann (1, FMNH).

Distribution. Known only from thee localities in Brazilian states Paraná and Santa Catarina.

***Microsynodites,* new genus** (Fig. 21-22)

Description. Body oval or short oval, small (PPL 1.5-2 mm). Body surface smooth, with abundant punctures and numerous short erect setae, mainly dorsally. Head with prominent separate latero-marginal frontal carinae, frontal stria incomplete. Faces of mandible bases with deep funnel-like depression and uncut edge. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral striae complete, anterior stria interrupted medially and represented by fragments along anterior pronotal angles or absent entirely. Pronotal disc with large punctures, dense or more scattered. Elytron with complete set of dorsal striae, complete outer subhumeral, 1st-5th dorsal and sutural, and abbreviated extra stria between 5th dorsal and sutural, occasionaly striae obscured by dense punctures. Dorsal striae with large, circular or elongate punctures, sometimes each stria with 2-3 punctures rows. Elytro-epipleural border sharp, angulate along subhumeral stria. Propygidium densely punctuate, with marginal stria along basal and lateral margins. Pygidium densely punctuate, in females with modifications (smooth oculae, longitudinal striae) in apical part. Prosternal lobe with complete marginal stria, deep longitudinal sutures, preapical foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triangular process. Marginal lateral stria of mesosternum present as indistinct lateral fragments, discal marginal stria complete or obscured by dense punctures. Metasternal disc flat or slightly convex, often densely punctate, unmodified in males. Outer lateral metasternal striae present consistently, inner lateral and longitudinal discal striae of metasternum either distinct or obscured

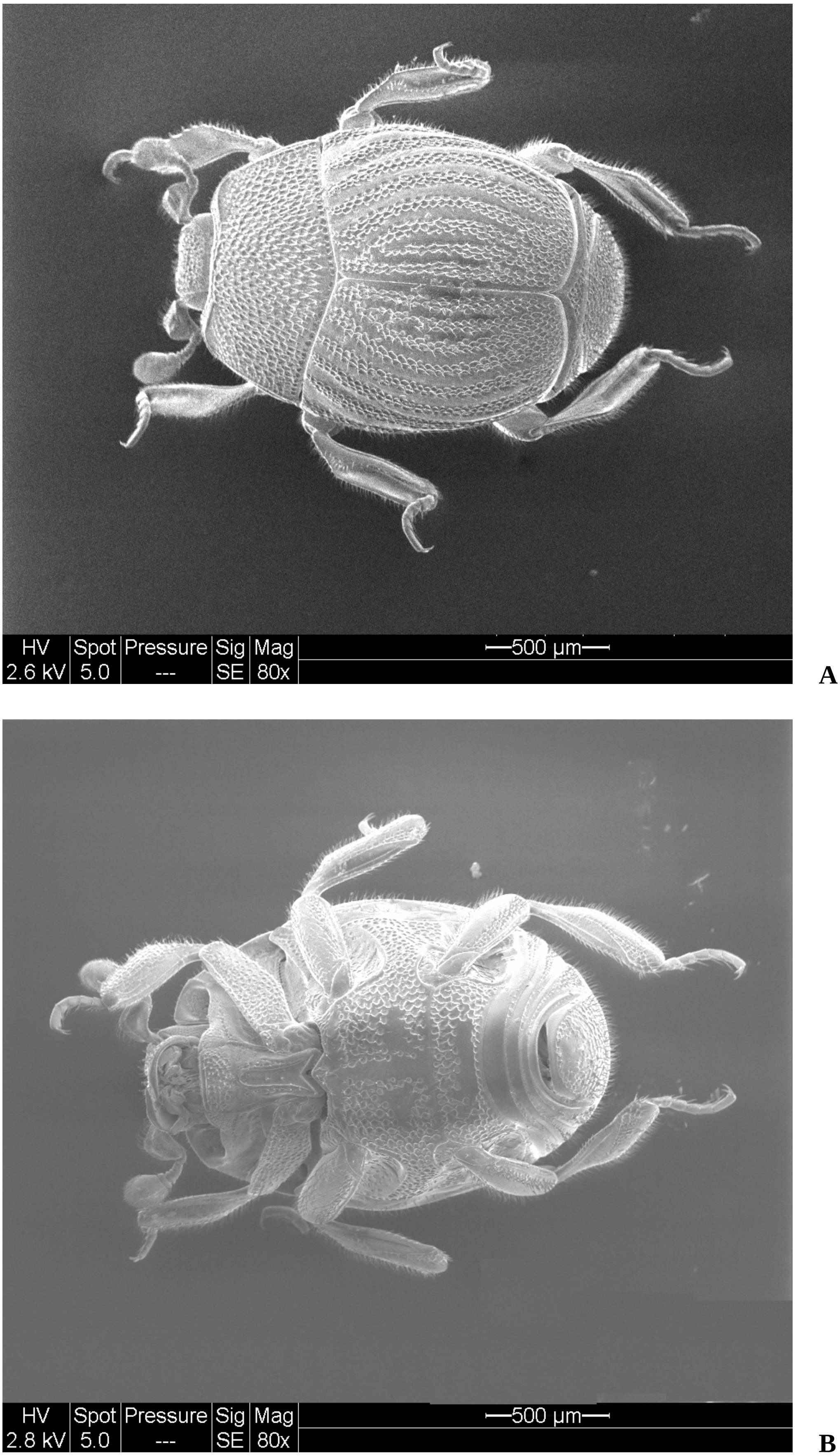


Fig. 21. Habitus of *Microsynodites schmidti*. A. Dorsal aspect; B. Ventral aspect.

by dense punctures. First abdominal sternite with distinct long postmetacoxal stria, its lateral stria may be obscured by dense punctation. Legs relatively long, tibia paddle-like. Protibia with 5-8 short spines, meso- and metatibia with central tooth and occasionally few spines on outer margins. Aedeagus with parameres short, laterally flattened, drop-shaped in profile, with no fusion present. Penis aligned perpendicularly to the longitudinal paramere axis. Basal piece long, with shallow and wide dorsal apical emargination. Male 8th sternite with separate, not reduced in size halves and pair of regular-sized velae. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male 9th sternite with spoon-shaped "handle". Male 9th tergite with small ventral apodeme and long basal projection, long thin apical projections with angulate or rounded apices and without ventral process. Halves of male 9th tergite narrowly fused, bridge with large square projection on posterior margin, 10th tergite absent (or incorporated into mentioned projection). Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles and separate median sclerite. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, fused into U/V-shaped figure.

Type species. *Mesynodites schmidti* Lewis, 1893

Etymology. The genus name represents a combination of the Greek word "mikros" meaning "small" and a part of the generic name *Mesynodites*, reflecting consistently small body sizes of the genus members. Gender is masculine.

Remarks. Small size, short oval shape, a full set of regular dorsal striae and strong development of punctures along with a combination of several genital characters (not

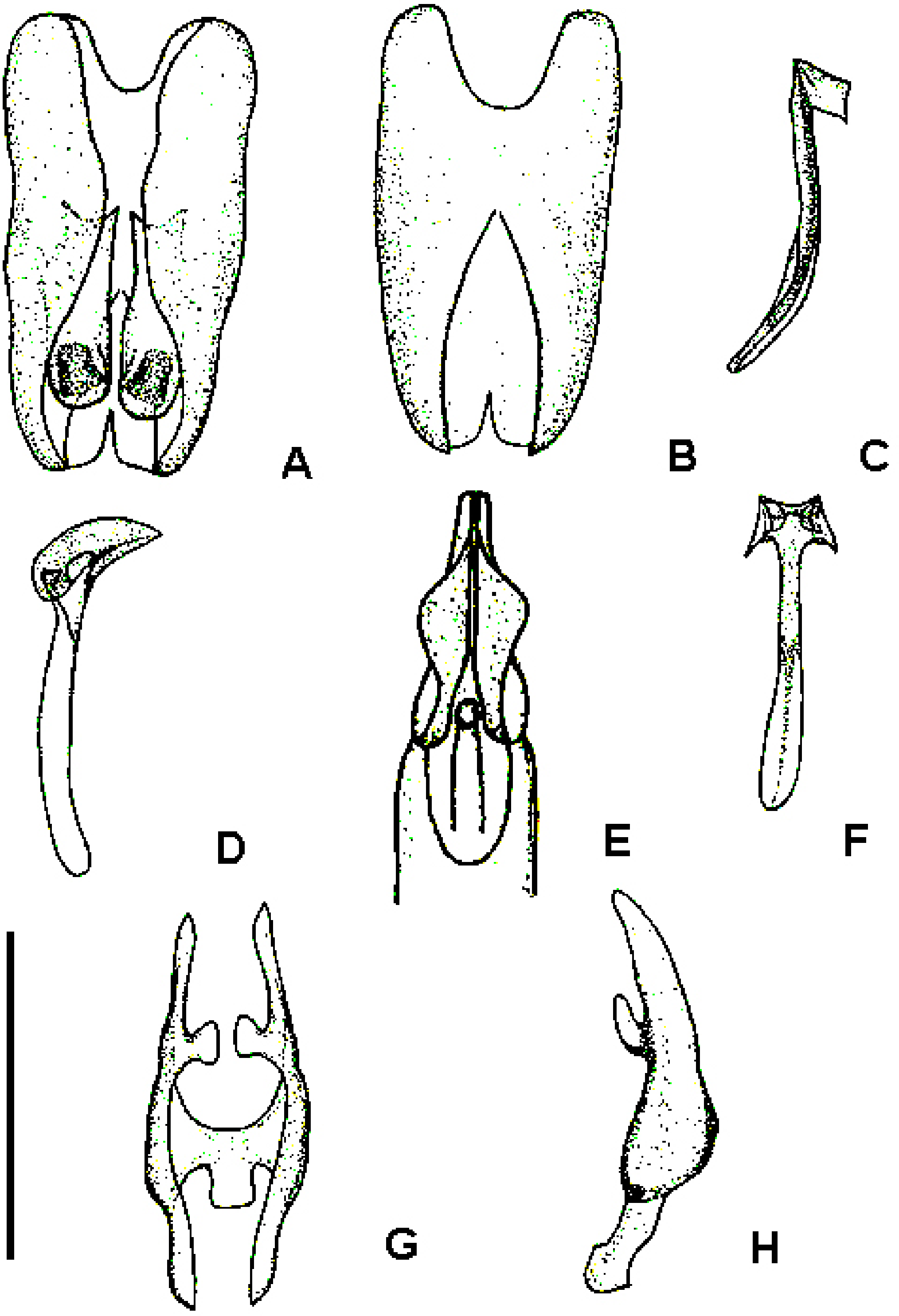


Fig. 22. Male genitalia of *Microsynodites schmidti*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

reduced halves of male 8th sternite, male 9th sternite posessing long and narrow basal projections, long thin apical projections with obtuse apices and prominent rectangular prosess of the sternite body, but lacking ventral processes, fused female genital sclerites) distinguish this genus from other related genera in the (*Monotonodites* - *Mesynodites evanescens*) clade.

List of Species.

Microsynodites ciliatus (Bruch, 1923) new combination

Bruch 1923: 192 (as *Synodites*), 1929: 433. Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point, with a cardboard-mounted worker of *Eciton dulcius* under it, and labeled “Alta Gracia Córdoba 4.XII.21 C.B. / Typus / *Synodites ciliatus* Bruch / PICHADO / Mus. Arg. Cs. Nat./ LECTOTYPE S*ynodites ciliatus* Bruch A.Tishechkin des. 2002” (MACN). Paralectotypes: 3 males and 1 female mounted on points and labeled as the lectotype, but with the “Paralectotype…” instead of the “Lectotype…” labes (MACN); 3 females mounted on points and labeled as previous lectotypes but with the “Cotypus” instead the “Typus” labels (MACN); female mounted on point and labeled as previous lectotypes but collected on 4.I.1922 (MACN).

Other Material. **ARGENTINA: Córdoba:** Alta Gracia, C.Bruch (3, FMNH; 1, ZIN); with *Eciton dulcius* Forel, 21.I.1924, C. Bruch (2, FMNH; 1, PWK); with *E. dulcius*, I.1926, C.Bruch (2, USNM).

Distribution. Numerous specimens (20 syntypes mentioned in original description) are known only from the type locality in northetn Argentina. Also reported from the Argentinian province Catamarca with *Neivamyrmex strobeli* Mayr as a host without any additional data (Bruch, 1929). I did not see any specimens with such labels, so I suggest to take this report cautiously as there are some apparently undescribed sibling species in this group.

Microsynodites schmidti (Lewis, 1893) new combination (Fig. 19-20)

Lewis, 1893: 423 (as *Synodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Synonym: *Mesynodites scaber* Reichensperger, 1931: 275, new synonym.

Reichensperger, 1931: 275. Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Holotype: male mounted on point and labeled "Bahia A. Cr. / *Synodites* new species (the 7th !) / *Synodites schmidti* Lewis Type" (NHML); Lectotype of *Mesynodites scaber*: female mounted on point with a major worker of *Nomamyrmex hartigi* Westwood and labeled "Campinas Goyaz, Schwarzmaier / *Eciton schlechtendali* 26.IV.29 / Type ! Reichensperger / *Mesynodites scaber* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites scaber* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted on point and labeled "Campinas Goyaz, Schwarzmaier / *Eciton crassicorne* 29.I.29 / Paratype ! Reichensperger / *Mesynodites scaber* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites scaber* Reich. A.Tishechkin des. 2002" (FIMAK); female mounted on point and labeled: "*Eciton schlechtendali* 26.IV.29 / Paratype ! Reichensperger / *Mesynodites scaber* Reichensp. / CNHM Colln. (Ex. Coll. C.A.Ballou) / PARALECTOTYPE *Mesynodites scaber* Reich. A.Tishechkin des. 2002" (FMNH).

Other Material. **BOLIVIA: Santa Cruz:** 3.7 km SSE Buena Vista, Hotel Flora & Fauna, 17º29.95'S 63º53.15'W, 405 m, 5-15.XI.2001, M.C. Thomas, B.K. Dozier (1, FSCA). **BRAZIL: Goiás:** Campinas, with *Nomamyrmex esenbecki*, P.

Schwarzmaier (3, FIMAK); with *N. esenbecki*, 15.X.1935, P.Schwarzmaier (9, AKT and FIMAK) with *N. esenbecki*, 12.XI.1935, P.Schwarzmaier (1, FIMAK); with *N. esenbecki*, 8.XI.1936, P.Schwarzmaier (4, AKT and FIMAK). **Pará:** Tucurui, 3º45'S 49º40'W, flight intercept trap, VI.1985, N.Dégallier (1, ND); flight intercept trap, 16-29.VII.1985, N.Dégallier (1, ND).

Distribution. Known with certainty from scattered locations in central South America, in the Bolivian departament of Santa Cruz and the Brazilian states Bahia, Goiás and Pará. Lewis' records from 'Bahia' are somewhat ambiguous (see discussion under *Euclasea tuberculata*), but in the context of the species range, reference of 'Bahia' as Brazilian state is more plausible than the Atlantic coast of Honduras.

Remarks. Type specimens of *M. schmidti* and *M. scaber* differ slightly in density and development of elytral and metasternal punctures. However, their conspecificity seems to be well established thanks to availability of numerous specimens from different, widely separated localities. Specimens from different populations exibit continuous variability in punctures development and conservative morphology of male genitalia, supporting the status of a single, somewhat variable species at the present level of knowledge.

Microsynodites strigilatus **(Reichensperger, 1931) new combination**

Reichensperger, 1931: 274 (as *Mesynodites*). Mazur, 1984: 309 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites striguslatus,* sic!). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: female mounted on point and labeled "Campinas Goyaz, Schwarzmaier / *Eciton schlechtendali* 26.IV.29 / Type ! Reichensperger / *Mesynodites* *strigilatus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites strigilatus* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other Material. **BRAZIL: Goiás:** Campinas, with *Nomamyrmex hartigi,* 26.IV.1929, P.Schwarzmaier (1, FMNH).

Distibution. Known only from the type locality in the Brazilian state Goiás.

***Monotonodites* (Reichensperger, 1939)**

Type species: *Mesynodites levis* Reichensperger, 1939

Reichensperger, 1939: 131 (as *Mesynodites* [*Monotonodites*]). Mazur, 1984: 309 (as *Mesynodites* [*Monotonodites*]). Helava *et al.*, 1985: 282-284. Mazur, 1997: 154.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985). The following is additional descriptive information. Female 8th sternite with deeply emarginated apical margin, distinct basal bridge with briefly angulate lateral parts and rounded basal angles and separate median sclerite. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, fused into U/V-shaped figure.

List of Species

***Monotonodites levis* (Reichensperger, 1939)**

Reichensperger, 1939: 132 (as *Mesynodites*). Mazur, 1984: 309.(as *Mesynodites*). Helava *et al.*, 1985: 284. Mazur, 1997: 155.

Lectotype: male mounted on point, with a worker of *Neivamyrmex alfaroi* Emery cardboard-mounted under it, and labeled "San Jose Costa Rica H.Schmidt / *Ac. alfaroi* Em. / *Mesynodites Monotonodites levis* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites levis* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted and labeled as the lectotype, but with lectorype label instead paratype; 3 females, one mounted on point and two mounted on the same cardboard, labeled "San Jose Costa Rica H.Schmidt / *Ac. alfaroi* Em. / Paratype ! Reichensperger / *Mesynodites Monotonodites levis* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites levis* Reichen. A.Tishechkin des. 2002" (FIMAK); female mounted on point and labeled "San Jose Costa Rica H.Schmidt / *castaneum* Borgm. *A. opacithorax* / A.Reichensperger / *Mesynodites Monotonodites levis* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites levis* Reichen. A.Tishechkin des. 2002" (FIMAK); male mounted on point, with a worker of *Neivamyrmex alfaroi* cardboard-mounted under it, and labeled "San Jose Costa Rica H.Schmidt / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites levis* Reichen. A.Tishechkin des. 2002" (FIMAK);

Other material. **COSTA RICA: San Jose:** San Jose, H.Schmidt (2, FMNH); with *Neivamyrmex alfaroi*, H.Schmidt (2, AKT; 5, FIMAK). **PANAMA: Colón:** 15 km N junction of Escobal and Piña Roads, 30 m, flight intercept trap, 2-11.VI.1996, J.Ashe, R.Brooks (1, SEC).

Distribution. Known only from two localities in central Costa Rica and central Panama.

Monotonodites nitidus (Reichensperger, 1923)

Reichensperger, 1923: 244 (as *Synodites*). Mazur, 1984: 309.(as *Mesynodites*). Helava *et al.*, 1985: 284. Mazur, 1997: 155.

Lectotype: male mounted on point and labeled "Rio Negro Paraná 1923 P.M.Witte / *Eciton quadriglumme* / A.Reichensperger / Paratypus 1923 / *Mesynodites* 1923 *nitidus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Synodites nitidus* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: female mounted on point and labeled as previous specimen, but with paralectotype label (FIMAK);

female mounted on point and labeled as previous specimen, but without "Paratypus 1923" label (FIMAK); male mounted on point and labeled "*Eciton* 1923 *quadriglumme* R. Negro Paraná / *Mesynodites nitidus* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Synodites nitidus* Reichen. A. Tishechkin des. 2002" (FIMAK); female mounted on point and labeled "Rio Negro Paraná coll. Reichensperger / *Eciton 4glumme* / *Mesynodites nitidus* Reichensp. / P.TYPUS / WMMann Coll. 1954 / PARALECTOTYPE *Synodites nitidus* Reichen. A.Tishechkin des. 2002" (USNM); 3 females mounted on point and labeled "[golden circle] / Rio Negro Paraná coll. Reichensperger / *ex nido Ecitonis quadriglumis* / *Synodites nitidus* Reichensp. Paratype / PARALECTOTYPE *Synodites nitidus* Reichen. A.Tishechkin des. 2002" (ZIN).

Other material. **BRAZIL: Paraná,** Rio Negro (1, CMN); with *Eciton quadriglumme*, 5.I.1929 (1, FMNH). **Santa Catarina**, Nova Teutonia, with *E. quadriglumme*, F.Plaumann (1, FIMAK).

Distibution. Known only from two localities in the Brazilian states Paraná and Santa Catarina.

Monotonodites pauperella (Lewis, 1893) new combination

Lewis, 1893: 424 (as *Euclasea*). Mazur, 1984: 306 (as *Euclasea*). Helava *et al.*, 1985: 254 (as *Euclasea*). Mazur, 1997: 150. (as *Euclasea*).

Lectotype: male mounted on point and labeled "Bahia Tabac. 89 / Type / George Lewis Coll. B.M. 1926-369. / *Euclasea pauperella* Type. Lewis / LECTOTYPE *Euclasea pauperella* Lewis A.Tishechkin des. 2002" (NHML).

Distribution. Probably, the Brazilian state Bahia, but see discussion under *Euclasea tuberculata*.

Monotonodites raptantis **(Reichensperger, 1925) new combination**

Reichensperger, 1925: 353 (as *Euclasea*). Mazur, 1984: 306 (as *Euclasea*). Helava *et al.*, 1985: 254 (as *Euclasea*). Mazur, 1997: 150. (as *Euclasea*).

Holotype: male mounted on point, with a worker of *Neivamyrmex raptans* Forel cardboard-mounted under it, and labeled "*Acam. raptans* Porto Alegre P.Buck 9.7.24 / coll. Reichensperger Type. desc. 1925 / *Euclasea raptantis* n. Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Distribution. Known only from type locality in the Brazilian state Rio Grande do Sul.

Monotonodites subopacus **Reichensperger (1939)**

Reichensperger, 1939: 133 (as *Mesynodites*). Mazur, 1984: 309 (as *Mesynodites*). Helava *et al.*, 1985: 284. Mazur, 1997: 155.

Holotype: female mounted on point and labeled "San Jose Costa Rica H.Schmidt / *E. (Acamat.) humile* Borgm. / Type ! Reichensperger / *Mesynodites Monotonodites subopacus* Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Other material. **COSTA RICA: San Jose:** San Jose, with *Neivamyrmex humilis* Borgmeier, H.Schmidt (1, FIMAK).

Distribution. Known only from type locality in the Costa Rican province San Jose.

Mutodites, **new genus** (Fig. 23-24)

Description. Body oval or short oval, small to medium sized (PPL 1.5-2.5 mm). Body surface smooth, shiny, asetose, without punctures or with weakly developed dorsal punctures. Head without latero-marginal frontal carinae, frontal stria complete. Faces of mandible bases with deep funnel-like depression and uncut edge. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal outer lateral and anterior striae complete. Pronotal disc with small punctures, dense or scattered and obscure. Elytron with relatively complete set of dorsal striae, outer subhumeral always complete, 5th dorsal and sutural consistently absent or strongly reduced. Dorsal striae mostly thin impunctate, occasionally with elongate punctures, especially basally. Elytro-epipleural smooth, gradually rounded. Propygidium with or without punctures, with marginal stria along apical, basal and lateral margins. Pygidium with or without punctures, without modifications in females. Prosternal lobe with complete marginal stria, thin longitudinal sutures, small and inconspicuous preapical foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triagular process. Marginal lateral stria of mesoternum present as indistinct lateral fragments, discal marginal stria interrupted medially or complete. Metasternal disc flat or slightly convex, without punctures, unmodified in males. Outer lateral and inner metasternal and longitudinal discal striae striae present consistently. Outer lateral stria without recurrent arm, longitudinal discal stria variable, sometimes abbreviated apically. First abdominal sternite with distinct long lateral and postmetacoxal stria. Legs relatively long, tibia paddle-like. Protibia with 5-8 short spines, meso- and metatibia without cenral tooth and few spines on outer margins. Aedeagus with parameres short, laterally flattened, drop-shaped in profile, with no fusion present. Penis aligned almost perpendicularly to the longitudinal paramere axis. Basal piece long, with shallow and wide dorsal apical emargination. Male 8th sternite with separate, normal-sized halves and pair of normal-sized velae. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male

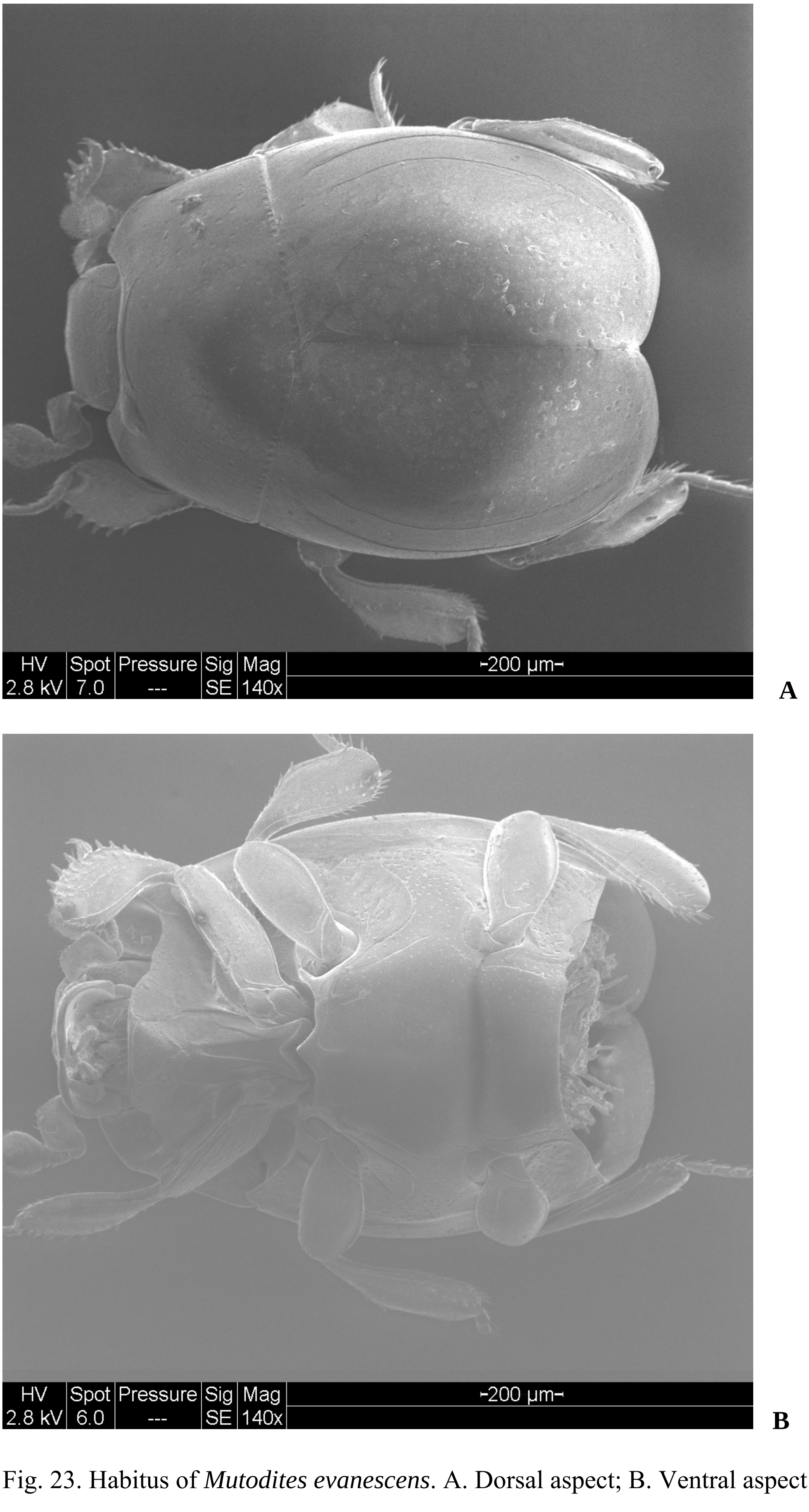


Fig. 23. Habitus of *Mutodites evanescens*. A. Dorsal aspect; B. Ventral aspect.

9th sternite with spoon-shaped “handle”. Male 9th tergite with long thin ventral apodeme and long basal projection, long thin apical projections with angulate apices and with short membranous ventral process. Halves of male 9th tergite narrowly fused, bridge with small rectangular or triangular projection on posterior margin, 10th tergite absent (or incorporated into mentioned projection). Female 8th sternite with deeply emarginate apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles and separate median sclerite. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, fused into U/V-shaped figure.

Type species. *Mesynodites evanescens* Reichensperger, 1935

Etymology. The genus name represents a combination of Latin word “muto” meaning “alter, exchange” and a part of the generic name *Mesynodites*, reflecting an apparent spectacular host shift within the genus. The gender is masculine.

Remarks. The combination of smooth shiny body surface with limited presence of punctures and complete absence of setae, complete anterior stria of pronotum, excavate base of mandible with uncut edge, prosternal lobe with longitudinal sutures and basal foveae and full set of metasternal striae allows a recognition of the genus externally. The rudimentary membranous ventral processes of male 9th tergite and long thin ventral apodemes are two genitalic autapomorphies of *Mutodites* within the (*Monotonodites – Mesynodites evanescens*) clade.

List of Species.

***Mutodites evanescens* (Reichensperger, 1935) new combination** (Fig. 21-22)

Reichensperger, 1935: 31 (as *Mesynodites*). Mazur, 1984: 308. (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 151. (as *Mesynodites*).

Lectotype: male mounted on point and labeled “Mendes, Rio Brasil X.33 Eidm./ Dr. Eidmann legit. / *Mesynodites evanescens* Reichensp. / Ko.Type ! Reichensperger / Nat. Hist. Mus. Basel – 1972 coll. H.Eidmann / LECTOTYPE *Mesynodites evanescens* Reichen. A.Tishechkin des. 2002” (NHMB).

Other Material. **BRAZIL: Rio de Janeiro:** Mendes, with *Atta sexdens* L. (1, FMNH).

Distibution. Known only from the type locality in the Brazilian state Rio de Janeiro.

***Mutodites megacantha* (Reichensperger, 1938)** new combination

Reichensperger, 1938: 90 (as *Mesynodites*). Mazur, 1984: 308. (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152. (as *Mesynodites*).

Holotype: male mounted on point and labeled “Bella Vista, Goyas Schwarzmaier [the rest - on the other side of the label] 533 *E. crassic.* 26.XII.34 / *Eciton crassicorne* / Type ! Reichensperger / *Mesynodites megacantha* Reichensp. / MUSEUM KOENIG BONN“ (FIMAK).

Distibution. Known only from the type locality in the Brazilian state Goiás.

***Mutodites semistriatus* (Bruch, 1933)** new combination

Bruch, 1933: 30 (as *Mesynodites*). Mazur, 1984: 309. (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152. (as *Mesynodites*).

Synonym: *Mesynodites eidmanni* Reichensperger, 1935a: 28, new synonym. Reichensperger, 1935a: 28. Mazur, 1984: 307. (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 151. (as *Mesynodites*). Holotype: female mounted on point and labeled “Est. Exp. Loreto Misiones Dr. A.Ogloblin / con *Atta sexdens* / Typus / *Mesynodites semistriatus* typus C. BRUCH DETERM. / PICHADO / Mus. Arg. Cs. Nat.” (MACN). Lectotype of *M. eidmanni*: female mounted on point and labeled “Mendes Rio. Bras. 27.9.33 / *Atta sexdens* / Type ! *Eidmanni*

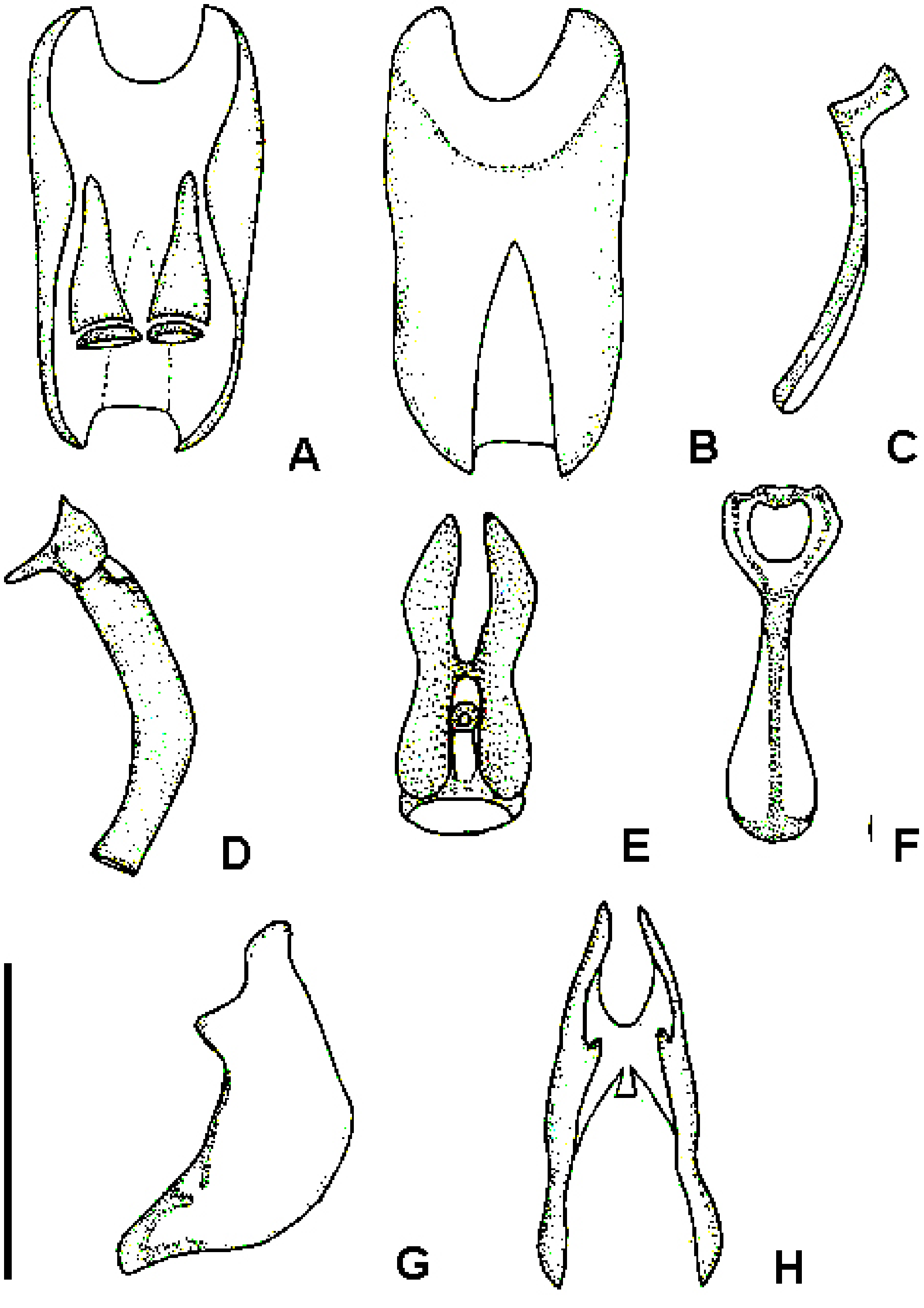


Fig. 24. Male genitalia of *Mutodites evanescens*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

Reichensp./ *Mesynodites eidmanni* Reichensp. / LECTOTYPE *Mesynodites eidmanni* Reichen. A.Tishechkin des. 2002" (NHMB).

Distibution. Known only from two localities northern Argentina (Misiones Province) and southern Brazil (Rio de Janeiro State).

Remarks. Comparison of the type specimens has revealed conspecificity of the species. This discovery was a great surprise to me as Reichensperger was in regular communication with Bruch and discussed *M. semistriatus* in his paper. Apparently, Reichensperger did his comparison using only the description and was not able to correctly assess the differences between specimens apparent from the paper.

Mutodites speculum **(Reichensperger, 1931)** new combination

Reichensperger, 1931: 280 (as *Mesynodites*). Mazur, 1984: 309. (as *Mesynodites*). Helava *et al.*, 1985: 337 (as *Mesynodites*). Mazur, 1997: 152. (as *Mesynodites*).

Holotype: male mounted on the same point with a worker of *Nomamyrmex esenbecki* and labeled "Campinas Goyaz, Schwarzmaier / *Eciton crassicorne* / Type ! Reichensperger / *Mesynodites speculum* n Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Distribution. Known only from the type locality in the Brazilian state Goiás.

Remarks. The original description states the type locality as "Inhacimas [= Inhumas], Goyaz" without any date and mentions "*Eciton crassicorne* [=*Nomamyrmex esenbecki*]" as a host. The "Inhacimas" name could be traced to unclear label handwriting of "Inhumas" by P. Schwarzmaier, also occasionally interpreted as "Inhaumas" by Reichensperger (own observations). The actual specimen corresponds well with the description and photograph in Reichensperger (1931), and has been long known as the single specimen of the species (Dégallier, 1993; personal communication). Given these facts as well as Reichensperger's ususal sloppiness with labels, I am sure that this specimen is the holotype.

***Nicolasites,* new genus** (Figs. 25-26)

Description. Body elongate oval, small (PPL ca. 1.5 mm), convex dorsally. Body surface smooth and shiny, asetose. Head with frons convex, without latero-marginal frontal carina, frontal stria incomplete. Frons and clypeus in different planes, the angle between them almost 90°. Faces of mandible bases with deep funnel-like depression and uncut edge. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral stria complete, anterior stria interrupted medially and represented by long fragments along anterior pronotal angles or absent entirely. Pronotal disc with large sparse punctures. Elytron with incomplete set of dorsal striae, complete outer subhumeral, fragments and traces 1st-5th dorsal and and sutural, and additional irregular, more or less transverse arcs or rows of elongate punctures. Remnants of dorsal striae with large shallow elongate or arc-shaped punctures. Elytro-epipleural border smooth, gradually rounded. Propygidium sparsely punctate, with marginal stria complete along entire margins. Pygidium impunctate, without modifications in females. Prosternal lobe with complete marginal stria, deep longitudinal sutures, preapical foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triangular process. Marginal lateral stria of mesosternum present as indistinct lateral fragments, discal marginal stria complete. Metasternal disc flat, impunctuate, unmodified in males. Outer and inner lateral and longitudinal discal metasternal striae present, complete. Inner lateral striae without

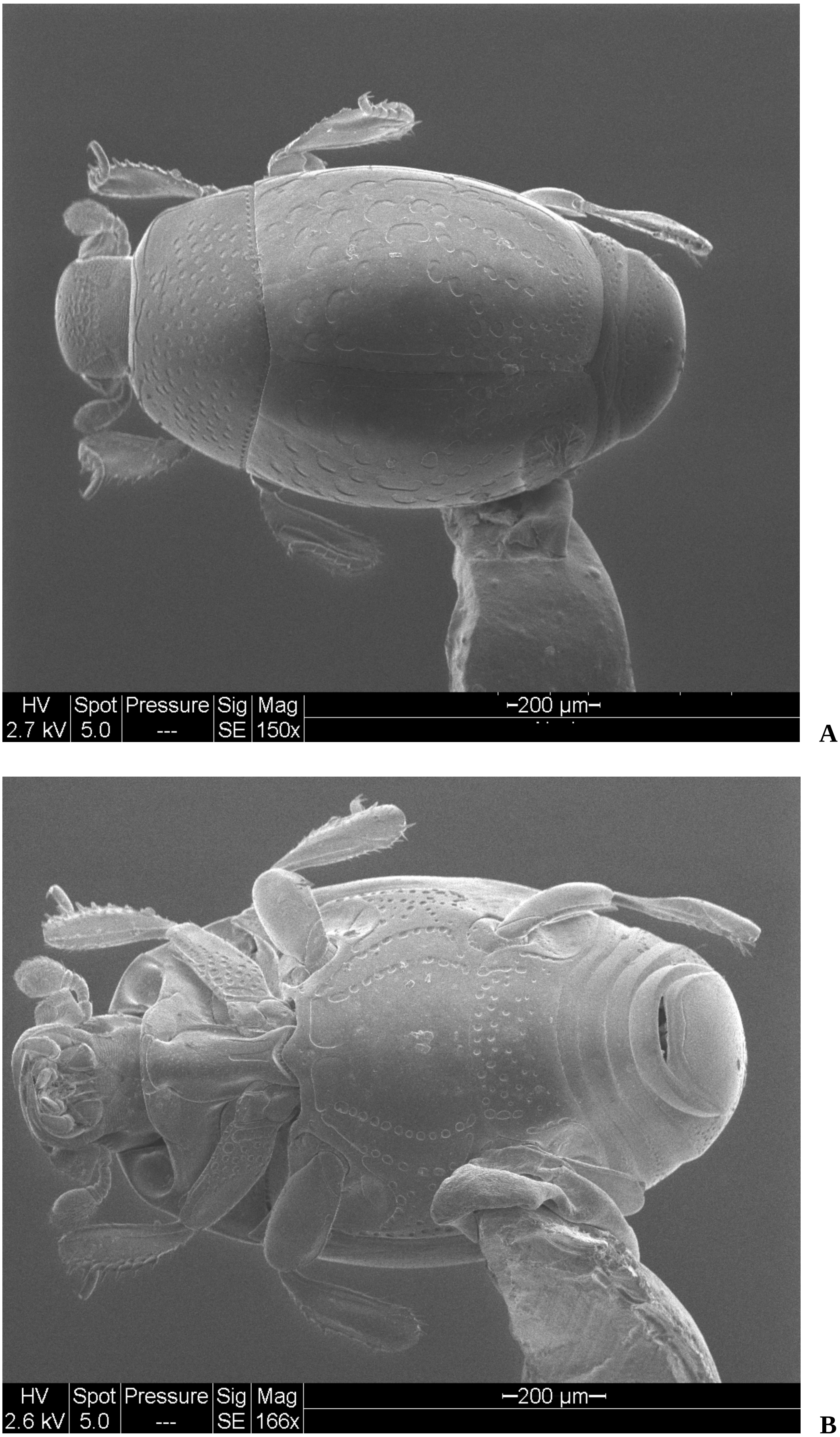


Fig. 25. Habitus of *Nicolasites graniformis*. A.Dorsal aspect; B.Ventral aspect.

recurrent arms. Both inner lateral and longitudinal discal metasternal striae arched outwardly. First abdominal sternite sparsely punctate, with distinct long lateral and postmetacoxal striae. Legs relatively long, tibia paddle-like. Protibia with 7-8 short spines, meso- and metatibia with central tooth and few spines on outer margins. Aedeagus with parameres short, laterally flattened, drop-shaped in profile, with no fusion present. Penis aligned perpendicularly to the longitudinal paramere axis. Basal piece long, with shallow and wide dorsal apical emargination. Male 8th sternite with separate, normal-sized halves and pair of normal-sized velae. Male 8th tergite with TAS and transverse posterior suture present complete narrow intra-TAS plate and a pair of extra preapical sclerites. Male 9th sternite with spoon-shaped “handle”. Male 9th tergite with small ventral apodemes and long and very wide basal projections, long thin apical projections with acute apices and with long sclerotized dorso-ventrally flattened ventral processes. Halves of male 9th tergite narrowly fused, bridge with narrow bifurcate projection on posterior margin, 10th tergite absent (or incorporated into mentioned projection). Female 8th sternite with deeply emarginated apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites simple, elongate, separate.

Type species. *Mesynodites graniformis* (Schmidt, 1893)

Etymology. The genus name represents a combination of a part of the generic name *Mesynodites* and Nicolas Dégallier’s name, honoring his remarkable contribution to the studies of inquilinous histerids. The gender is masculine.

Remarks. Characteristic elytral striation and arched subparallel inner lateral and longitudinal discal striae allow recognition of *Nicolasites* among other genera in

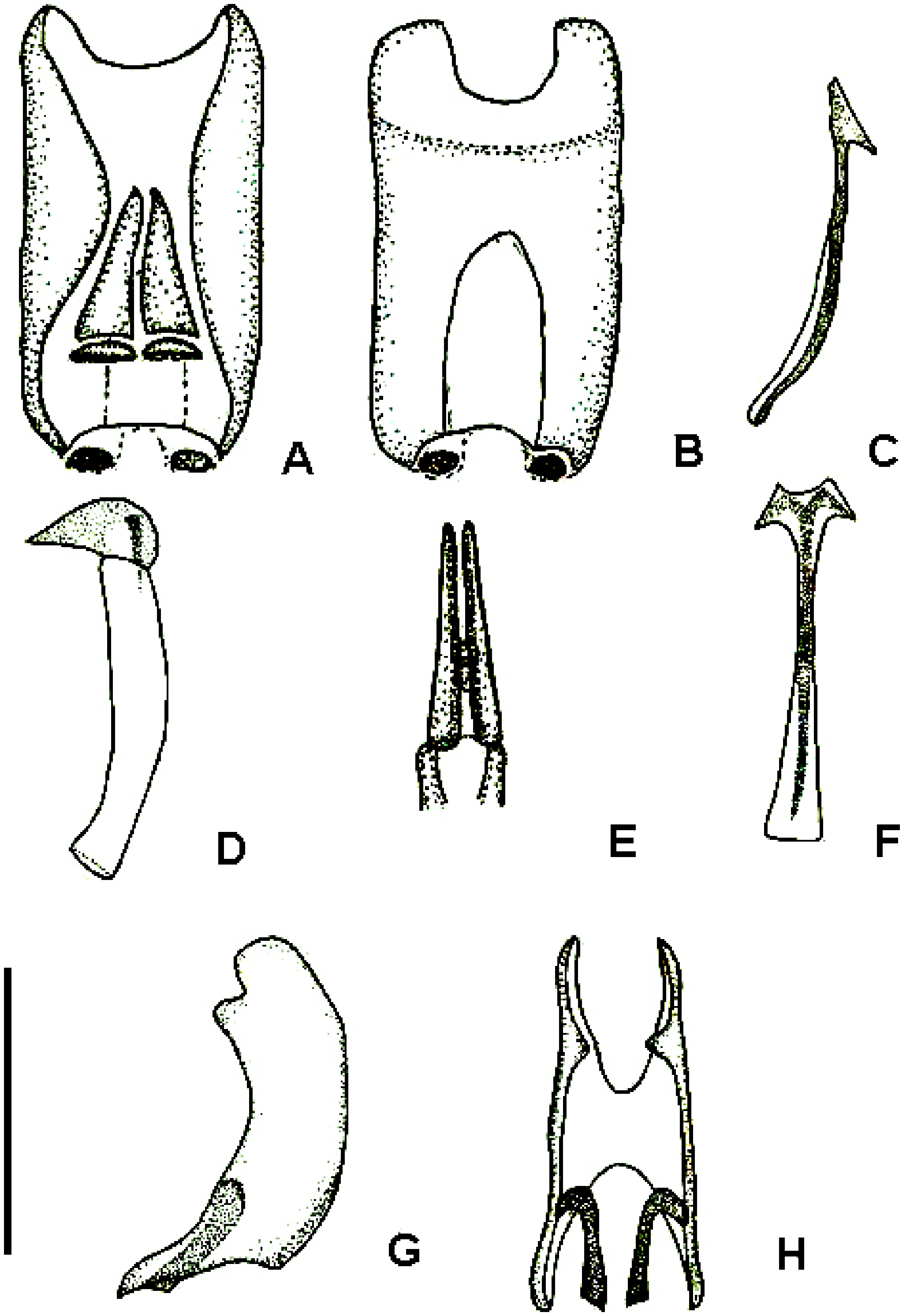


Fig. 26. Male genitalia of *Nicolasites graniformis*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.

the (*Monotonodites - Mesynodites evanescens*) clade. Important diagnostic autapomorphic (at least within the mentioned clade) genital characters include male 8th tergite with narrow and long TAS plate and extra preapical sclerites, male 9th tergite with very wide long basal projections, long triangular apical projections, bifurcate posterior process of the tergite body and long sclerotized ventral processes, lack of median sclerite of female 8th sternite and separate female genital sclerites.

List of Species.

Nicolasites graniformis (Schmidt, 1893) new combination (Fig. 25-26)

Schmidt, 1893: (as *Synodites*). Mazur, 1984: 308. (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites grandiformis,* sic!). Mazur, 1997: 151. (as *Mesynodites*).

Holotype: female mounted on point and labeled "Sumatra / Type / coll. J.Schmidt / *Synod. graniformis*" (HUB).

Other Material. **FRENCH GUIANA:** Mt. La Fumée near Saül, 3º39'46"N 53º13'19"W, 490 m, flight intercept trap, 1-8.VI.1997, J.Ashe, R.Brooks (1, SEC). **BRAZIL: Pará:** Altamira – Maraba, km 18, 3º09'S 54º20'W, flight intercept trap, 10-23.IX.1985, N.Dégallier (18, AKT, FMNH, MZSP, ND); Carajas (Serra Norte), 6º04'S 50º12'W, flight intercept trap, X.1984, N.Dégallier (1, ND); flight intercept trap, 16.IX.-6.X.1986, N.Dégallier (2, ND); flight intercept trap, VIII.1986, N.Dégallier (1, ND); Monte Alegre, 1º43'S 54º20'W, flight intercept trap, 17.VI.-3.VII..1992, N.Dégallier (5, AKT, MZSP, ND); Melgaço Distr., Rio Marinau, flight intercept trap, 27.X.-3.XI.1993, N.Dégallier (2, ND); Tucurui, 3º45'S 49º40'W, flight intercept trap, VI.1985, N.Dégallier (17, AKT, FIMAK, FMNH, HUB, ND); flight intercept trap, 16-29.VII.1985, N.Dégallier (11, MHNG, ND); flight intercept trap, 27.X.-9.XI.1985, N.Dégallier (4, ND); flight intercept trap, V.1986, N.Dégallier (5, ND); flight intercept trap, 20.V.-5.VI.1986, N.Dégallier (6, ND, MZSP); flight intercept trap, 1-15.IX.1987, N.Dégallier (1, ND); Utinga (I.P.E.A.N.), Belem, 1º27'S 48º26'W, flight intercept trap, VIII.1984, N.Dégallier (1, ND); flight intercept trap, V.1985, N.Dégallier (1, ND); flight intercept trap, VII.1985, N.Dégallier (2, ND); flight intercept trap, X.1986, N.Dégallier (2, ND). **GUYANA: Region 8:** Iwokrama Forest, 1 km W Kurupukari, Iwokrama Field Station, 4º40'19"N 58º41'4"W, 60 m, flight intercept trap, 30.V.-2.VI.2001, R.Brooks, Z.Falin (1, SEC). **VENEZUELA: Bolivar:** 20 km S Tumeremo, flight intercept trap, 24.VI.-12.VII.1987, S. & J.Peck (1, CMN).

Distribution. The type specimen was mislabeled. For no apparent reason, Mazur (1984, 1997) gave Mexico (with a questionmark in the second source) as a distributional area. The species is known from multiple localities in north-eastern South America, from Bolivar Province in Venezuela, through Guianas to Pará State in Brazil.

Nymphister Reichensperger, 1933

Type species: *Nymphister simplicissimus* Reichesperger, 1933

Reichensperger, 1933: 188. Mazur, 1984: 299. Helava *et al.*, 1985: 300-302. Mazur, 1997: 156.

Description. The genus was described in detail, diagnosed and illustrated by Helava *et al.* (1985). The following is additional descriptive information. Female 8th sternite with deeply emarginated apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present as 2 lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, simple, elongate.

List of Species.

Nymphister monotonus (Reichesperger, 1938) new combination

Reichesperger, 1938: 83 (as *Cheilister*). Mazur, 1984: 300. (as *Cheilister*). Helava *et al.*, 1985: 321 (as *Cheilister*). Mazur, 1997: 158. (as *Cheilister*).

Types. Two specimens from Hamburg Farm, Costa Rica, are mentioned in the original description, but could not be located and were reported as lost (Dégallier, 1993). However, a specimen found among unidentified/poorly labeled material of Reichensperger in FIMAK was positively assigned to this species. It has an original teal Nevermann's label "Hamburg Farm Reventazon Ebene Limon", additional rectangular piece of red cardboard and cardboard with a head of an *Eciton hamatum* F. major worker pinned beneath the geographic label. It is in complete agreement with the original description.

Other material. **COSTA RICA: Heredia:** LaSelva Biol. Station, 10º26'N 84º01'W, with *Eciton hamatum*, 25.VI.1998, A.Tishechkin (1, LSAM). **GUATEMALA:** Tikal, with *Eciton hamatum*, 12.I.1974, D.H. & A.C.Kistner (2, FMNH).

Distribution. Known from three locations in Central America, from Guatemala to central Costa Rica.

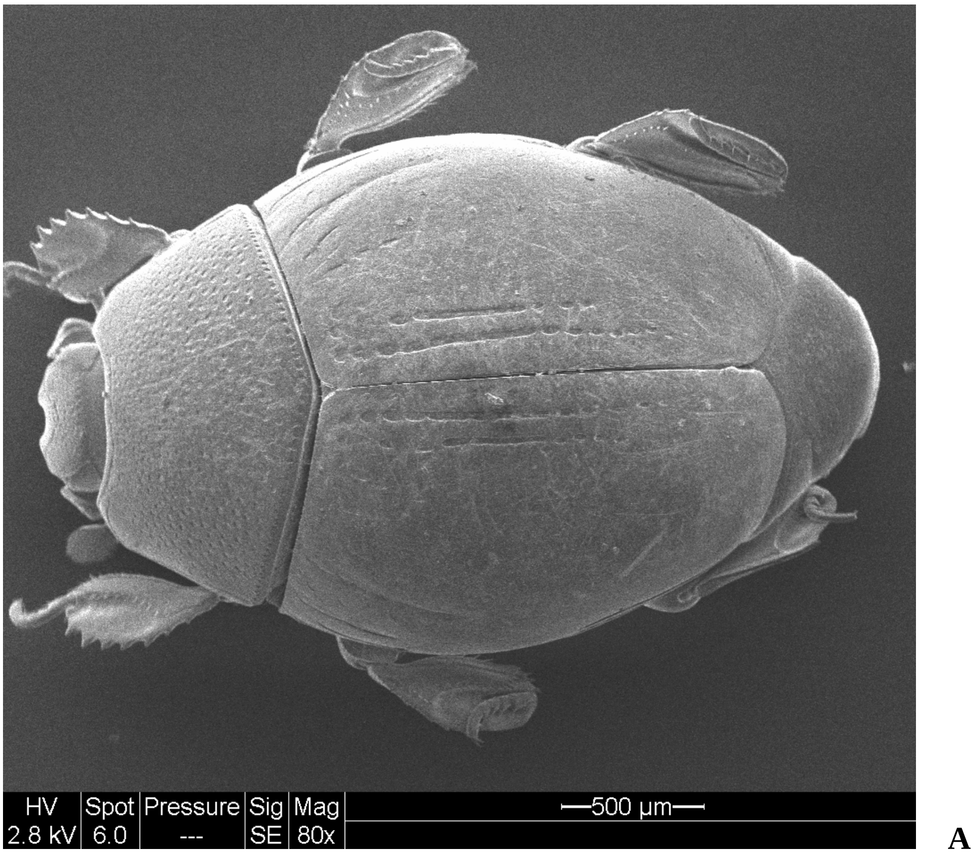
Nymphister simplicissimus Reichesperger, 1933

Reichesperger, 1933: 189. Mazur, 1984: 300. Helava *et al.*, 1985: 302. Mazur, 1997: 156.

Remarks. Distribution and host associations of the species have been reviewed recently (Tishechkin, 2003).

***Reichenspergerites,* new genus** (Fig. 27-28)

Description. Body oval, large (PPL 3.5 mm) and robust, convex dorsally. Body surface smooth, mostly covered with small dense background punctures, asetose. Head with prominent separate latero-marginal frontal carinae, frontal stria interrupted. Mandibles with faces of bases unmodified. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral stria complete, anterior stria interrupted medially and represented by fragments along anterior pronotal angles. Pronotal disc with dense large punctures in addition to background punctures. Elytron with strongly reduced set of impunctate dorsal striae, only outer subhumeral complete and sutural and presumably 5th represented by long fragments. Elytro-epipleural border smooth, gradually rounded. Propygidium with marginal stria only along parts of lateral margins, in females with weak median conical elevation near posterior margin. Pygidium in females with a pair of short longitudinal striae. Prosternal lobe with complete marginal stria and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triangular process. Marginal lateral stria of mesoternum present as indistinct lateral fragments, discal marginal stria complete. Metasternal disc convex, with dense large punctures, not modified in males. Outer lateral striae of metasternum complete, inner lateral stria represented by short basal fragment. First abdominal sternite with distinct and long lateral and postmetacoxal striae. Legs relatively short, tibia paddle-like. Protibia with 8 short spines, meso- and metatibia with central tooth and few spines on outer margins. Aedeagus with parameres short, dorso-ventrally flattened, with narrow basal



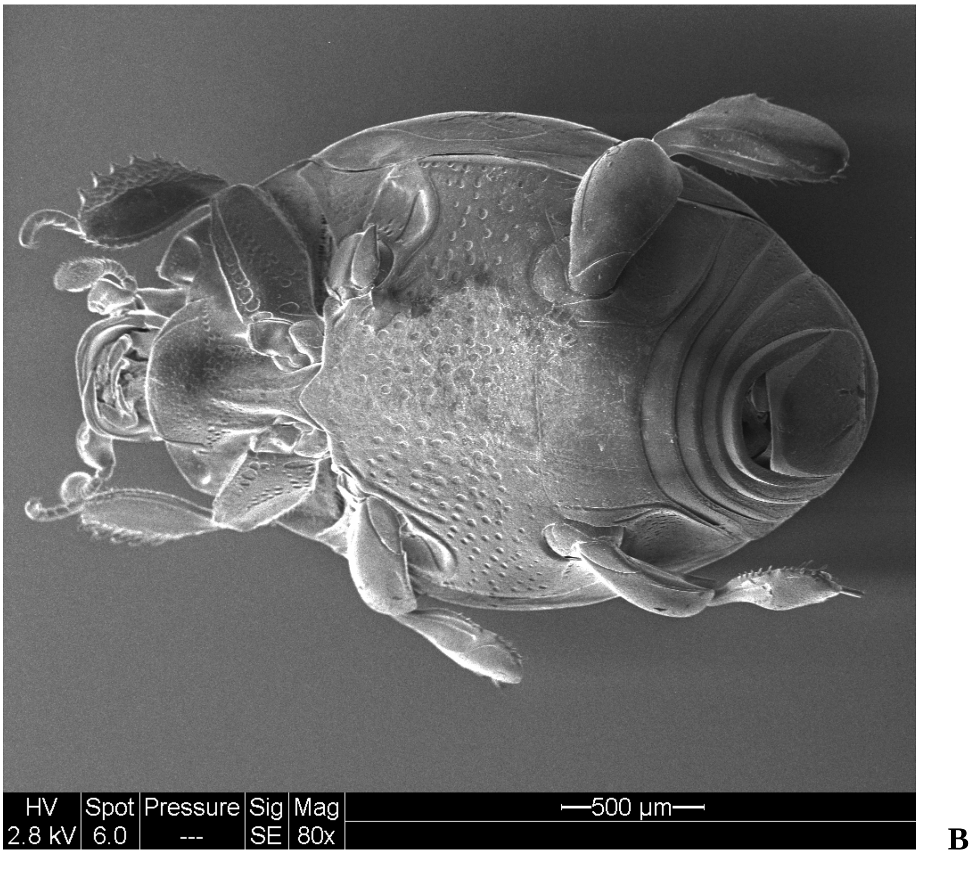


Fig. 27. Habitus of *Reichenspergerites robustus*. A. Dorsal aspect; B. Ventral aspect.

fusion dorsally. Penis aligned along the longitudinal paramere axis. Basal piece with shallow and wide dorsal apical emargination. Male 8th sternite with separate, normal-sized halves and pair of normal-sized velae. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male 9th sternite with stick-shaped “handle”. Male 9th tergite with small ventral apodeme and long basal projection, long thin apical projections with obtuse apices and with short sclerotized ventral processes. Halves of male 9th tergite narrowly fused, tergite body with wide rectangular projection on posterior margin, 10th tergite absent (or incorporated into mentioned projection). Female 8th sternite with deeply emarginated apical margin, distinct basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present as a single plate. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, simple, elongate.

Type species. *Mesynodites robustus* Reichensperger, 1939.

Etymology. The genus name represents a combination of a part of the generic name *Mesynodites* and August Reichensperger’s name, honoring his outstanding contribution to the studies of inquilinous beetles. The gender is masculine.

Remarks. The genus is easy to recognize through its large and robust body with consistent background punctures, reduction of dorsal and metasternal striae and dense large metasternal punctures. The genital characters reflect its intermediate phylogenetic position in that the parameres and male 9th sternite are of the *Mesynodites s.str.* type, male 9th tergite of the (*Monotonodites – Mesynodites evanescens*) clade type and the female genitalia are of generalized type characteristic for many taxa in the (*Mesynodites attaphilus – Voratister*) clade.

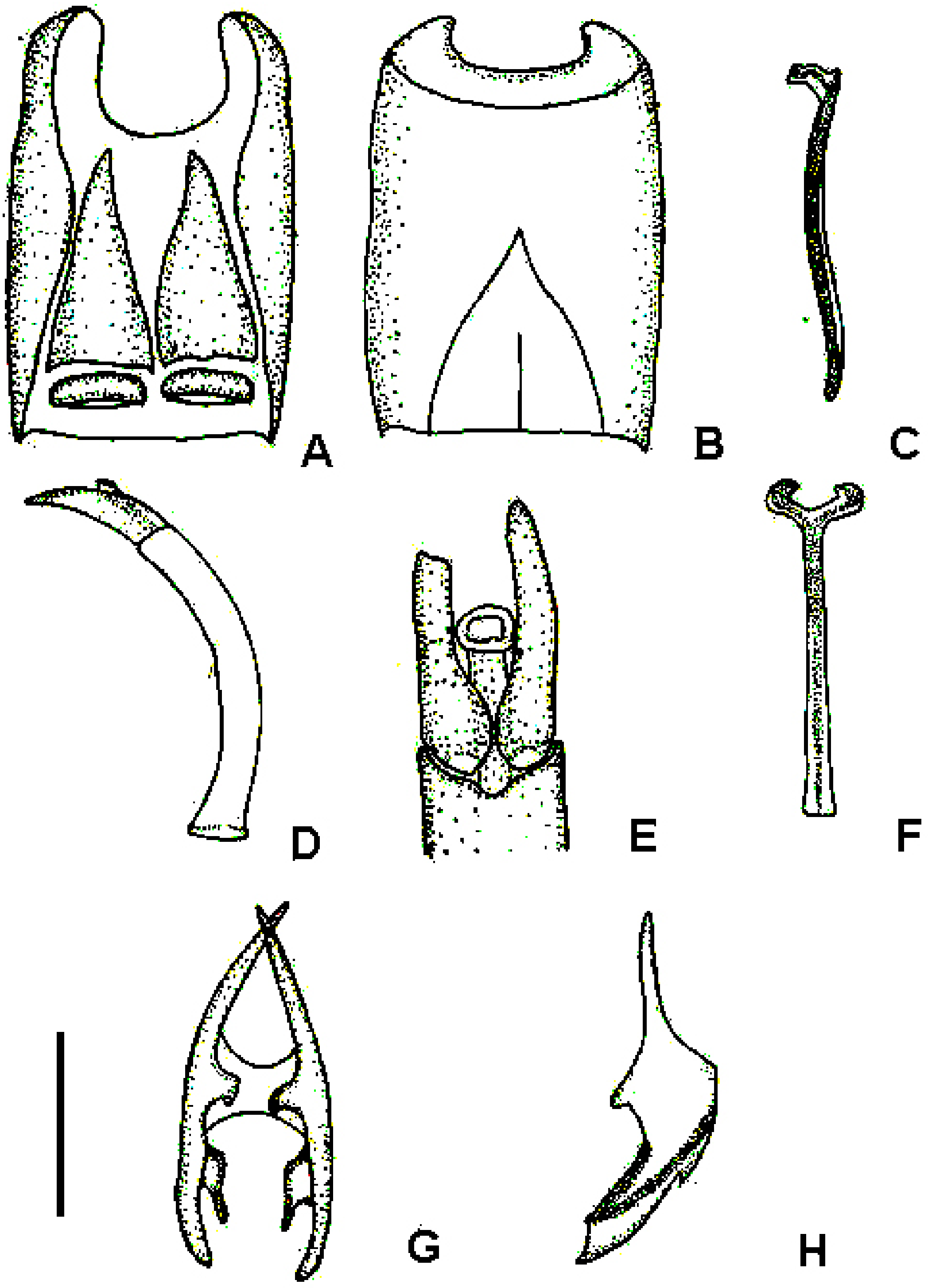


Fig. 28. Male genitalia of *Reichenspergerites robustus*. A. 8th sternite- tergite complex, ventrally; B. Same, dorsally; C. 9th sternite, laterally; D. Aegeagus, laterally; E. Same, apex dorsally; F. 9th sternite, dorsally; G. 9th tergite, ventrally; H. 9th tergite, laterally. Scale bar: all but D – 0.5 mm, D - 0.25 mm.
List of Species.

List of Species.

Reichenspergerites robustus **(Reichensperger, 1939) new combination**

Reichensperger, 1939: 107 (as *Mesynodites*). Mazur, 1984: 308. (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152. (as *Mesynodites*).

Holotype: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / Type ! Reichensperger / *Mesynodites robustus* Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Other material. **BRAZIL: Santa Catarina**: Nova Teutonia, F.Plaumann (1, FMNH); V.1953, F.Plaumann (1, FMNH); with *Labidus praedator*, 17.VI.1939, F.Plaumann (1, FMNH).

Distribution. Known only from type locality on the Brazilian state Santa Catarina.

Trichoreninus **Lewis 1891** (Fig. 29-30, ***297***)

Type species: *Trichoreninus flohri* Lewis

Lewis, 1891: 107. Mazur, 1984: 313. Helava *et al.*, 1985: 168-170 (in error). Mazur, 1997: 136.

Description. Body oval oval, convex dorsally, medium to large (PPL 2-3.5 mm). Body surface smooth, often with microsculpture and small secondary punctures, with or without setae. Head with prominent separate latero-marginal frontal carinae united medially, frontal stria incomplete. Mandibles with faces of bases unmodified. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral stria complete, anterior stria interrupted medially and represented by fragments along anterior pronotal angles or absent entirely. Pronotal disc with numerous large circular or drop-shaped punctures. Elytron with complete set of dorsal striae, only 5th dorsal stria abbreviated basally. Dorsal striae with large, sometimes deep, elongate punctures. Elytro-epipleural border sharp, angulate along subhumeral striae. Propygidium punctuate, with marginal stria along basal and lateral margins. Pygidium without punctures, without striate modifications in females. Prosternal lobe with complete marginal stria, lateral foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging and united into acute angle anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as prominent triagular process. Marginal lateral stria of mesoternum present as indistinct lateral fragments, discal marginal stria complete. Metasternal disc flat or convex, in males with variable median depression. Outer lateral stria of metasternum complete. Inner lateral stria complete or abbreviated posteriorly, always with separate recurrent arm. Longitudinal discal stria absent, sometimes present as short apical fragment. First abdominal sternite with distinct and long lateral and postmetacoxal striae. Legs relatively short, tibia paddle-like. Protibia with 7-9 short spines, meso- and metatibia with spines on outer margins, occasionally with central tooth. Aedeagus with parameres short, subcylindrical, with narrow basal fusion ventrally. Penis aligned along the longitudinal paramere axis. Basal piece with shallow and wide dorsal apical emargination. Male 8th sternite with separate, reduced halves and pair of normal-sized velae. Male 8th tergite with TAS and transverse posterior suture present and without intra-TAS plate, occasionally represented by a pair of tiny fragments along anterior part of TAS. Male 9th sternite with spoon-shaped “handle”. Male 9th tergite with small ventral apodeme and long basal projection, long heavily sclerotized pointed apical projections with basal notches, and membranous traces of ventral process. Halves of male 9th tergite fused, 10th tergite absent. Female 8th sternite with deeply emarginated apical margin, distinct

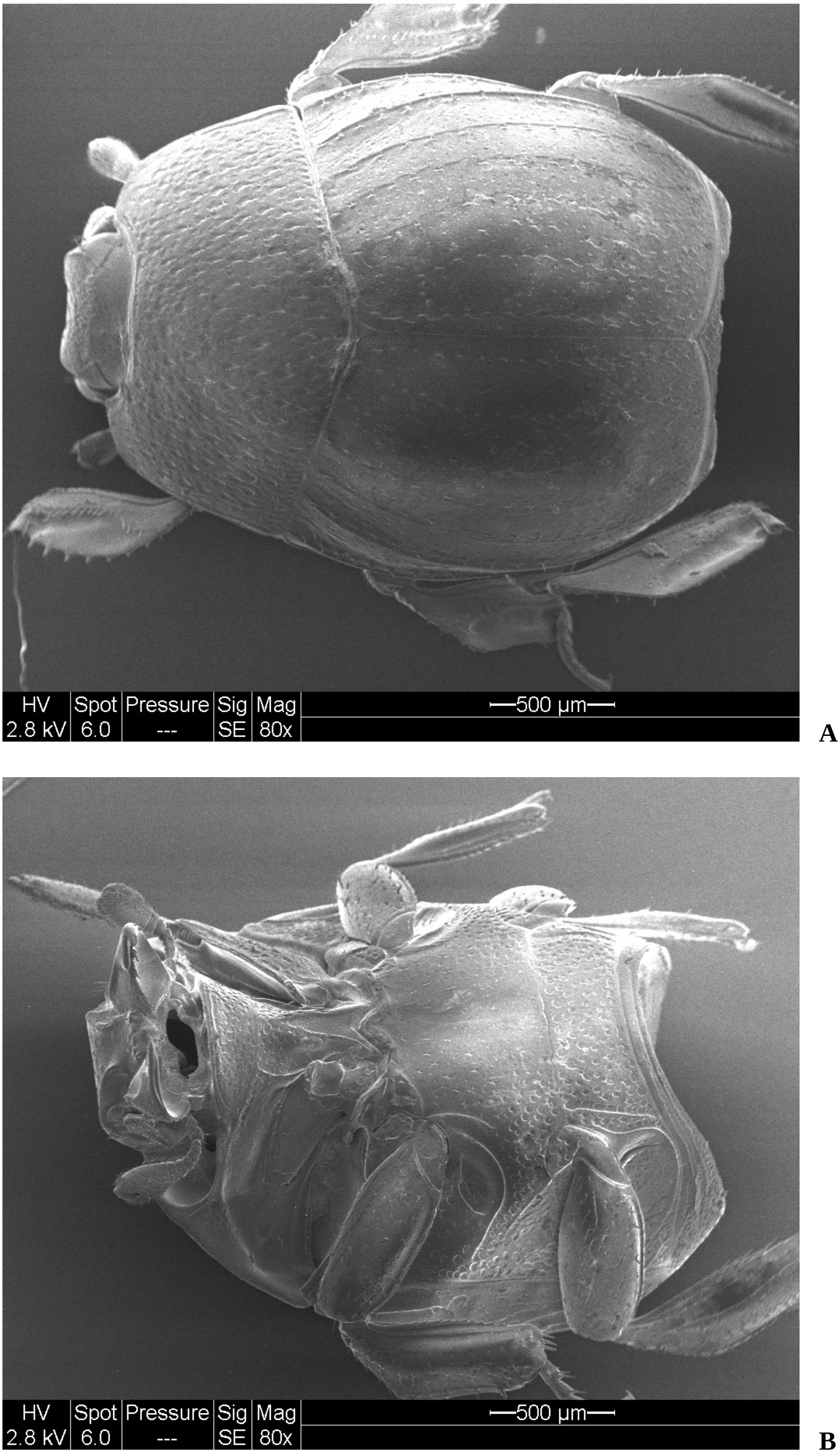


Fig. 29. Habitus of *Trichoreninus flohri*. A. Dorsal aspect; B. Ventral aspect.

basal bridge with shortly angulate lateral parts and rounded basal angles. Female 8th tergite present as 2 lateral sclerites. Coxites connected by dorsal bridge only. Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, simple, elongate.

Remarks. Original description (Lewis, 1891) is very precise and inadequate. Subsequent descriptions of other species of *Trichoreninus* (Lewis, 1893; Bruch, 1939) did not add anything substantial to the generic diagnosis. For no apparent reason, Helava *et al.* (1985) based their concept of the genus on a single female specimen of an undescribed species without studying authentic material of any described *Trichoreninus* species. Consequently, their understanding of the genus was completely wrong.

Representatives of *Trichoreninus* are variable regarding body surface microsculpture, punctures and development of setae. However, all of them fit well the general type of relatively large beeles with punctate pronotal disc, full set of punctate dorsal striae, modified female pygidium, concave male metasternum and particular pattern of metasternal striae. Male and female genitalia are uniform throughout the genus and provide numerous synapomorphies, supporting its current status and species composition.

List of Species

***Trichoreninus exclamationis* (Reichensperger, 1931)** new combination Reichensperger, 1931: 279 (as *Mesynodites*). Mazur, 1984: 308. (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1984: 151. (as *Mesynodites*).

Holotype: female mounted on point with a worker of *Nomamyrmex hartigi* and labeled “Campinas Goiaz Schwarzmaier [on the other side of the label] 26.IV.29

E. schlecht. / *Eciton schlechtendali* / Type ! Reichensperger / *Mesynodites exclamationis* Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Other Material. **BRAZIL: Goiás:** Campinas, P.Schwarzmaier (1, FIMAK); with *Nomamyrmex esenbecki*, P.Schwarzmaier (2, AKT and FIMAK); with *Eciton dulcius*, 4.X.1935, P.Schwarzmaier (1, FIMAK); with *N. hartigi*, 10.XII.1937, P.Schwarzmaier (2, FIMAK); with *Labidus coecus*, 30.I.1938, P.Schwarzmaier (1, FMNH).

Distribution. Known only from the type locality in the Brazilian state Goiás.

Trichoreninus flohri **Lewis, 1891** (Fig. 29)

Lewis 1891: 107. Mazur, 1984: 313. Helava *et al.*, 1985: 120. Mazur, 1997: 136.

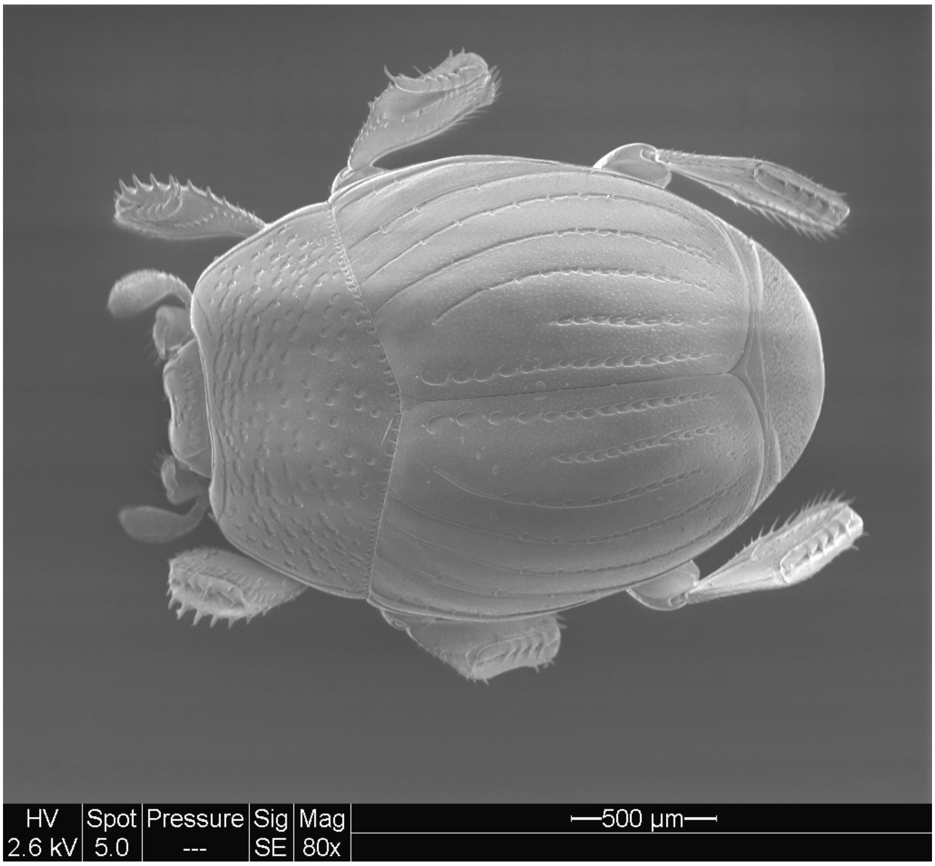
Lectotype: male mounted on point and labeled "Atliaco Flohr / Type / *Trichoreninus Flohri* Type Lewis / G.Lewis Coll. B.M. 1926-369. / Syntype / LECTOTYPE *Trichoreninus flohri* Lewis. A.Tishechkin des. 2003" (NHML). Paralectotype: female mounted on point and labeled "Guanajuato / G.Lewis Coll. B.M. 1926-369. / Syntype / *Trichoreninus Flohri* Lewis / PARALECTOTYPE *Trichoreninus flohri* Lewis. A.Tishechkin des. 2003" (NHML).

Distribution. Known only from the type localities in the Mexican states Guanajuato and Toluca.

Trichoreninus geminus **(Reichensperger, 1935)** new combination (Fig. 30)

Reichensperger, 1935b: 193 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 151. (as *Mesynodites*).

Holotype: female mounted on point and labeled "Costa Rica Nevermann 29.IX.1933 / *Eciton burchelli* / Paratype ! Reichensperger / *Mesynodites geminus* n. Reichensp. / MUSEUM KOENIG BONN" (FIMAK).



A

B

Fig. 30. Habitus of *Trichoreninus geminus*. A. Dorsal aspect; B. Ventral aspect.

Other Material. **COSTA RICA: Guanacaste:** Est. Las Pailas, 800 m, 1-22.VII.1992, D.Garcia (1, INBIO); Patilla Biological Station, 10º59’22”N 85º25’33”W, 610 m, 3-15.VII.2000, J.Ashe, R.Brooks, Z.Falin (2, SEC); 3 km SE R. Naranjo, 15-19.I.1993, F.D.Parker (PWK). **Limon:** Hamburg Farm, wih *Eciton* Other Material. **COSTA RICA: Guanacaste:** Est. Las Pailas, 800 m, 1-22.VII.1992, D.Garcia (1, INBIO); Patilla Biological Station, 10º59’22”N 85º25’33”W, 610 m, 3-15.VII.2000, J.Ashe, R.Brooks, Z.Falin (2, SEC); 3 km SE R. Naranjo, 15-19.I.1993, F.D.Parker (PWK). **Limon:** Hamburg Farm, wih *Eciton burchelli* (1, FIMAK). **Puntarenas:** Las Cruces Biological Station, 1200 m, flight intercept trap, VII.1982, B.Gill (1, CMN); flight intercept trap, 17.VIII.-12.IX.1982, B.Gill (1, CMN); flight intercept trap, 22.II.-3.III.1983, B.Gill (4, AKT and BDG); 1000 m, flight intercept trap, 2-10.IV.2002, A.Cline, A.Tishechkin (6, AKT and LSAM); Osa Peninsula, 7 km W Rincon, 50 m, flight intercept trap, 21-25.VI.1997, S. & J.Peck (2, AKT and SEC); Osa Peninsula, Rancho Quemado, 200 m, VII.1991, F.Quesada (1, INBIO). **NICARAGUA: Rio San Juan:** El Castillo, flight intercept trap, 22-25.II.2000, E.Barbero, F.Penati (1, FP). **PANAMA: Chiriqui:** 4 km N Sanata Clara, Hartmann’s Finca, 1500 m, flight intercept trap, 30.VI.-14.VII.1982, B.Gill (1, SM). **Veraguas:** Cerro Tute, 8º30’26”N 81º06’49”W, 915 m, 24-26.VII.1999, J.B.Wooley (1, TAMU).

Distribution. One of the most common species of Hetaeriinae in collections, known from multiple localities from eastern Nicaragua to central Panama.

***Trichoreninus imbricatus* Lewis, 1893**

Lewis 1893: 422. Mazur, 1984: 313. Helava *et al.* 1985: 120. Mazur, 1984: 136.

Type locality: “Bahia.”

Remarks. The species is listed here formally, but the type specimen was not studied. The original description contains information casting serious doubt on this generic placement (Lewis, 1893; Helava *et al.*, 1985). This problem will be dealt with in a separate study in collaboration with N.Dégallier.

Trichoreninus major **(Bruch, 1923)** new combination

Bruch, 1923: 189 (as *Synodites*), 1929: 433. Reichensperger, 1931: 282 (as *Mesynodites major* var. *crassicornis*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on point, with a worker of *Eciton dulcius* cardboard-mounted under it, and labeled "Alta Gracia Córdoba 4.I.922 Bruch / Pigidio liso / Typus / *Synodites major* Bruch 1926 Syntypus / *Synodites major* Bruch C. BRUCH DETERM. / PICHADO / Mus. Arg. Cs. Nat. / LECTOTYPE S*ynodites major* Bruch A.Tishechkin des. 2002" (MACN). Paralectotype: female mounted on point, with a worker of *Eciton dulcius* cardboard-mounted under it, and labeled "Alta Gracia Córdoba 4.I.922 Bruch / Pigidio arrugado / Typus / *Synodites major* Bruch 1926 Syntypus / PICHADO / Mus. Arg. Cs. Nat. / PARALECTOTYPE S*ynodites major* Bruch A.Tishechkin des. 2002" (MACN).

Other Material. **ARGENTINA: Córdoba:** Alta Gracia, with *Eciton dulcius*, C.Bruch (1, FIMAK); Cabana (Unquillo), with *E. dulcius*, 1926, C.Bruch (3, FIMAK, FMNH and USNM). **BRAZIL: Goiás:** Campinas, with *Nomamyrmex esenbecki*, 10.XII.1929, P.Schwarzmaier (1, FIMAK); with *E. dulcius*, 4.XII.1933, T.Borgmeier (2, FMNH and FIMAK).

Distribution. Known only from two localities, in northern Argentina (Córdoba Province) and southern Brazil (Goiás State).

Trichoreninus schwarzmaieri **(Reichensperger, 1931)** new combination

Reichensperger, 1931: 277 (as *Mesynodites*). Mazur, 1984: 309 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Holotype: female mounted on point with a worker of *Nomamyrmex esenbecki* and labeled “Inhumas Goyaz Schwarzmaier 27.XII.28 / *Eciton crassicorne* / Type ! Reichensperger / *Mesynodites schwarzmaieri* Reichensp. / MUSEUM KOENIG BONN” (FIMAK).

Other Material. **BRAZIL: Goiás:** Campinas, with *Nomamnyrmex esenbecki*, P.Schwarzmaier (3, AKT, FIMAK and FMNH); with *N. esenbecki*, 16.II.1937, P.Schwarzmaier (2, FIMAK).

Distibution. Known only from two localities in the Brazilian state Goiás.

Trichoreninus vianai Bruch, 1939

Bruch, 1939: 259. Mazur, 1984: 313. Helava *et al.* 1985: 120. Mazur, 1984: 136. Type locality: “’El Sauce’, Departamento Calamuchita de Córdoba”

Remarks. This species is listed formally. The type specimen was not studied and some information in the original description as well as unpublished data suggests that the species does not belong to the genus in its current sense (Bruch, 1939; Dégallier, personal communication). The status of *T. vianai* will be addressed in a separate study in preparation by Dégallier and Tishechkin.

Tribe Hetaeriini Marseul, 1857

Diagnosis. Parameres long, basal piece either long or short, male 10th tergite usually present (if absent, 9th tergite present as two separate pieces).

Type Genus: *Hetaerius* Erichson.

Remarks. Hetaeriini cannot currently be defined other than a tribe uniting genera that do not belong to either of the above tribes. This is a paraphyletic assemblage uniting the bulk of hetaeriine genera, Groups B-D of Helava *et al.* (1985). It is characterized by a wide diversity of external and genital morphologies. Hetaeriini will split into several component tribes, when phylogenetic analyses of the entire subfamily is undertaken. To provide some practical internal resolution, I organize below the genera in their assignments to Helava *et al.*'s Groups.

List of genera. Group B: *Chelyocephalus* Schmidt, *Cachexia* Lewis, *Coelister* Bickhardt, *Colonides* Schmidt, *Cossyphodister* Reichensperger, *Discoscelis* Schmidt, *Enicosoma* Lewis, *Euxenister* Reichensperger, *Homalopygus* Boheman, *Inquilinister* Helava, *Kleptisister* Helava, *Lissosternus* Lewis, *Neocolonides* Dégallier, *Notocoelis* Lewis, *Paroecister* Reichensperger, *Pelatetister* Reichensperger, *Procolonides* Reichensperger, *Scapicoelis* Marseul, *Scapolister* Borgmeier, *Terapus* Marseul, *Termitolister* Bruch, *Termitoxenus* Schmidt, *Thaumataerius* Mann, *Tylois* Marseul.

Group C: *Aristomorphus* Lewis, *Bastactister* Reichensperger, *Convivister* Reichensperger, *Eretmotus* Lewis, *Hetaerius* Erichson, *Glyptosister* Helava, *Iugulister* Reichensperger, *Pinaxister* Reichensperger, *Plaumannister* Reichensperger, *Pterotister* Reichensperger, *Satarpes* Schmidt, *Sternocoelis* Lewis, *Synetister* Reichensperger, *Ulkeopsis* Helava, *Ulkeus* Horn.

Group D: *Brasilister* Dégallier, *Euclasea* Lewis, *Chelonosternus* Bickhardt, *Fistulaster* Helava, *Hemicolonides* Reichensperger, *Hetaeriobius* Reichensperger, *Hippeutister* Reichensperger, *Murexus* Lewis, *Nevermannister* Reichensperger, *Troglosternus* Bickhardt, *Opadosister* Helava, *Parasynodites* Bruch, *Parodites* Reichensperger, *Plagioscelis* Bickhardt, *Reninoides* Helava, *Reninopsis* Helava, *Reninus* Lewis, *Synoditinus* Reichensperger, *Teratosoma* Lewis, *Xenister* Borgmeier.

Euclasea* Lewis, 1888** (Fig. 31, ***299)

Type species: *Euclasea godmani* Lewis

Lewis, 1988: 220-221. Mazur, 1984: 306. Helava *et al.* 1985: 252-254 (in error). Mazur, 1997: 150.

Description. Body oval or elongate oval, convex dorsally, sometimes drop-shaped, minute to large (PPL 1-3.5 mm). Body surface smooth and usually shiny, rarely setose and/or punctate. Head with or without latero-marginal frontal carina, frontal stria complete or interrupted. Mandibles with faces of bases unmodified. Antennal clubs with dense pubescence except for large sclerotized areas on dorsal, outer lateral and ventral surfaces. Pronotum with marginal and outer lateral stria complete, anterior stria variable, sometimes absent. Elytron usually with reduced set of dorsal striae, regularly only outer subhumeral stria complete. Dorsal striae, if present, thin and impunctate. Elytro-epipleural border smooth, gradually rounded. Propygidium with marginal stria along basal and lateral margins. Pygidium in females sometimes with surface modifications such as punctate oculae or longitudinal striae. Prosternal lobe with complete marginal stria, lateral foveae and lateral notches. Prosternal keel narrow, flat, with distinct, narrowly separated carinal striae, converging or parallel and angularly or roundly united anteriorly. Lateral prosternal striae distinct and short. Mesosternum narrow, its anterior margin produced medially as a prominent triagular process. Marginal lateral stria of mesosternum present as indistinct lateral fragments, discal marginal stria usually absent. Metasternal disc in males often modified, with median depression and/or small acute medial tooth. Lateral and longitudinal discal striae of metasternum variable and usually reduced present, only outer lateral stria present consistently. First abdominal sternite with distinct and long lateral and postmetacoxal striae. Legs relatively short, tibia paddle-like, sometimes wide. Protibia with 6-10 short spines, meso- and metatibia sometimes with central tooth and without spines on outer margins. Aedeagus with parameres long, occasionally shorter, dorso-ventrally flatened, with long basal fusion ventrally

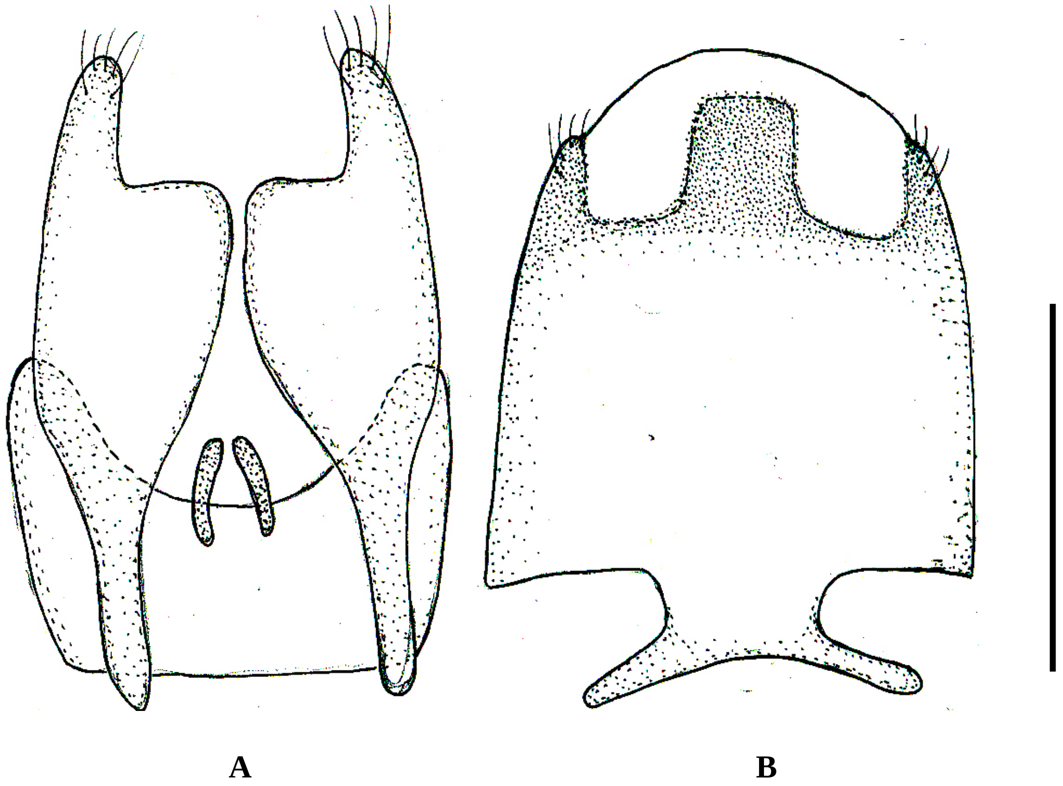


Fig. 31. Female genitalia of *Euclasea diadochus*. A. Genitalia with 8th sternite omitted, dorsally. B. 8th sternite, ventrally. Scale bar – 0.5 mm.

and dorsally. Penis aligned along the longitudinal paramere axis. Basal piece long, with shallow and wide dorsal apical emargination, its posterior opening elongate oval, in ventral position. Male 8th sternite with fused full-sized halves, pair small or medium of velae and a tuft of setae in each of latero apical angles. Male 8th tergite with TAS and transverse posterior suture present and complete intra-TAS plate. Male 9th sternite with spoon-shaped "handle". Male 9th tergite with small ventral apodeme, long basal projection, rudimentary apical projections and large sclerotized fused ventral process. Halves of male 9th tergite separate, 10th tergite present. Female 8th sternite with continuous heavily sclerotized apical margin, distinct basal bridge with shortly lateral parts elongate into proximal apodemes and rounded basal angles. Female 8th tergite present as sigle plate. Coxites connected both by 2 dorsal bridges.

Female 9th tergite present as single plate connected to coxites by its base. Female genital sclerites separate, comma-shaped.

Remarks. The genus *Euclasea* has not been diagnosed adequately since its establishment. The original description is too concise and appeared before most of the hetaeriine diversity had been discovered and documented. The history of confusion with the genus began in 1893, when Lewis added new species of *Euclasea* and placed some of them in the genus inappropriately (Lewis, 1893). Almost at the same time Schmidt described a true *Euclasea* species in *Mesynodites* (*Synodites* than; Schmidt, 1893). Reichensperger (1924a, 1925, 1938, 1939) did not clarify the situation and placed all his species affiliated in one or another way with *Euclasea* in the wrong genera, adding *Cheilister* and *Monotonodites* (then a subgenus of *Mesynodites*) to a list of genera involved in these misplacements. Helava *et al.* (1985) followed the tradition and based their *Euclasea* description on a female of an undescribed species that belonged to a different genus, apparently also undescribed (Tishechkin, unpublished). This last concept was accepted and followed by Kovarik and Caterino (2001).

The current definition of *Euclasea* is based exclusively on numerous synapomorphies in morphology of both male and female genitalia, specifically long, almost completely fused, dorsoventrally flattened parameres with vertical lateral appendages, basal piece with elongate oval posterior opening in dorsal position, fused halves of male 8th sternite with a pair of latero-apical setose tufts, presence of male 10th sternite, continuous and heavily sclerotized apical margin of female 8th sternite etc. (see Chapter 3). The external morphology of *Euclasea* is variable and often similar to other genera (*e.g.*, some *Helavadites*, *Euclasea sensu* Helava *et al.*). The typical habitus of *Euclasea*, smooth shiny impunctate beetles with strong reduction of striation both dorsally and ventrally, represented, among others, in the type species, *E. godmani*, seems to be a dominant form in terms of species numbers. However, several species represent different degrees of background sculpture and punctures, setae and strial development, both ventrally and dorsally. Also, there is potentially meaningful variation in a few male genitalic morphologies (female genitalia were not widely studied) including relative length of parameres, degrees of development of paramere lateral appendages and the 10th sternite. Given the scope of this study and a substantial number of undescribed species, I chose a somewhat conservative generic approach until a special revisionary study of *Euclasea* and related genera such as *Hemicolonides* can be underdaken.

List of Species

***Euclasea arcanus* (Reichensperger, 1939)** new combination

Reichensperger, 1939: 122 (as *Mesynodites*). Mazur, 1984: 307. (as *Mesynodites*). Helava *et al.*, 1985: 335 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on a cardboard with a female of the same species and minor worker of *Labidus coecus* and labeled “San Jose Costa Rica H.Schmidt / *Eciton coecum* 9.37 / Type ! Reichensperger / *Mesynodites arcanus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites arcanus* Reich. A.Tishechkin des. 2002” (FIMAK).

Other material. **COSTA RICA: San Jose:** San Jose, H.Schmidt, (15, AKT and FIMAK); with *Labidus coecus*, H.Schmidt (8, AKT, FIMAK and FMNH); 1937, with *Labidus coecus*, H.Schmidt (4, FIMAK). **Limon:** Hamburg Farm, F.Nevermann (1, FIMAK).

Distribution. Known from two localities in the Costa Rican provinces of San Jose and Limon.

Euclasea acamati **(Reichensperger, 1939)** new combination

Reichensperger, 1939: 124 (as *Mesynodites*). Mazur, 1984: 307 (as *Mesynodites*). Helava *et al*., 1985: 335 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point and labeled “San Jose Costa Rica H.Schmidt / *Ac alfaroi* Em. / Paratype ! Reichensperger / *Mesynodites acamati* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites acamati* Reichen. A.Tishechkin des. 2002” (FIMAK). Paralectotypes: male and female mounted on the same cardboard and female mounted on point, all labeled “San Jose Costa Rica H.Schmidt / *Ac alfaroi* Em. / Type ! Reichensperger / *Mesynodites acamati* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites acamati* Reichen. A.Tishechkin des. 2002” (FIMAK).

Other material. **COSTA RICA: San Jose:** San Jose, H.Schmidt (3, FIMAK); with *Neivamyrmex alfaroi,* H.Schmidt (1, FIMAK); with *Labidus coecus*, H.Schmidt (7, AKT and FIMAK).

Distribution. Known from a single locality in central Costa Rica (San Jose Province).

Euclasea detritus **(Schmidt, 1893)** new combination

Schmidt, 1893: (as *Synodites*). Mazur, 1984: 307. Helava *et al*., 1985: 335 (as *Mesynodites*). Mazur, 1997: 151.

Synonym: *Euclasea obliqua* Lewis, 1893, new synonym.

Lewis, 1893: 425. Mazur, 1984: 306. Helava *et al*., 1985: 254. Mazur, 1997: 150.

Lectotype: female mounted on point and labeled “Mexico / coll. J.Schmidt / Type / *Syn. detritus* / LECTOTYPE *Synodites detritus* Schmidt A.Tishechkin des. 2002” (HUB). Lectotype of *Euclasea obliqua* Lewis: male labeled “Mexi...[illegible] /

Type / George Lewis Coll. B.M. 1926-369. / *Euclasea obliqua* Type. Lewis / LECTOTYPE *Euclasea obliqua* Lewis A.Tishechkin des. 2002" (NHML).

Remarks. The two species placed in synonymy were described during the same year, but in different genera. Apparently, no one questioned their validity and suspected their synonymy. Comparison of the lectotypes has clearly revealed their conspecificity.

Distribution. The only distributional information available is the country record (Mexico).

***Euclasea diadochus* (Reichensperger, 1939)** new combination (Fig. 31)

Reichensperger, 1939: 113 (as *Mesynodites*). Mazur, 1984: 307 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton quadriglume* 6.I.37 / Type ! Reichensperger / *Mesynodites diadochus* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites diadochus* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: male mounted on point and labeled as previous specimen, but with paralectotype instead lectotype label (FIMAK); male mounted on point and labeled "F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* 13.II.37 / Paratype ! Reichensperger / *Mesynodites diadochus* Reichensp. / MUSEUM KOENIG BONN / PRALECTOTYPE *Mesynodites diadochus* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other material. **BRAZIL: Santa Catarina**, Nova Teutonia, I.1953, F.Plaumann (7, FMN, SM, USNM and ZIN); 15.XII.1950, F.Plaumann (2, FMNH); Ibicare, IX.1960, F.Plaumann (1, FMNH).

Distribution. Known from two lacalities in the Brazilian state Santa Catarina.

Euclasea godmani Lewis, 1888

Lewis, 1888: 221. Mazur, 1984: 306. Helava *et al.*, 1985: 254. Mazur, 1997: 150.

Holotype: female mounted on point labeled "Chiacaman, Vera Paz Champion / Sp. figured / B.C.A., Col., II, (1). / Syntype / Type / *Euclasea Godmani* Lewis Type" (NHML).

Other material. **BELIZE: Cayo:** Las Cuevas Research Station, 16º43.99'N 88º59.20'W, 550 m, with *Eciton burchelli*, 25.V.2000, M.Caterino (2, NHML). **MEXICO: Veracruz:** Canyon Rio Metlac near Fortin, 975 m, with *E. burchelli*, 28.VII.-1.VIII.1973, A.F.Newton (3, AKT and FMNH).

Distribution. Known from southern Mexico (Chiapas State), Belize and Guatemala.

Euclasea inops (Reichensperger, 1935) new combination

Reichensperger, 1935b: 196 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 151 (as *Mesynodites*).

Holotype: male mounted on point and labeled "Costa Rica F.Nevermann 29.IX.1933 / *Eciton burchelli* / Type ! Reichensperger / *Mesynodites inops* n. sp. Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Other material. **COSTA RICA: San Jose:** San Jose, with *Labidus coecus*, 1937, H.Schmidt (2, FIMAK); with *Eciton burchelli,* IX.1935, H.Schmidt (1, FIMAK). **Puntarenas:** Las Cruces Biological Station, 8º47'N 82º57'W, 1100 m, flight intercept trap, 30.III.-1.IV.2002, A.Cline, A.Tishechkin (1, LSAM); Monte Verde, 1520 m, flight intercept trap, 21.V.1989, J.Ashe, R.Brooks, R.Leschen (1, SEC); Sirena Station, upper Ollas Trail, 8º29'7"N 83º34'39"W, 140 m, flight intercept trap, 24-28.VI.2000, Z.H.Falin (1, SEC); Sirena Station, upper Rio Claro Trail, 8º28'29"N 83º35'8"W, 100 m, flight intercept trap, 28.VI.-1.VII.2000, Z.H.Falin (1, SEC); **HONDURAS: El Paraiso:** Cerro Monserrat, 13º55’N 86º24’W, 1760 m, flight intercept trap, 7-10.VI.1994, J.Ashe, R.Brooks, (1, SEC). **PANAMA: Chiriqui:** 4 km N Sanata Clara, Hartmann’s Finca, 1500 m, flight intercept trap, 30.VI.-13.VII.1982, B.Gill (2, AKT and BDG); **Panama:** Barro Colorado Island, flight intercept trap, 3-14.VI.1983, B.Gill (1, BDG); flight intercept trap, 15.VII.1994, D.Banks (1, SEC).

Distribution. Central America from Honduras to central Panama, both in lowland and montane forests.

***Euclasea novaeteutoniae* (Reichensperger, 1939)** new combination

Reichensperger, 1939: 109 (as *Mesynodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on point and labeled “F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.37 / *Mesynodites Novae-Teutoniae* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Mesynodites novaeteutoniae* Reichen. A.Tishechkin des. 2002” (FIMAK). Paralectotypes: female mounted on point and labeled “F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* II.36 / Type ! Reichensperger / *Mesynodites Novae-Teutoniae* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites novaeteutoniae* Reichen. A.Tishechkin des. 2002” (FIMAK); female mounted on point and labeled “F.Plaumann Nova Teutonia Brasilien / *Eciton praedator* 12.II.37 / Paratype ! Reichensperger / *Mesynodites Novae-Teutoniae* Reichensp. / MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites novaeteutoniae* Reichen. A.Tishechkin des. 2002” (FIMAK); female mounted on cardboard and labeled “*Mesynodites Novae-Teutoniae* Reichensp. / *Eciton praedator* II.36 / F.Plaumann Nova Teutonia Brasilien / Paratypus

/ MUSEUM KOENIG BONN / PARALECTOTYPE *Mesynodites novaeteutoniae* Reichen. A.Tishechkin des. 2002" (FMNH).

Other material. **BRAZIL: Santa Catarina**, Nova Teutonia, F.Plaumann (1, FMNH); II-V.1941, F.Plaumann (6, FMNH); V.1953, F.Plaumann (9, FMNH and USNM); with *Labidus praedator*, F.Plaumann (7, FIMAK and FMNH); with *L. praedator*, 14.II.1936, F.Plaumann (15, AKT and FIMAK); with *L. praedator*, IV.1952, F.Plaumann (11, FMNH and ZIN); with *L. praedator*, III.-IV.1952, F.Plaumann (4, FMNH); with *Eciton* prey, II.1959, F.Plaumann (11, FMNH and SM). **PARAGUAY:** Horqueta, with *Labidus*, XII.1936, A.Schulze (1, FMNH).

Distribution. Known from three localities, two in southern Brazil (Santa Catarina State) and one in Paraguay.

Euclasea pumilis **(Reichensperger, 1926)** new combination

Reichensperger, 1926: 192 (as *Synodites*). Mazur, 1984: 308 (as *Mesynodites*). Helava *et al.*, 1985: 336 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Holotype: female mounted on point with a minor worker of *Labidus praedator* and labeled " Passa Quatro Minas. Brasil J.F.Zikán 3.20 / bei *Eciton praedator* Sm. / TYPUS / coll. Reichensperger 1925 descr. / *Synodites pumilus* n. sp. Reichensp. Type / MUSEUM KOENIG BONN" (FIMAK).

Other material. **BRAZIL: Rio de Janeiro:** Itatiaya, 1100 m, with *Labidus praedator*, 3.III.1931, W.Zikán (1, FIMAK). **Santa Catarina:** Nova Teutonia, 1953, F.Plaumann, (5, FMNH and SM); V.1953, F.Plaumann, (2, FMNH); I.1954, F.Plaumann, (1, FMNH); IX.1959, F.Plaumann, (1, FMNH); with *Labidus praedator*, F.Plaumann, (2, FIMAK).

Distribution. Southern Brazil (Minas Gerais, Rio de Janeiro and Santa Catarina States).

***Euclasea sphaeroides* (Reichensperger, 1938)** new combination

Reichensperger, 1938: 85 (as *Cheilister*). Mazur, 1984: 300 (as *Chelister*). Helava *et al.*, 1985: 321 (as *Cheilister*). Mazur, 1997: 158 (as *Chelister*). Dégallier, 1998c: 354 (as *Chelister*).

Lectotype (designated by Dégallier, 1998c): male mounted on point and labeled "Hamburg-Farm Costa Rica 8a Nevermann 8.XI / *E. (Acamatus) pilosum* c. Reichensperger / Type ! 2 Reichensperger / *Cheilister sphaeroides* Reichensp. / MUSEUM KOENIG BONN / (FIMAK). Paralectotype (designated by Dégallier [1998c]): female mounted on point, with a cardboard-mounted worker of *Neivamyrmex pilosus* beneath it, and labeled "Hamburg-Farm Costa Rica 8a Nevermann 8.XI / *E. (Acamatus) pilosum* c. Reichensperger / Paratype ! Reichensperger / *Cheilister sphaeroides* Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Distribution. Known from a single locality in central Costa Rica (Limon Province).

***Euclasea splendens* (Reichensperger, 1924)** new combination

Reichensperger, 1924a: (as *Synodites*). Bruch, 1926b: 19, 1929: 433. Mazur, 1984: 309 (as *Mesynodites*). Helava *et al.*, 1985: 337 (as *Mesynodites*). Mazur, 1997: 152 (as *Mesynodites*).

Lectotype: male mounted on point and labeled "1923 *Eciton quadriglumme* R.Negro, Paraná / A.Reichensperger / Paratypus 1923 / *Synodites splendens* Reichensp. / MUSEUM KOENIG BONN / LECTOTYPE *Synodites splendens* Reichen. A.Tishechkin des. 2002" (FIMAK). Paralectotypes: male and female mounted on points and labeled "1923 *Eciton quadriglumme* R.Negro, Paraná / A.Reichensperger / *Synodites splendens* Reichensp. / MUSEUM KOENIG BONN /

PARALECTOTYPE *Synodiyes splendens* Reichen. A.Tishechkin des. 2002" (FIMAK).

Other material. **BRAZIL: Paraná:** Rio Negro, with *Eciton quadriglumme*, I.1930 (1, FIMAK). **Satna Catarina:** Blumenau, with *E. quadriglumme*, P.M.Witte (1, FIMAK).

Distribution. Known from two localities in southern Brazil (Paraná and Santa Catarina States). Reports of the species from northern Argentina (Reichensperger, 1924a; Bruch, 1926b, 1929) were based on a closely related undescribed species to be dealt with elsewhere. Above lectotype specimens from Rio Negro were chosen for designation as Reichensperger put "Typus" after mentioning Rio Negro in a row of distributional localities in his description.

Euclasea tuberculata Lewis, 1893

Lewis, 1893: 425. Mazur, 1984: 306. Helava *et al.*, 1985: 254. Mazur, 1984: 150.

Lectotype: female mounted on point and labeled "Bahia A Cr / Type / George Lewis Coll. B.M. 1926-369. / *Euclasea tuberculata* Type. Lewis / LECTOTYPE *Euclasea tuberculata* Lewis A.Tishechkin des. 2002" (NHML).

Other material. **HONDURAS: Atlantida:** 13 km E La Ceiba, 150 m, flight intercept trap, 15-19.VI.1996, R.Lehman (1, AKT); flight intercept trap, VII.1996, R.Lehman (1, TAMU).

Distribution. Known with certainty only from the single locality in Honduras. The type locality is somewhat ambiguous, and is presumed to be either the Brazilian state of Bahia or Islas de la Bahia near the Atlantic coast of Honduras (see discussion in Helava *et al.*, 1985: 253-254). The recent record makes the second alternative more plausible.

***Euclasea verruculosus* (Reichensperger, 1939)** new combination

Reichensperger, 1939: 125 (as *Mesynodites*). Mazur, 1984: 309. (as *Mesynodites*). Helava *et al.*, 1985: 263 (as *Oudaimosister*, in error). Mazur, 1997: 152 (as *Oudaimosister*).

Holotype: male mounted on point and labeled "Hamburg-Farm Costa Rica 16 Nevermann 24/XI 35 / *Eciton praedator* / Type ! Reichensperger / *Mesynodites verruculosus* Reichensp. / MUSEUM KOENIG BONN" (FIMAK).

Other material. **VENEZUELA: Miranda:** Guatopo N. P., El Lucero, 700 m, flight intercept trap, 7-14.VI.1987, S. & J.Peck (1, CMN).

Distribution. Known from two localities, in central Costa Rica and northern Venezuela.

Genera Insertae Cedis

Remarks. Here are listed genera, tribal assignments of which are uncertain due to unknown location of type material and/or lack of either males available for study or previous studies.

List of genera. *Alienister* Reichensperger, *Aneuterapus* Reichensperger, *Attalister* Bruch, *Hesperodromus* Schmidt, *Hetaeriodes* Schmidt, *Hetaeriomorphus* Schmidt, *Morphotaerius* Reichensperger, *Nomadister* Borgmeier, *Pselaphister* Bruch, *Teratolister* Bruch, *Tubulister* Borgmeier, *Wasmannister* Bruch.

4.5. Key to the Genera of Nymphisterini

1 (2). Legs long and thin, subcylindrical, tibia elongate, stick-shaped (Fig. ***19, 290***) 3

2 (1). Legs shorter, femora wide and stout, tibia at most moderately elongate, narrowly triangular or paddle-shaped (Fig. 28) 11

3 (4). Lateral sides of pronotal disc with wide and high longitudinal elevations (Fig. ***224, 290***) 5

4 (3). Lateral sides of pronotal disc without longitudinal elevations 7

5 (6). Lateral longitudinal elevations of pronotal disc rectangular in cross-section, their dorsal surfaces more or less flat, granular, with numerous trichomes in the form of compact tufts of long golden setae. Similar trichomes also present on propygidium, pygidium and along apical and lateral edges of elytra. Elytral disc outside trichomes only with minute depressed setae (Fig. ***224***) .... *Symphilister* Reichensperger

6 (5). Lateral longitudinal elevations of pronotal disc semicircular in cross-section, their convex dorsal surfaces as well as elytral disc, propygidium and pygidium uniformly covered with sparse, long, erect setae (Fig. ***290***) ....
.... *Pulvinister* Reichensperger

7 (10). Pronotal disc strongly convex. Dorsal surface with granulate microsculpture, uniformly covered with long, erect setae 8

8 (9). Mandibles short, bent mesially at midpoints. Prosternal lobe weakly concave. Basal "handle" of male 9th sternite strap-shaped. Ventral processes of male 9th tergite long and narrow, heavily sclerotized, movable (Fig. ***293, 294***) ....
.... *Chrysetaerius* Reichensperger

9 (8). Mandibles elongate, bent mesially near apices. Prosternal lobe deeply concave, lateral apical parts forming pointed lobes. Basal "handle" of male 9th sternite spoon-shaped. Ventral processes of male 9th tergite short and membranous (Fig. ***242, 243***)
.... *Latronister* Reichensperger

10 (7). Pronotal disc flat, with weak longitudinal impressions along midline. Dorsal surface, except for lateral longitudinal areas sides, alutaceous, sometimes locally with few tiny semi-erect setae (Fig. ***266***) .... *Sternocoelopsis* Reichensperger

11 (12). Lateral surface of mandible near base with deep funnel-like impression, often almost perforated, sometimes also deeply and narrowly incised. Prosternal lobe with deep longitudinal sutures along midline (Fig. ***213, 214, 221, 222***) 13

12 (11). Lateral surface of mandible near base unmodified, rarely with shallow depression. Prosternal lobe without deep longitudinal sutures along midline 31

13 (14). Lateral surface of mandible near base deeply and narrowly incised (Fig. ***213, 214***) 15

14 (13). Lateral surface of mandible near base without incision 23

15 (16). Body form oval, convex 17

16 (15). Body form truncate oval, sometimes almost rectangular, depressed (Fig. ***205, 208***) 19

17 (18). Pronotal disc mostly covered with large, shallow punctures, without inner lateral striae. Elytral disc smooth, shiny, sometimes with very fine alutaceous microsculpture locally (Fig. ***212***) .... *Metasynodites* Reichensperger

18 (17). Pronotal disc without large, shallow punctures, with sinuous inner lateral striae. Elytral disc with striate microsculpture (Fig. ***216***) .... *Aristonister* Dégallier

19 (20). Pronotal disc regularly convex, with numerous large punctures. Lateral sides of pronotum regularly, arcuately narrowed apically, widest at the base (Fig. ***205***) .... *Leptosister* Reichensperger

20 (19). Pronotal disc more or less flat, only with minor impressions/elevations slightly above/below plain of disc, without punctures. Lateral margins of pronotum slightly expanded near base, then gradually, weakly narrowed apically, widest around basal third (Fig. 12, ***208***)... 21

21 (22). Elytra costate, surfaces shiny. Pronotal disc without longitudinal striae. Longitudinal sutures of prosternal lobe without foveae (Fig. ***208, 209***) .... *Eurysister* Reichensperger

22 (21). Elytra not costate, surfaces mostly alutaceous. Pronotal disc on each side with a pair of longitudinal striae. Longitudinal sutures of prosternal lobe continuous across deep, large preapical foveae (Fig. 12) .... *Guianahister* gen. n.

23 (24). Dorsal surface with short to medium erect or semi-erect setae, densely covering pronotal disc and elytral striae. Pronotum completely covered with rather dense punctures. Each elytron with full set of unabbreviated dorsal and sutural striae, sometimes with additional abbreviated stria in apical half of sutural area composed of shallow conjunct elongate punctures. Sometimes elytral surface nearly covered with dense punctures that obscure dorsal striae 25

24 (23). Dorsal surface without setae, occasionally with a few isolated, inconspicuous setae. Pronotum with few punctures, at most with sparse shallow punctures on disc. Elytral set of striae never complete, striae often abbreviated, broken, irregular or absent, always so in sutural area 27

25 (26). Complete longitudinal discal metasternal striae double, forming long, narrow loops. Ventral processes of male 9th tergite short and membranous (Fig. 6, 7) .... *Bruchodites* gen. n.

25 (26). Longitudinal discal metasternal striae either present or absent, but never double, loop-like. Ventral processes of male 9th tergite absent (Fig. 19, 20) .... *Microsynodites* gen. n.

27 (28). Preapical foveae small and incospicuous. Elytra with thin simple dorsal striae, set either complete or reduced in scutellar and discal area. Dorsal striae never

broken into series of punctures and never obscured by interval punctation (Fig. 21) .... *Mutodites* gen. n.

28 (27). Preapical foveae large and conspicuous. Dorsal striae ether absent or reduced to few remnant punctures along imaginary dorsal striae, or confused by breaks and interval punctures (especially in mesal areas) (Fig. 23, ***220***) 29

29 (30). Carinal striae close, their anterior connection forming an acute angle. Both inner and longitudinal discal metasternal striae complete, bent laterally. Set of dorsal striae complete, although striae are broken, abbreviated and/or confused with interval punctures, especially in sutural area. Separate central sclerite of female 8th sternite absent (Fig. 23) .... *Nicolasites* gen. n.

30 (29). Carinal striae absent, or, if present, widely spaced, their anterior connection forming obtuse angle or semicircular arch. Inner metasternal striae absent or complete, longitudinal discal metasternal striae absent or present as a basal fragment, both striae straight. Set of dorsal striae substantially reduced, at most represented by few remnant punctures, often absent completely. Separate central sclerite of female 8th sternite present (Fig. ***220***) .... *Monotonodites* Reichensperger

31 (32). Proepisternum with setose patch or fossa (Fig. ***103, 228***) 33

32 (31). Proepisternum without setose patch or fossa 37

33 (34). Pronotum with inverted U-shaped stria on disc in addition to somewhat irregular striae parallel to lateral margins. Almost complete outer dorsal striae (1st and 2nd) present (Fig. ***231***) .... *Oaristes* Helava

34 (33). Pronotum without inverted U-shaped striae on disc 35

35 (36). Dorsal surface without setae. Elytra smooth, without microsculpture. Dorsal striae represented by a few short basal fragments (Fig. ***227***) .... *Panoplitellus* Hedicke

36 (35). Dorsal surface with numerous, dense setae, many in compact tufts. Elytra with distinct dense microsculpture of punctures and/or longitudinal wrinkles. Outer dorsal striae, at least 1st, long, reaching apical half of elytra (Fig. ***235***) .... *Aemulister* Reichensperger (part)

37 (38). Prosternal keel with a pair of longitudinal rows of long erect setae parallel to carinal striae (Fig. ***236***) 39

38 (37). Prosternal keel without longitudinal rows of setae 41

39 (40). Lateral margins of pronotum swollen into high longitudinal elevations (Fig. ***235***) .... *Aemulister* Reichensperger (part)

40 (39). Pronotum without lateral longitudinal elevations, regularly weakly convex (Fig. ***239***) .... *Daptesister* Helava

41 (42). Carinal striae narrowly spaced, convergent apically and forming a narrow acute angle at apical connection (Fig. ***252, 263***) 43

42 (41). Carinal striae widely spaced, parallel, either connected by arched or angular line or not connected at apices (Fig. ***279, 287***) 65

43 (44). Body almost spherical. Entire body surface covered with dense punctate microsculture. Lateral sides of propygidium each with a tubercle (Fig. ***286***) 45

44 (43). Above combination of characters absent 47

45 (46). Pronotum, meso- and metasterna, propygidium and pygidium with scattered, dense, circular or elongate, tiny, shiny setiferous tubercles. On elytra, such tubercles tightly arranged along a full set of dorsal striae. Prosternal keel in profile with median triangular elevation. Lateral margins of pronotum each with a tubercle basally (Dégallier, 1998b) .... *Cyclechinus* Bickhardt

46 (45). Body surface without scattered shiny granular tubercles. Dorsal striae marked by weak, shallow punctures. Prosternal keel in profile flat. Lateral margins of pronotum without tubercles .... *Ecclisister* Reichensperger

47 (48). Elytron with numerous secondary longitudinal striae, given the impression of 12-14 dense dorsal striae or dense striate microsculpture with traces of dorsal striae. Head, pronotum, pygydia, meso- and metasterna and 1st abdominal sternite with dense, large, elongate oval or drop-shaped punctures (Fig. ***262, 263***) .... *Alloiodites* Reichensperger

48 (47). Above combination of characters absent 49

49 (50). Body surface smooth and shiny, impunctate. Dorsal, inner lateral and longitudinal discal metasternal striae absent. Intra-TAS plate of male 8th sternite substantially reduced, almost entirely absent. Male 9th sternite with apical projections robust, heavily sclerotized, with apices pointed (Fig. ***246, 247***) .... *Nymphister* Reichensperger (part)

50 (49). Above combination of characters absent 51

51 (52). Disc and sides of metasternum covered with large, shallow, circular or oval, dense punctures. Inner lateral metasternal striae absent, longitudinal discal metasternal striae represented only by short basal fragments. Body large (PEL ca. 3 mm), stout, its surface asetose. Parameres of aedeagus flattened dorsoventrally (Fig. 25) .... *Reichenspergerites* gen. n.

52 (51). Above combination of characters absent, at least either inner lateral or longitudinal discal metasternal lateral striae always complete or nearly complete ... 53

53 (54). Metasternal striae arranged as follows: inner lateral metasternal short and close to mesocoxae, outer lateral metasternal short, with recurrent arm, located near midline of metasternum, far anteriad posterior margin. Longitudinal discal

metasternal striae short, abbreviated posteriorly. Two additional pairs of striae present on metasternum: short fragments between inner and outer lateral striae, close to mesocoxae, and innermost pair of long and irregularly S-shaped striae. Body shape elongate oval, convex, body surface asetose. Legs short and wide. Pronotum with distinct dense punctures. Elytra with full set of dorsal striae represented by close elongate shallow punctures (Helava, 1989) .... *Voratister* Helava

54 (53). Above combination of characters absent 55

55 (56). Lateral sides of metasternal disc with odd-shaped wide striate loops, irregularly inverted B- or O-shaped, formed by longitudinal discal metasternal and additional discal striae. Body shape elongate oval, body surface asetose. Pronotum with distinct, dense punctures. Elytra with full set of dorsal striae, elytral intervals distinctly convex (Fig. ***251***) .... *Paratropinus* Reichensperger

56 (55). Lateral sides of metasternal disc without wide striate loops. Sometimes longitudinal discal metasternal striae are double and may form narrow, parallel-sided, straight or slightly bent stick-shaped loops 57

57 (58). Longitudinal discal metasternal striae either absent entirely or represented by short apical fragments next to metacoxa 59

58 (57). Longitudinal discal metasternal striae present, complete 61

59 (60). Inner lateral metasternal striae present. Longitudinal discal metasternal striae either absent entirely or represented by short apical fragments next to metacoxa. Body large, oval and robust (PEL 2.5-3.5 mm), set of dorsal striae always entire or nearly entire, punctures setae variable. Intra-TAS plate of male 8th sternite substantially reduced, almost entirely absent. Male 9th sternite with apical projections short, robust, heavily sclerotized, with acute apices (Fig. 27, 28, ***297***) .... *Trichoreninus* Lewis

60 (59). Inner lateral and longitudinal discal metasternal striae entirely absent. Body small (PEL ca. 1 mm) and convex, teardrop-shaped. Entire body surface densely covered with fine small punctures. Set of dorsal striae substantially reduced, at most 1st and 2nd dorsal striae more or less complete. Intra-TAS plate of male 8th sternite present, variably cut along TAS and midline. Male 9th sternite with apical projections very long, thin, moderately sclerotized (Fig. 16) .... *Helavadites* gen. n. (part)

61 (62). Entire body surface densely covered with fine background punctures. Body elongate oval, small (PEL 1.5-2 mm), asetose. Longitudinal discal metasternal striae simple, always straight. Intra-TAS plate of male 8th sternite present, variably incised along TAS and midline. Male 9th sternite with ventral apodemes present, ventral processes absent, apical projections very long, thin, moderately sclerotized, with acute apices (Fig. 15, 16) .... *Helavadites* gen. n. (part)

62 (61). Body surface without background punctures, usually smooth, often shiny between major punctures and striae, rarely almost completely covered with dense punctures that obscure striae. Body oval, mostly shorter and more robust, often larger (PEL up to 3.5 mm), mostly with numerous erect or semierect setae. Longitudinal discal metasternal striae mostly modified, keeled or double, often bent. Male genitalia characters different 63

63 (64). Inner lateral and longitudinal discal metasternal striae keeled. Body large (PEL 3 mm and more), surface always shiny, with numerous deep, large punctures and long setae. Basal piece of aedeagus with wide, shallow dorsal apical emargination and without collar of basal opening. Male 8th sternite with substantially enlarged velae. Male 9th sternite with ventral apodemes present, ventral processes long and robust (Fig. 6, 7) .... *Alienodites* gen. n.

64 (63). Inner lateral and longitudinal discal metasternal striae never keeled, longitudinal discal striae often double. Body size variable, but PEL rarely more then 3 mm, surface rarely shiny, punctures variable, but setae usually less prominent. Basal piece of aedeagus with narrow and deep dorsal apical emargination and with a collar of basal opening. Male 8th sternite with small velae. Male 9th sternite with ventral apodemes, and ventral processes absent (Fig. 19, 20) .... *Mesynodites* Reichardt

65 (66). Carinal striae connected at apices 67

66 (65). Carinal striae not connected at apices 69

67 (68). Prosternum between carinal striae flat. Pronotal disc more or less convex, unmodified (Fig. ***274, 275***) .... *Daitrosister* Helava

68 (67). Prosternum between carinal striae deeply concave. Pronotal disc more or less flat, with median H-shaped depression and setose patches/tufts (Fig. ***270, 271***) .... *Aphanister* Reichensperger

69 (70). Body surface almost entirely covered with dense background punctures. Body shape subspherical. Both lateral margins of propygidium and pronotum each with a tubercle (Fig. ***286***) .... *Clientister* Reichensperger

70 (69). Above combination of characters absent 71

71 (72). Surface of elytra, meso- and metasterna and disc of 1st abdominal sternite with dense striate microsculpture. Pronotal disc convex, smooth and shiny, with sparse shallow punctures. Lateral sides of pronotum slightly swollen and bent upwards, separated from the rest of disc by shallow longitudinal depressions (Fig. ***258***) .... *Anasynodites* Reichensperger

72 (71). Above combination of characters absent, striate microsculpture on upper and lower body surfaces always absent 73

73 (74). Dorsal striae and punctures of body surface absent, only a few scattered shallow punctures tracing the position of dorsal striae may be present on elytra, especially in sutural area. Body globular, subspherical (Fig. ***247***) .... *Nymphister* Reichensperger (part)

74 (73). At least basal halves of three outer dorsal striae present. Body shape more elongate and less convex 75

75 (76). Full set of dorsal striae usually present on elytra, sutural striae always complete. Anterior parts of inner lateral and longitudinal discal metasternal striae originate in the same point, descend posteriorly forming acute angle (Fig. ***255***) .... *Psalidister* Reichensperger

76 (75). Only basal halves of 3 outer dorsal striae present on elytra, sutural striae absent. Inner lateral and longitudinal discal striae not connected anteriorly, completely parallel to each other (Fig. ***278***) .... *Cheilister* Reichensperger

CHAPTER 5. EVOLUTION OF HOST-GUEST RELATIONSHIPS IN NYMPHISTERINI

5.1. Evolution of Host Use

Before this analysis was done, I realized that it would be of limited application due to at least two major drawbacks resulting from problems with identification of the sister taxon of Nymphestirini and incomplete taxon sampling. I sampled consistently, but selectively within Group E of Helava *et al.* (1985) and included a maximum of four genera for the remainder of the Hetaeriinae, *Synoditulus* and one genus in each of Groups B-D. Group E is probably not basal within Hetaeriinae and most host diversity (termites and miscellaneous ants other than army and leaf-cutter ants) is within taxa entirely outside this clade (Helava *et al.*, 1985). Thus, chances that the (*Hemicolonides – Mesynodites diadochus*) clade is the sister group of Nymphestirini, as my analyses suggested, are low. This is an important caveat because outgroup seriously affects character optimization (*e.g.*, Brooks & MacLennan, 2002).

Selection of the taxa within the ingroup was driven by two factors, balanced representation of Group E subgroups and *Mesynodites s.l.* representation, and specimen availability. Several guest genera appeared to be associated with more than one host genus (see below, Table 5), so changing one of two (on average) representative species per genus in such multi-host taxa would affect character mapping. The same is true of including or omitting a particular genus as a representative of a subgroup. Finally, lack of host information for some old specimens or specimens collected recently by flight intercept traps is another source of ambiguity in host use optimization. Nevertheless, some insights are apparent from this limited analysis (Fig. 30).

Ancestral host of Nymphisterini. Optimization (Fig. 30) suggests *Labidus* (which is represented overwhelmingly by *L. praedator* in this data set) is the ancestral host. Inspection of alternative phylogenetic results (Fig. 2, Chapter 3.3.1), provide only one potential alternative, *Eciton*. In an analysis of alternative phylogenies, internal resolution of host optimization did not improve because *Eciton*-specialized basal clades, (*Mesynodites bifurcatus – Mesynodites amazonicus*) = *Alienister, Anasynodites – Cheilister,* and/or (*Mesynodites bifurcatus – Cheilister*), are sisters to clades, *Mesynodites s. str.* and/or (*Eurysister – Mesynodites evanescens*), where basal lineages have multiple hosts almost exclusively other than *Eciton* (Figs. 2, 32).

Either of the genera implied as ancestral hosts have representative species, *E. burchelli* and *L. praedator* that could be considered suitable candidates for the ancestral hosts of inquilinous histerids according to Helava *et al.*'s (1985) hypothesis. They hypothesized that ancestral inquilines colonized ant refuse deposits first, then switched to termite colonies and interiors of ant colonies. Both *E. burchelli* and *L. praedator* are swarm raiders with broad generalized diets (Gottwald, 1995). As a result, they exploit prey resources effectively and attain high and predictable densities and large colony sizes (Gottwald, 1995), factors favoring colonization and survival by would-be-guests (Wilson, 1971). Furthermore, unlike other army ants specialized on soft-bodied larvae of other ants and social wasps, *E. burchelli* and *L. pradeator* prey on a diversity of hard-bodied arthropods and produce substantial refuse deposits during statary phases of life cycles because they utilize heavily chitinized food items completely (Gottwald, 1995). This last fact points to *E. burchelli* and *L. pradeator* as better candidates for basal hetaeriine hosts, as argued by Helava *et al*. (1985) and Wilson (1971). In fact, *Synoditulus*, apparently the basal hetaeriine (see Chapter 3.3.3), is found both with *E. burchelli* and *L. pradeator.*

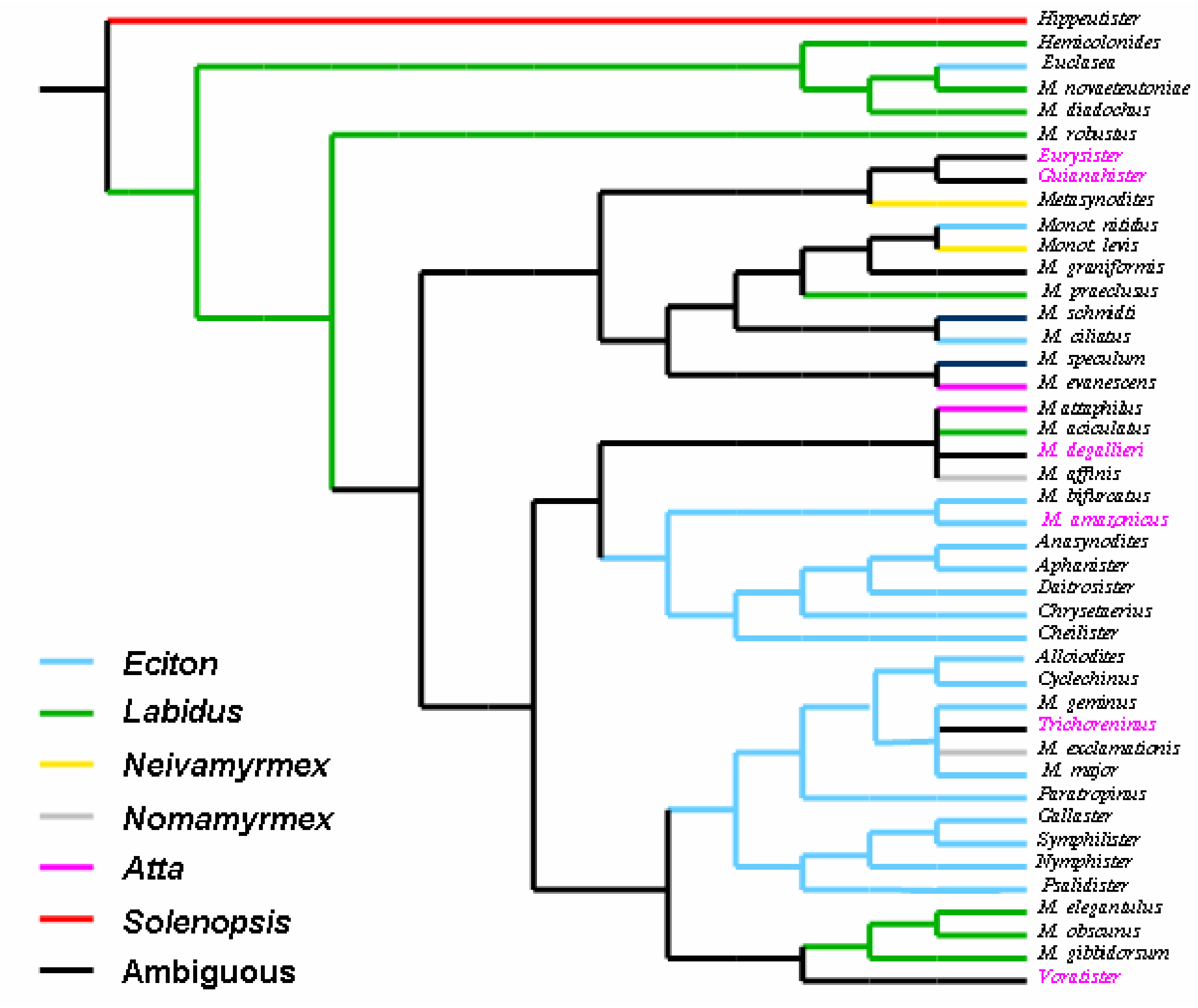


Fig. 32. Results of the optimization of ant host information (at the genus level) onto the phylogeny of Nymphisterini using MacClade. Terminal taxa without host information and Ecitoninae hosts are highlighted.

Host specificity at the generic level. The results of this analysis allow a critical evaluation of a long standing dogma of high host specificity at the genus-to-genus level within Hetaeriinae (Kistner, 1979, 1982; Helava *et al*., 1985). These authors reported only one hetaeriine genus other than *Mesynodites* with more than one social insect host genus. By contrast, my results reveal that several lineages of closely related species, *e.g. Mesynodites s.str.*, *Microsynodites, Monotonodites, Mutodites, Trichoreninus*, are associated with multiple ant host genera (Fig. 32 and Chapter 4). In fact, lack of strict specificity seems to be a rule outside the

(*Alloidites – Voratister*) and (*M. bifurcatus – Cheilister*) clades, which evolved almost exclusively with *Eciton*. Presumably, these intrageneric switches are relatively recent events facilitated by rich local assemblages of sympatric army ant species with different life styles (*e.g*., diurnal vs. nocturnal activities, surface vs. subterranean nesting/foraging) (Watkins, 1976; Gottwald, 1995).

Origin of associations with leaf-cutter ants. The group in question is associated almost exclusively with army ants (Ecitoninae). However, four described species of *Mesynodites s.l.* are associated with subterranean refuse chambers of leaf-cutter ants (Bruch, 1933; Reichensperger, 1935), a habitat supporting few, but very specialized hetaeriines (Helava *et al*., 1985). Tracing the affinities of these species and evolution of this odd association within a clade dominated by army ant hosts was one of the exciting challenges of this analysis.

The results suggest two switches to *Atta* hosts within Nymphisterini (Fig. 32), one within *Mesynodites s.str*. and another within *Mutodites*. In *Mutodites*, the switch to *Atta* took place almost certainly from *Nomamyrmex,* the only other known host for the genus (Chapter 4). The situation with *Mesynodites s.str*. is not so clear because its hosts include two species of *Labidus* and *Nomamyrmex esenbecki*. The nature of these switches to *Atta* can be formally studied with an application of appropriate methods of cladistics and historical ecology, but a switch from *Nomamyrmex* seems to be reasonable preliminary hypothesis.

A couple of empirical facts may shed light on the mechanism of this switch and provide additional support for its validity. *Nomamyrmex* ants are mainly subterranean nesters and nocturnal foragers (Gottwald, 1995). An observational report exists of *Neivamyrmex,* a genus very similar in habits to *Nomamyrmex,* establishing a bivouac inside subterranean chambers of an *Atta* colony in Louisiana (Moser, 1963). This provides a circumstantial case where such a switch could be accomplished. Furthermore, *N. esenbecki* on Barro Colorado Island, Panama, are known to attack *Atta* colonies on a regular basis and are able to wipe out mature colonies in the course of multi day battles (Elie Clark, Smithsonian Tropical Research Institution, personal communication). These cases provide insight into possible circumstances of the host switch process, stressing the significance of close colony proximity in subterranean ants, current host ants' predation on potential hosts and the initial invasion of weakly guarded refuse deposits by inquilines.

5.2. Host Specialization and Speciation in Hetaeriinae

Much literature exists dealing with the relationship between the degree of specificity and patterns of speciation in symbiotic organisms. Despite increased recent attention by researchers to the topic, no clear consensus exists about whether narrow specialization is an evolutionary dead end or a new adaptive zone (Mayr, 1963; Futuyma & Moreno, 1988; Siddall *et al*, 1993; Thompson, 1994; Robinson *et al.*, 1996; Kelley & Farrel, 1998). In the first case, lineages/species become more prone to extinction due to exclusive use of more limited resources, lower adaptability to substantial environmental changes affecting their availability and low possibility of reverse evolution from extreme specialization. In the latter, enhanced speciation results in wide radiations into new niches not available for less specialized competitors and unfamiliar to existing natural enemies. A number of species per lineage (*e.g.*, per genus) may be used to measure evolutionary success because it reflects the balance between speciation and extinction. Below, I investigate a relationship between numbers of species per genus in strictly specialized and more generalized Hetaeriinae to test whether narrow host specialization is correlated with increased or decreased species numbers.

Data were derived from published and revised species counts and known host genera for a selection of 54 genera of neotropical Hetaeriinae (Table 5). Numbers of guest species per genus vary substantially, from 1-15 (24) species in host specialists and from 1-13 (79) species in generalists (revised species counts in parentheses). However, a comparison of the average number of species per guest genus of host-specialized versus host-generalized hetaeriines (Table 6) provides a clear picture. On average, guest genera with 2+ hosts have 1.6-2.9 times more species than specialized genera, differences being significant or almost significant (Table 6). The results are surprisingly consistent among three analytical categories used (Nymphestirini, all ecitophiles and all Hetaeriinae) and published and revised species counts.

The use of improved taxonomy makes the trend more pronounced, but slightly changes the results for Nymphisterini (Table 6). Consideration of potential trends related to the results of these analyses in light of further taxonomic improvement (*e.g.*, splitting some apparently non-monophyletic 'oversized' genera with multiple hosts such as *Euclasea, Homalopygus, Reninus*) suggests that the pattern probably would persist. These revisions will result either in splitting small, often monotypic lineages from more diverse genera or subdividing them into several component genera that mostly would be comparable to, or even more diverse than average generalized host genera. Both scenarios will contribute to maintenance of the observed pattern. Another argument that improved taxonomy will provide the same result is a disproportional increase in average number of species per genus in generalized vs. specialized hetaeriines in revised species counts (*i.e.*, 2.8-4.3 vs. 2.1-2.5, respectively, Table 6).

Table 5. Host relationships and species diversity of selected hetaeriine genera. Sources of methods for obtaining host and species counts information are described in Chapter 2.10.

Hetaeriine Genus	Published Species Count	Revised Species Count	Host Genus/Genera
Aemulister	2	2	*Eciton, Neivamyrmex*
Alloiodites	3	12	*Eciton, Labidus*
Anasynodites	1	1	*Eciton*
Aphanister	1	3	*Eciton*
Aristomorphus	5	14	*Labidus*
Bactactister	1	2	*Neivamyrmex*
Bruchodites	1	3	*Labidus*
Cheilister	1	1	*Eciton*
Chrysetaerius	2	1	*Eciton, (Neivamyrmex)*
Clientister	2	3	*Eciton*
Colonides	3	4	*Eciton*
Convivister	1	1	*Eciton, Labidus*
Daitrosister	6	18	*Eciton*
Daptesister	1	1	*Eciton*
Ecclisister	1	3	*Eciton*
Euclasea	12	79	*Eciton, Labidus, Neivamyrmex*
Euxenister	4	4	*Eciton, Ectatomma*
Glyptosister	1	1	*Nomamyrmex*
Hetaeriobus	2	2	*Neivamyrmex*
Hippeutister	5	5	*Solenopsis*
Homalopygus	12	12	*Crematogaster, Nasutitermes*
Latronister	2	4	*Eciton*
Mesynodites	7	22	*Atta, Labidus, Nomamyrmex*
Metasynodites	3	10	*Neivamyrmex*
Microsynodites	3	12	*Eciton, Nomamyrmex*
Monotonodites	5	15	*Eciton, Neivamyrmex*
Mutodites	4	4	*Atta, Nomamyrmex*
Nevermannister	1	5	*Labidus*
Nicolasites	5	24	*Labidus*
Notocoelis	1	1	*Cornitermes*
Nymphister	1	14	*Eciton*
Oaristes	2	2	*Eciton*
Panoplitellus	1	1	*Eciton*
Paratropinus	2	3	*Eciton*
Parodites	1	4	*Eciton, Labidus*
Pelatetister	1	2	*Neivamyrmex*
Pinaxister	4	6	*Pheidole*
Procolonides	1	1	*Neivamyrmex, Solenopsis*
Psalidister	6	10	*Eciton*
Pterotister	2	3	*Neivamyrmex*
Reichenspergerites	1	2	*Labidus*

Table 5. (Continued).

Hetaeriine Genus	Published Species Count	Revised Species Sount	Host Genus/Genera
Reninus	13	15	*Acromyrmex, Atta*
Pulvinister	1	2	*Eciton*
Scapolister	1	2	*Syntermes*
Sternocoelopsis	3	3	*Eciton*
Symphilister	2	2	*Eciton*
Synoditulus	2	5	*Eciton, Labidus*
Teratosoma	2	2	*Neivamyrmex*
Terapus	15	24	*Pheidole*
Trichoreninus	5	14	*Eciton, Nomamyrmex*
Troglosternus	4	11	*Eciton, Labidus, Nomamyrmex*
Ulkeopsis	1	1	*Neivamyrmex*
Ulkeus	6	18	*Neivamyrmex*
Undescribed genus	-	1	*Eciton*

Limited availability of host and phylogenetic information prevents a rigorous test of the trends accounting for potential phylogenetic constraints (*i.e*., based on sister taxa differing in host specialization). This approach may be used only in an illustrative manner as I was able to find only three genera pairs that satisfied criteria of relatively confidently proven sister relationship and different host specialization. These pairs are *Alloiodites* and *Cyclechinus*, *Monotonodites* and *Bruchodites*, *Troglosternus* and *Nevermannister* (this study and Helava *et al*., 1985: 150; generalists listed first). The results for these genera are completely consistent with the previously discussed trend: genera with multiple hosts are 2-5 times more speciose, and two pairs of three exceed the typical differences by two-fold (Tables 5, 6). Given the limits of this analysis (limitations in taxon sampling, taxonomic information, host records and use of phylogenetic framework), the increased species diversity of hetaeriine genera with multiple hosts (or decreased diversity in specialized genera) found may be considered as a working hypothesis to be tested on an improved dataset using phylogenetically independent comparisons. The

Table 6. Average number of species per genus in selected genera of neotropical Hetaeriinae with specialized and generalized host use, presented as Average±SD (N). Differences tested by the Wilcoxon paired test.

Categories of Analysis	Published Species Count			Revised Species Count		
	Specialists	Generalists	P	Specialists	Generalists	*P*
Nymphisterini	2.1±1.7 (20)	3.9±1.9 (8)	0.04	5.3±6.3 (21)	11.6±6.8 (8)	0.06
All Ecitophiles	2.2±1.7 (31)	3.6±3.2 (11)	0.02	5.3±6.1 (31)	15.5±22.9 (10)	0.03
All Hetaeriinae	2.6±1.7 (36)	4.8±4.0 (17)	0.03	5.4±6.4 (38)	13.3±18.6 (16)	0.03

discussions of possible mechanisms of this phenomenon are premature as many factors may be involved. These include number of host shifts, host species diversity, colony sizes, and nesting and food habits. A couple of examples demonstrate some potential deviations from an average pattern, apparently due to some factors imposed by different hosts.

An average number of species per specialized genus is about five (Table 6). However, limited information available on some particular hosts suggests potential for disparate, host-specific variability. Termite specialists living with *Cornitermes* and *Syntermes* average just 1.5 species per genus, while specialized guests of *Pheidole* ants have 15 species. Although these figures are based on very small samples, other available data that did not qualify for this analysis generally support this pattern. The documented and suspected termite specialist genera that were not included in the analysis due to doubts about host affiliation and limited host records (*e.g.*, *Coelister*, *Cossyphodister*, *Discoscelis*, *Paroecister, Thaumataerius*) have no more than two species each (Helava *et al*., 1985; Tishechkin, unpublished). Alternatively, analyzed *Pheidole* specialists account for the half of the known specialized hetaeriine guest genera for these ants. With inclusion of *Parasynodites* and *Synoditinus* into the analysis, with one and four known species, respectively (Helava *et al*., 1985; Tishechkin, unpublished) a number of 8.75 species per genus of *Pheidole* specialists results, well above an average value. These genera make the list of known specialized hetaeriine *Pheidole* guests complete, but they do not meet minimal criteria for formally including them in the results as each has only a single host record.

The pattern observed for hetaeriine termite guests is similar to the situation observed in termitophilous Staphylinidae (Kistner, 1979) that are strictly host specific (often at the host species level) and represent low numbers of guest species/genus. An obvious explanation for the situation with *Pheidole* specialists postulates higher levels of specialization (at the species or species group level) in a superdiverse host genus, as *Pheidole* represents (Wilson, 2003). However, guests of another extremely diverse ant genus, *Neivamyrmex* (Wilson, 2003), contain a more modest number of species per genus, approximately five (Table 6). Whether these examples represent real patterns and what the actual situation is with hetaeriine species in relation to host specificity remain to be uncovered with the use of additional research tools and better sampling.

REFERENCES

Agosti D., D. Grimaldi and J.M. Carpenter. 1997. Oldest known ant fossil discovered. Nature 391: 447.

Akre R.D. 1968. The behavior of *Euxenister* and *Pulvinister*, histerid beetles associated with army ants. Pan-Pacific Entomologist 44: 87-101.

Akre R. D. and C. W. Rettenmeyer. 1966. Behavior of Staphylinidae associated with army ants (Formicidae: Ecitonini). Journal of the Kansas Entomological Society 39: 745-782.

Akre R. D. and C. W. Rettenmeyer. 1968. Trail-following by guests of army ants (Hymenoptera: Formicidae: Ecitonini). Journal of the Kansas Entomological Society 41: 165-174.

Bikhardt H. 1914. Die System der Histeriden (Vorläufige Mitteilung). (22. Beitrag zur Kenntnis der Histeriden). Entomologischer Blätter 10: 305-308.

Borgmeier T. 1929. Um novo histerideo ecitophilo. Boletím Biologico (São Paolo) 16: 85-91.

Borgmeier T. 1930. Eine neue termitophile Histeridengattung aus Brasilien. Zoologischer Anzeiger 88: 33-39.

Borgmeier T. 1948. Zur Kenntnis der bei *Eciton* lebenden myrmecophilen Histeriden (Col.). Revista de Entomologia 19: 377-400.

Brady S. G. 2003**.** Evolution of the army ant syndrome: The origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. Proceedings of the National Academy of Sciences 100: 6575-6579.

Brooks D. R. and D. A. McLennan. 2002. The nature of diversity. An evolutionary voyage of discovery. Univ. Chicago Press, Chicago, IL.

Bruch C. 1922. Dos nuevos coleópteros mirmecóphilos. Physis 5: 296-300.

Bruch C. 1923. Estudios mirmecológicos con la descripción de neuvas especies de dipteros ("Phoridae") por los RR. PP. H. Schmitz y Th. Borgmeier y de une araña ("Gonyleptidae") por El. Doctor Mello-Leitão. Revista del Museo de La Plata 28: 172-209.

Bruch C. 1926a. Coleópteros mirmecóphilos de Córdoba. Revista de la Sociedad Entomologica de Argentina 1: 3-12.

Bruch C. 1926b. Nuevos histéridos ecotófilos (Col.). Revista del Museo de La Plata 29: 17-33.

Bruch C. 1929. Neue myrmecophile Histeriden und Verzeichnis der aus Argentinien bekannten Ameisengäste. Zoologischer Anzeiger 82: 421-437.

Bruch C. 1933. Coleópteros mirmecóphilos de Misiones (Staph. Pselaph. Hister.). Revista de Entomologia 3: 12-37.

Bruch C. 1939. Un neuvo histérido mirmecófilo (Coleopt.). Notas del Museo de La Plata 4: 259-262.

Carpenter J. M. and H. R. Hermann. 1979. Antiquity of sociality in insects. Pp. 81-89 in: H. R. Hermann (ed.) Social Insects. Vol. I. Academic Press, New York.

Caterino M. S. 1999. The taxonomy and phylogenetics of the *coenosus* group of *Hister* Linnaeus (Coleoptera: Histeridae). University of California Publication. Entomology 119: 1-75.

Caterino M. S. and A. P. Vogler. 2002. The phylogeny of the Histeroidea (Staphyliniformia). Cladistics 18 (4): 394-415.

Colwell R. K. 1996. Biota: The Biodiversity Database Manager. Sinauer Associates, Sunderland, MA.

Dégallier N. 1993. Catalogue des Coleoptera Histeridae conserves dans la collection du laboratorie d'entomologie du Zoologisches Forschungsinstitut & Museum Alexander König, Bonn, Allemagne. Revista Brasileira de Entomologia 37: 117-123.

Dégallier N. 1997. Analyse d'ouvrage. Helava (J.V.T.), Howden (H.F.) & Ritchie (A.J.), 1985. - A review of New World genera of myrmecophilous and termitophilous subfamily Hetaeriinae (Coleoptera: Histeridae). – Sociobiology, California State University – Chico, 10 (2): 127-382. Nouvelle Revue d'Entomologie (N.S.) 4: 220.

Dégallier N. 1998a. Notes taxonomiques et faunistiques sur les Histeridae néotropicaux avec la description de *Brasilister flechtmanni* nov. gen, nov. sp. et *Terapus flechtamnni* nov. sp. (Coleoptera, Histeridae). Nouvelle Revue d'Entomologie (N.S.) 15: 45-62.

Dégallier N. 1998b. Notes taxonomiques sur les Coleoptera Histeridae Hetaeriinae du Muséum d'Histoire Naturelle de Berlin (MNHUB). Mitteilungen der Museum für Naturunde zu Berlin 74: 129-143.

Dégallier N. 1998c. Coleoptera Histeridae Hetaeriinae: description de nouveaux taxons, désignation de lectotypes et notes taxonomiques. Bonner Zoologischer Beitrag 47: 345-349.

Dégallier N. and Y. Gomy. 1983. Caractères gènéraux et techniques de récolte des Coléoptéres Histeridae. L'Entomologiste 39: 9-17.

De Marzo L. and P.Vienna. 1982. Studio morfologico della spermateca in Coleotteri Isteridi, con particolare attenzione alla tribù Saprinini. Entomologica 18: 163-179.

Farris J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist 106: 645-668.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using bootstrap. Evolution 39: 783-791.

Foerster A. 1868. Synopsis der Familien und Gattungen der Ichneumonen. Verhandlungen des Naturhistorischen Vereins Preußischen Rheinlandes und Westfalen 25: 135-221.

Forey P. L. and I. J. Kitching. 2000. Experiments in coding multistate characters. Pp. 54-80 in: R. Scotland and R. T. Pennington (eds.) Homology and systematics. Coding characters for phylogenetic analysis. Taylor & Francis, London – New York.

Futuyma D. J. and G. Moreno. 1988. The evolution of ecological specialization. Annual Revue of Ecology and Systematics 19: 207-233.

Gottwald W. H. 1995. Army ants. The biology of social predation. Cornell Univ. Press, Ithaca and London.

Grimaldi D. and D. Agosti. 2000. A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. Proceedings of the National Academy of Sciences 97: 13678-13683.

Hansen M. 1997. Phylogeny and classification of staphyliniform beetle families. Biologiske Skrifter 48: 1-339.

Helava J. V. T. 1989. A new genus and two new species of ant-associated histerids from Panama (Coleoptera: Histeridae: Hetaeriinae). Coleopterists Bulletin 43: 121-126.

Helava J. V. T., H. F. Howden and A. J. Ritchie. 1985. A review of New World genera of myrmecophilous and termitophilous subfamily Hetaeriinae (Coleoptera: Histeridae). Sociobiology 10: 127-386.

ICZN. 1999. International Code of Zoological Nomenclature. 4th Edition. The International Trust for Zoological Nomenclature, London.

Kanaar P. 1997. Revision of the genus *Paratropus* Gerstaecker (Coleoptera: Histeridae). Zoologische Verhandelingen 315: 1-185.

Kelley S. and B. D. Farrell. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52: 1731-1743.

Kistner D. H. 1979. Social and evolutionary significance of social insect symbionts. Pp. 339-413 in: H. R. Hermann (ed.) Social Insects. Vol. I. Academic Press, New York.

Kistner D. H. 1982. The socials insects' bestiary. Pp. 1-244 in: H. R. Hermann (ed.) Social Insects. Vol. III. Academic Press, New York.

Kovarik P. W. and M. S. Caterino. 2001. Histeridae. Pp. 212-227 in R. H. Arnett & M. C. Thomas (eds.). American Beetles. Vol. 1. CRC Press, Boca Raton – London – New York – Washington.

Kovarik P. W., D. S. Verity and J. C. Mitchell. 1999. Two new saprinine histerids from southwest North America. Coleopterists Bulletin 53: 187-198.

Krishna K. and R. Weesner. 1970. Biology of termites. Vol. II. Academic Press, New York.

Kryzhanovkij O. L. and A. N. Reichardt. 1976. Beetles of the superfamily Histeroidea (families Sphaeritidae, Histeridae, Synteliidae). Fauna of the USSR V (4): 1-434 (in Russian).

Lackner, T. and T.Yélamos. 2001. Contribution to the knowledge of the Moroccan fauna of *Sternocoelis* Lewis, 1888 and *Eretmotus* Lacordaire, 1854 (Coleoptera: Histeridae). Zapateri. Revista Aragonesa de Entomologia 9: 99-102.

Lewis G. 1888. Fam. Histeridae. Biologia Centrali-Americana 2 (1): 182-244.

Lewis G. 1891. On new species of Histeridae. Annales and Magazine of Natural History (6) 8: 381-405.

Lewis G. 1893. On new species of Histeridae, and notes on others. Annales and Magazine of Natural History (6) 11: 417-430.

Maddison D. R. and W. P. Maddison. 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Version 4. Sinauer Associates, Sunderland, MA.

Mann W. 1925. Guests of *Eciton hamatum* (Fab.) collected by professor W.M.Wheeler. Psyche 32: 166-177.

Mayr E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, MA.

Mazur S. 1981. Histeridae – gnilikowate (Insecta: Coleoptera). Fauna Polski 9: 1-204 (in Polish).

Mazur S. 1984. A World catalogue of Histeridae. Polskie Pismo Entomologiczne 54: 1-379.

Mazur S. 1997. A World catalogue of the Histeridae (Coleoptera: Histeroidea). Biologica Silesiae, Wroclaw, Poland.

Meacham C. A. 1986. The role of hypothesized direction of characters in the estimation of evolutionary history. Taxon 33: 26-38.

Moser J. C. 1963. Contents and structure of *Atta texana* nest in summer. Annales of the Entomological Society of America 56: 286-291.

Nixon K. M. and J. M. Carpenter. 1993. On outgroups. Cladistics 9: 413-426.

Ôhara M. 1994. A revision of the superfamily Histeroidea of Japan [Coleoptera]. Insecta Matsumurana (N.S.) 51: 1-283.

Prendini L. 2001. Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. Systematic Biology 50: 290-300.

Reichardt A. 1924. Zwei neue Histeriden aus Turkestan. Entomologischer Blätter 20: 162-166

Reichardt A. 1941. Coleoptera. Sphaeritidae and Histeridae. Fauna of the USSR V (3): 1-420 (in Russian).

Reichensperger A. 1923. Neue südamerikanische Histeriden als Gäste von Wandermeisen und Termiten. Zeitschrift für Wissenschaftliche Insekten-Biologie 18: 243-252.

Reichensperger A. 1924a. Das Weibchen von Eciton quadriglume Hal., einige neue ecitophile Histeriden und allgemeine Benerkingen. Zoologischer Anzeiger 60: 201-213.

Reichensperger A. 1924b. Neue südamerikanische Histeriden als Gäste von Wandermeisen und Termiten. Revue Siusse de Zoologie 31: 117-152.

Reichensperger A. 1925. Weitere Histeriden-Beiträge. Entomologische Mitteilungen 14: 351-357.

Reichensperger A. 1926. Neue Beiträge zur Artenkenntnis and zur Lebenweise myrmekophiler Histeriden. Verhandlingen der III International Kongress der Entomologie 2: 184-203.

Reichensperger A. 1929. Systematische und ökologische Myrmekophilen-Beiträge (Staph., Hist., Pauss.) Zoologischer Anzeiger 82: 257-268.

Reichensperger A. 1931. Die Wirte der *Mesynodites*-Gruppe nebst Beschreibung neuer ecitophiler und termitophiler Histeridenarten. (Col. Hist.). Zoologischer Jahrbücher. Systematik. 61: 263-284.

Reichensperger A. 1933. Ecitophilen aus Costa Rica (II), Brasilien und Peru (Staph., Hist., Clavig.). Revista de Entomologia 3:179-194.

Reichensperger A. 1935a. Beitrag zur Kenntnis der Myrmekophilenfauna Brasiliens und Costa Ricas III. Arbeiten über Morphologische und Taxononomische Entomologie 2:188-218.

Reichensperger A. 1935b. Beitrag zur Kenntnis attaphiler Histeriden aus Brasilien. Revista de Entomologia 5: 25-32.

Reichensperger A. 1938. Beiträge zur Kenntnis der Myrmekophylen- und Termitophilenfauna Brasiliens und Costa Ricas V. (Col. Hist., Staph.). Revista de Entomologia 9: 74-97.

Reichensperger A. 1939. Beiträge zur Kenntnis der Myrmekophylen- und Termitophilenfauna Brasiliens und Costa Ricas VI. (Col. Hist., Staph.). Revista de Entomologia 10: 97-137.

Reichensperger A. 1958. Zwei neue Gattungen myrmekophiler Hetaeriomorphini (Col. Hist.) nebst Bemerkungen über *Terapus gracilipes* Bruch (*Aneuterapus* nov. gen.). Studia Entomologica (N.S.) 1: 279-286.

Rettenmeyer C. W. 1961. Arthropods associated with neotropical army ants with a review of the behavior of these ants (Arthropoda: Formicidae: Dorylinae). Ph.D. Dissertation. Univ. Kansas.

Robinson B. W., D. S. Wilson, and G. O. Shea. 1996. Trade-offs of ecological specialization: an intraspecific comparison of pumpkinseed sunfish phenotypes. Ecology 77: 170-178.

Schmidt J. 1893. Myrmekophile Histeriden aus Amerika. Deutscher Entomologischer Zeitschrift 1893: 171-189.

Schneirla T. C. 1971. Army ants. A study in social organization. Freeman and Co., San Francisco, CA.

Seevers C. H. 1965. The systematics, evolution and zoogeography of staphylinid beetles associated with army ants (Coleoptera: Staphylinidae). Fieldiana. Zoology 47: 137- 351.

Siddall M. E., D. R. Brooks, and S. S. Dresser. 1993. Phylogeny and reversibility of parasitism. Evolution 47: 308-313.

Ślipiński S. A. and S. Mazur. 1999. *Epuraeosoma*, a new genus of Histeridae and phylogeny of the family Histeridae. Annales Zoologici 49: 209-230.

Swofford D. L. and D. P. Beagle. 1993. PAUP Users Manual. Center for Biodiversity, Illinois Natural History Survey, Champaign, IL.

Swofford D. L. 2001. Phylogenetic Analysis Using Parsimony (PAUP*). Version 4.0b10 for Macintosh (PPC/Altivec). Sinauer Associates, Sunderland, MA.

Thompson J. N. 1994. The coevolutionary process. Univ. Chicago Press, Chicago and London.

Tishechkin A. K. 2003. New distribution records of Neotropical Hetariinae (Coleoptera: Histeridae). Sociobiology 41: 673-683.

Vienna P. 1981. Coleoptera Histeridae. Fauna d'Italia 16: 1-386.

Watkins J. F. 1976. The identification and distribution of New World army ants (Dorylinae: Formicidae). Markham Press Fund of Baylor Univ. Press, Waco, TX.

Wasmann E. 1903. Zur näheren Kenntnis des echten Gastverhaltnisses (Symphilie) bei den Ameisen- und Termitengsten. Biologischer Zentralblätter 23: 63-72, 195-207, 232-248, 261-276, 298-310.

Wenzel R. L. 1939. A new genus and several new species of North American Histeridae (Coleoptera). Annals of the Entomological Society of America 32: 384-394.

Wenzel R. L. 1944. On the classification of the histerid beetles. Fieldiana. Zoology 28: 51-151.

Wenzel R. L. and H. S. Dybas. 1941. New and little known neotropical Histeridae (Coleoptera). Fieldiana. Zoology 22: 433-472.

Wheeler W. M. 1928. The social insects: their origin and evolution. Harcourt, New York, NY.

Wilson E. O. 1971. Insect societies. Belknap, Cambridge, MA.

Wilson E. O. 1985. Ants of the Dominican amber. 2. The first fossil army ants. Psyche 92: 11-16.

Wilson E. O. 2003. *Pheidole* in the New World. A dominant, hyperdiverse ant genus. Harvard Univ. Press, Cambridge, MA, and London.

Yélamos T. 1992. Revision del genero *Eretmotus* Lacordaire, 1854 (Coleoptera, Histeridae). Eos 68: 7-27.

Yélamos T. 1995. Revision of the genus *Sternocoelis* Lewis, 1888 (Coleoptera, Histeridae), with a proposed phylogeny. Revue Suisse de Zoologie 102: 113-174.

Yélamos T. 1997. Description of a new species of *Satrapes* Schmidt, 1885 with proposed phylogeny of the Palearctic genera of Hetaeriinae (Coleoptera: Histeridae). Sesie de Entomologia. ICHN-SCL 9: 63-74.

VITA

Alexey K. Tishechkin was born in Baranawiczi, Belarus (Byelorussian Soviet Socialist Republic of the USSR then) to the family of a military officer. When he was three years old, the Tishechkin family moved to Minsk, where he graduated from the High School No. 93 in 1978, and began his college studies at Belarusian State University that same year. He graduated from the Department of Biology of the mentioned university in 1983 with the diploma of 'Biologist, Teacher of Biology and Chemistry' (degree, approximately corresponding to a Master of Science degree). After graduation, he spent a year teaching in Mir High School in Baranawiczi Rajon (County) before beginning a career as a research biologist. In 1984-89, he was a part of scientific staff of the Berezinsky Biosphere Nature Reserve in northern Belarus, than worked eight years as a research biologist with the Institute of Zoology, National Science Academy of Belarus, in Minsk. He joined the Department of Entomology at Louisiana State University in the fall of 1997, where he will earn the degree of Doctor of Philosophy in entomology in May, 2005.