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THE UNIVERSITY OF ALBERTA

Systematics of Hymenoptera, with special reference to the superfamily Chalcidoidea and family Eupelmidae (Terebrantes)

by

© Gary A. P. Gibson

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Doctor of Philosophy

Entomology

EDMONTON, ALBERTA

Spring 1986

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ISBN 0-315-30320-4

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Gary A. P. Gibson

TITLE OF THESIS

Systematics of Hymenoptera, with special reference to the superfamily Chalcidoidea and family Eupelmidae (Terebrantes)

DEGREE FOR WHICH THESIS WAS PRESENTED Doctor of Philosophy

YEAR THIS DEGREE GRANTED Spring 1986

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Systematics of Hymenoptera, with special reference to the superfamily Chalcidoidea and family Eupelmidae (Terebrantes) submitted by Gary A. P. Gibson in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Supervisor

W. G. Evans

B. S. Heming

External Examiner

Date March 17, 1986

ABSTRACT

Four papers compose the thesis, "Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures"; "Evidence for monophyly and relationships of Chalcidoidea, Mymaridae, and Mymarommatidae (Hymenoptera: Terebrantes)"; "Mesothoracic skeletomusculature and mechanics of flight and jumping in Eupelminae (Hymenoptera: Chalcidoidea: Eupelmidae)"; and, "Revision of the world genera of Calosotinae Bouček and Metapelmatinae n. subf., with a preliminary analysis of phylogenetics and classification of the family Eupelmidae (Hymenoptera: Chalcidoidea)". In the first paper, distribution and hypothesized transformation of states of 14 structural features of adults are described for representatives of Hymenoptera, synapomorphies hypothesized and used to test previous hypotheses of relationships and classification in the order, prior use of terms reviewed, and a single set of terms proposed for use throughout the order. In the second paper, synapomorphies are hypothesized based on distribution of states of 23 characters of adults and larvae described for representatives of higher taxa of Terebrantes, and used to test previous hypotheses of relationships of Chalcidoidea, Mymaridae, and Mymarommatidae. Mymarommatidae is not assigned to superfamily, but is proposed as a monophyletic family based on 4 autapomorphies, and the sister taxon of Chalcidoidea based on states of 3 internal characters. Chalcidoidea is proposed as a monophyletic superfamily based on states of 3 external characters, with Mymaridae included as a monophyletic family, supported by 3 synapomorphies for members. In the third paper, muscles and external structure of the mesothorax of males and females of Eupelminae (Eupelmidae) are described. Ninteen muscles are documented and external features and dimorphism of the sexes are partly explained by differences in form and placement of muscles. Mechanics of flight and jumping in males, and of jumping in females is also described. The apomorphic mesothoracic structure of females is correlated with how they jump, and "contortion" of females explained as a consequence of their jumping mechanism. In the fourth paper, a new subfamily, Metapelmatinae, is established and included in Eupelmidae *s. l.* with Calosotinae, Eupelminae, and Tanaostigmatinae. World genera of Metapelmatinae and Calosotinae are revised, with the following new genera proposed (type species in parenthesis): *Lambdobregma* [*L. schwarzii* (Ashmead) n. comb.] (Metapelmatinae), and *Archaeopelma* [*A. tropeotergum* n.sp.], *Licrooides* [*L. umbilicatus* n. sp.], *Paraeusandalum* [*P. chilensis* n. sp.], and *Tanythorax* [*T. spinosus* n. sp.] (Calosotinae). Phylogenetic relationships between the 3 genera included in Metapelmatinae, between the 8 genera included in Calosotinae, and between Cleonyminae (Pteromalidae), Aphelinidae, Encyrtidae, and the four subfamilies assigned to Eupelmidae *s. l.*, are proposed based on synapomorphic states inferred from distribution of states of 35 characters shared between some or all members. Proper higher classification of aphelinids, encyrtids, and eupelmids (*s. l.*) in Chalcidoidea is also proposed based on inferred relationships. Illustrated keys are given to distinguish members of the four eupelmid subfamilies from each other, and from other chalcidoids, and to distinguish members of calosotine and metapelmine genera.

ACKNOWLEDGMENTS

Regulations of the Faculty of Graduate Studies prevented inclusion of a separate acknowledgment section for each paper. Consequently, individuals who aided the sepate studies are acknowledged below. Prior to these separate acknowledgments, I would like to thank those individuals who made this thesis possible, and who made my years at the Department of Entomology, University of Alberta, such an enjoyable experience. Foremost is G. E. [illegible] provided financial assistance for research that is unheard of at other universities, who is [illegible] instrumental in maintaining an environment for research that is unexelled elsewhere, and who by example teaches students to extend themselves and do the best work that they are capable of. Also important were the professional, technical, and office staff of the department, whose knowledge and support are an integral part of this thesis. A student, however, learns most from his fellow graduate students, and I would like to thank all who I have been associated with, both for discussions and exchange of ideas, and for their comradery. I would also like to thank the members of my committee for their interest and helpful suggestions: G. E. Ball and W. G. Evans (Department of Entomology, University of Alberta), J. G. Packer (Department of Botany, University of Alberta), and N. F. Johnson (Department of Entomology, Ohio State University).

Production of the thesis itself was aided by a computer program for thesis format text written by D. R. Maddison, (Department of Entomology, University of Alberta). J. E. O'Hara, of the same department, used the program to modify papers written for publication into a thesis-acceptable format. He also made necessary corrections to the thesis, and prepared and distributed penultimate copies to the committee members when I was absent from the University prior to defense of the thesis.

Finally, I would like to thank the friends, relatives, and colleagues who collected specimens for me, or who aided me in collecting trips or visits to museums. They are too numerous to list individually, but all are remembered.

The following sections acknowledge individuals who provided assistance in preparation of the separate papers written for the thesis. Chapter 2: I am grateful to the following individuals for providing specimens for dissection and identification of specimens: H. Goulet, L. Masner; and W. R. M. Mason, Biosystematics Research Institute; R. L. Westcott, Oregon Department of Agriculture; M. Sanborne, Carleton University; J. M. Cumming, University of Alberta, Edmonton; M. Day and J. Noyes, British Museum (Nat. Hist.), and C. van Achterberg, Rijksmuseum van Natuurlijke Historie. I thank A. P. Rasnitsyn, Palaeontological Institute, Leningrad, for bringing certain Russian literature to my attention and for making valueable comments on an early version of this paper. I am also indebted to J. M. Cumming for many helpful discussions and suggestions during the course of this study. He and colleagues in the Hymenoptera sections of the Biosystematics Research Institute, Ottawa, and the Systematic Entomology Laboratory, USDA, at the U. S. National Museum, Washington, D. C., and members of my Ph. D. examining committee, G. E. Ball, W. G. Evans, and J. G. Packer, University of Alberta, reviewed various versions of this manuscript. G. Braybrook, University of Alberta, Edmonton, assisted in preparation of the scanning electon micrographs.

Chapter 3: I am particularly grateful to Carl Yoshimoto, Biosystematics Research Institute (BRI), Ottawa, who first interested me in the problems of monophyly and relationships of Chalcidoidea. He also identified and provided specimens for study and SEM, in addition to supplying some photomicrographs from his own work for use in this paper. I am indebted to A. P. Rasnitsyn, Palaeontological Institute, Leningrad, for lending type specimens of serphitids and mymarommatids described by him and M. A. Kozlov, and to E. W. Valentine, Department of Scientific and Industrial Research, Auckland, for the gift of specimens of *Palaeomymar insulare*. Type material of other mymarommatids was generously loaned by P. Dessart, Institut Royal des Sciences Naturelles de Belgique, Brussels; L. De Santis, Facultad de Ciencias Naturales y Museo, La Plata; and E. Dahms, Queensland Museum, Brisbane. Fossil mymarommatids from Baltic amber were loaned by B. Petersen, Zoologisk Museum, Copenhagen. H. E. Bisdee, BRI, assisted in preparation of some of the photomicrographs using facilities provided by the Electron Microscope Center, Cell Biology Research Institute, Ottawa, and provided other assistance in preparation of this manuscript. D. A. Craig and D. R. Maddison, Department of Entomology, University of Alberta, Edmonton (UAE), assisted in photography using the Carl Zeiss Ultraphot II microscope; and J. S. Scott, UAE, drafted figure one. I also thank my Ph. D. examining committee, G. E. Ball, W. G. Evans and J. G. Packer (UAE), and the following colleagues for reviewing this paper and providing corrections and many helpful suggestions for its improvement: J. Huber and J. LaSalle, University of California, Riverside; Z. Bouček and J. S. Noyes, British Museum (Nat. Hist.), London; M. E. Schauff and E. E. Grissell, United States National Museum, Washington; J. M. Heraty, Univeristy of Guelph, Guelph; D. C. Darling, Oregon State University, Corvallis; and C. M. Yoshimoto, L. Masner, M. Sharkey, and W. R. M. Mason, BRI.

Chapter 4: I thank T. Tachikawa, Ent. Lab., Ehime Univ., Matsuyama, Japan, for the gift of *Cynipencyrtus flavus* Ishii; J. LaSalle, Dept. Ent., University of Riverside, USA, for identification of species of Tanaostigmatinae; D. D. Cass, Dept. Botany, University of Alberta, Edmonton (UAE), for use and operation of the Photomicroscope 1; and D. A. Craig, UAE, for taking the high speed photography of jumping. G. D. Braybrook, UAE, assisted in SEM photography of specimens, and H. E. Bisdee, Biosystematics Research Institute (BRI), Ottawa, provided various assitance in preparation of the manuscript. I also thank D. A. Craig, B. S. Heming (UAE) and K. G. A. Hamilton and M. Sharkey (BRI) for reviewing the manuscript, and members of my Ph. D. examining committee, G. E. Ball, W. G. Evans and J. G. Packer (UAE).

Chapter 5: I am grateful to the curators of collections listed in the "materials" section for loan of specimens, and to T. Tachikawa, Ent. Lab. Ehime Univ., Matsuyama, Japan, and J. Noyes, British Museum (Nat. Hist.), London, England, for the gift of some specimens required for dissection and SEM. I also thank the many curators and other personnel of museums who allowed me to examine collections under their care, and showed many other kindnesses during a nine week trip through western Europe in 1984. I would particularly like to thank Z. Bouček, Commonwealth Inst. Ent., London, England, for the stimulating lunch-hour discussions about eupelmids during my three weeks at the British Museum (Nat. Hist.), and for letting me examine specimens collected and identified by him as belonging to the type species of eupelmid genera described from Australia by A. A. Girault. G. D. Braybrook, Univ. Alberta, Edmonton, assisted in SEM photography of specimens, and H. E. Bisdee, Biosystematics Research Inst., Ottawa, Ontario, assisted in preparation of the illustratory material. I also thank the members of my Ph.D. examining committee, who reviewed a version of this manuscript and offered helpful suggestions: G. E. Ball and W. G. Evans, Dept. Ent., Univ. Alberta; J. G. Packer, Dept. Botany, Univ. Alberta; and N. F. Johnson, Dept. Ent., Ohio State Univ.

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1. INTRODUCTION

Higher classification of the superfamily Chalcidoidea (Hymenoptera: Terebrantes) is acknowledged to be "in a state of confusion" (Heraty and Darling 1984, p. 309). Chalcidoidea was the only superfamily of Apocrita for which Rasnitsyn (1980) did not hypothesize family-level relationships, stating that "The lack of data pertaining to the group discussed compels us to abandon any attempt at analyzing phylogenetic relationships within the superfamily..." (Rasnitsyn 1980, p. 99). Monophyly of Chalcidoidea itself is not documented, and there is disagreement about both the groundplan states and limits of the superfamily (*cf.* Königsmann 1978; Rasnitsyn 1980). Higher classification in the superfamily is also chaotic, with anywhere from nine (Riek 1970) to twenty-one (Peck 1963) families recognized, and a new classification proposed with each new catalog or major publication about chalcidoids (*cf.* Nikolskaya 1952, Peck 1963, Peck *et al.* 1964, Graham 1969, Riek 1970, Gordh 1979, Yoshimoto 1984).

Inconsistency of chalcidoid familial classification results partly because classifications are based on external structural features of adults, and adult chalcidoids are exceedingly plastic in external structure (Gordh 1979). Characters that are used to delimit higher taxa may work well for only one sex, and generally characters are not disjunctive, *i. e.*, they intergrade, and appear to "crop up from time to time where least expected" (Grissell 1980, p. 3). Disparate classifications also partly reflect differences of opinion about the significance of states used to differentiate or to associate members of higher taxa. For the most part, such differences of opinion result from a lack of critical evaluation of the level of apomorphy of states, *i. e.*, whether states are autapomorphic, synapomorphic, symplesiomorphic, or homoplasous.

The family Eupelmidae illustrates many of the problems inherent in present-day classifications of Chalcidoidea. The "family" is distinguished as a higher-level taxon primarily on basis of a number of striking mesothoracic characters that differentiate most members from most other chalcidoids. However, males of species assigned to the subfamily Eupelminae lack the distinguishing characters of the family, and are superficially indistinguishable from some chalcidoids assigned to the family Pteromalidae. On the other hand, female eupelmines not only share the primary distinguishing characters of the family with males and females of other "eupelmids", but in various combinations also with members of some other family-level taxa, such as encyrtids and some aphelinids. Consequently, in some classifications eupelmids are recognized as a family-level taxon [with tanaostigmatines included, or segregated as a separate family (*e. g.*, LaSalle 1984)], but in others are included as a subfamily of Encyrtidae (*e. g.*, Riek 1970), though Graham (1969, p. 7) suggested that Eupelmidae might be united with Pteromalidae for "a more mature classification" of Chalcidoidea.

The intent of this thesis is to investigate phylogenetics and classification of "eupelmids". However, it is my belief that accurate phylogenetics and stable classifications of taxa can not be obtained merely by study of character-state distribution in the taxa under consideration. In Hymenoptera, descriptions of character states and their distribution have been made over an extended period by innumerable individuals. Different descriptions and interpretations of structure, different terms for structure, and misidentifications of taxa have resulted in an accumulation of errors. Studies that rely on *a priori* hypotheses of character-state homology and distribution, or that ignore incongruencies in the literature, at whatever level, perpetuate and thereby further validate inaccuracies. I also believe that detailed analysis of the distribution, structure, and function of characters is necessary for rigorous phylogenetic studies. Detailed character-state analysis is required to differentiate homology (symplesiomorphy and synapomorphy) from homoplasy, to determine the number of series involved in and polarity of character transformations, and to determine the relationships between characters, *i. e.*, whether characters are independent or form functional complexes. I attempt to investigate phylogenetics of eupelmids using these principles. Consequently, this thesis is not concerned primarily with hypotheses of eupelmid relationships, but in justifying hypotheses, whether these are explicitly stated, or implicit in nomenclature and terms used. Because eupelmids are accorded higher-level status in Chalcidoidea mainly on basis of mesothoracic structure, particular emphasis is placed on studies of comparative and functional morphology of the mesothorax.

In chapter two of this thesis, selected external and internal mesosomal structures are compared throughout Hymenoptera in order to establish homology, probable groundplan states for Chalcidoidea, and correct use of terms. More diverse characters are analyzed in chapter three for evidence of monophyly of Chalcidoidea, in order to establish limits and probable groundplan states for the superfamily. In chapter four, mesothoracic skeletomusculature of eupelmids and other chalcidoids is studied in detail. External structure is correlated with placement and form of muscles in order to establish homology and standardize use of terms in the superfamily, and structure is correlated with function to determine functional complexes and establish why eupelmids are structured as they are. In chapter five I revise the genera of the world for two eupelmid subfamilies, Metapelmatinae and Calosotinae, and use data from this and the previous three studies to analyze subfamilial and familial relationships of Eupelmidae.

Information derived from the studies written as chapters 2-4 of this thesis was required to document the revisionary and phylogenetic studies of Eupelmidae written as chapter five. However, the former studies have additional, broader implications for systematics and comparative morphology of Hymenoptera. Because the individual studies are very diverse, each is written as a separate paper for publication. Style conforms to that of "The Canadian Entomologist", except for modifications required to conform to regulations (revised April 1985) of the Faculty of Graduate Studies and Research, University of Alberta.

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2. SOME PRO- AND MESOTHORACIC STRUCTURES IMPORTANT FOR PHYLOGENETIC ANALYSIS OF HYMENOPTERA, WITH A REVIEW OF TERMS USED FOR THE STRUCTURES[1]

2.1 Synopsis

The character-state distribution of various external and internal pro- and mesothoracic structures of Hymenoptera is described. Structures discussed are the transscutal articulation, axillae, notauli, median mesoscutal sulcus, parapsidal lines, pronotal lobe, postspiracular sclerite, prepectus, netrion, epicnemium, basalare, pronotal-mesothoracic attachment mechanism and two mesothoracic muscles, *viz.*, mesotrochanteral depressor and second-phragmal flexor. Ancestral state and transformation of the characters are hypothesized, and shared derived states of higher taxa are determined. Hypotheses of synapomorphy are based on the shared derived states, and these hypotheses used to test previous hypotheses of relationship and classification. Relationships of Symphyta to Apocrita and of Aculeata to Terebrantes are discussed, and various aspects of classification of Symphyta and Terebrantes are examined. Finally, prior use of terms is reviewed for the thoracic structures studied. A single set of terms is selected for use throughout the order based on original use of each term and on hypotheses of homology.

2.2 Introduction

Separate studies of systematics and morphology of Chalcidoidea include analysis of various thoracic characters. Most of the characters either had been discussed in recent phylogenetic treatments of Hymenoptera (*e. g.* Brothers 1975; Königsmann 1977, 1978a, b; Rasnitsyn 1980), or in recent comparative studies of morphology (*e. g.* Daly 1963; Shcherbakov

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[1] A version of this chapter has been accepted for publication in The Canadian Entomologist.

1980, 1981; Saini 1983). However, these works show some discrepancies in character states attributed to higher taxa, in interpretation of homology, and in terms used for structures. Furthermore, character states were unknown for a number of higher taxa, particularly in parasitic Hymenoptera (Terebrantes). It was therefore necessary to more accurately determine the distribution and homology of the character states before these could be assessed as phylogenetic indicators for Chalcidoidea.

The primary purpose of this paper is to describe the various states of the thoracic characters studied, and based on distribution of the states to propose probable transformation series, homologies, and phyletic relationships of taxa. Particular emphasis is placed on character-state distribution and transformation within Symphyta and Terebrantes. Survey of the large and diverse infraorder Aculeata is more superficial, the taxa examined primarily to help determine probable ancestral states for Apocrita.

Proposed relationships are based on hypothesized derived states shared by taxa, but it should be emphasized that such states can be the result of inheritance from a common ancestor (synapomorphy), or due to independent derivation (homoplasy). Because hypotheses of synapomorphy and homoplasy are made partly on the basis of congruence of character-state transformations using the principle of parsimony, such hypotheses should ideally be made only after a detailed analysis of as many characters as possible. Only a few characters are studied in this paper and proposed hypotheses of synapomorphy and relationship must be tested by congruence of other character states. Furthermore, generalizations about character-state distribution at the family level are based on relatively few taxa. This is inevitable due to the scope of the investigation, plus the rarity of representatives of some taxa or specimens suitably preserved for internal examination. I hope that the above-stated weaknesses of this paper will not lead to acceptance of inadequately proven generalizations and hypotheses, but will stimulate examination and description of characters in additional taxa.

The second purpose of this paper is to correct and standardize the present inconsistent and multiple use of morphological terms for the structures studied. A single set of terms representing homologous structures is essential to facilitate communication and understanding of the evolution of the order. Terms used by previous workers are reviewed and a single set is proposed for use throughout the order from those available.

2.3 Materials and methods

2.3.1 Materials

Because reduction or loss of wings is often reflected in a highly modified thorax (Reid 1941), only alates were dissected, unless noted otherwise in the text. Representatives of taxa dissected for the presence and state of muscles discussed under character 5 are listed in appendix 3.

Ethanol-preserved specimens were used for dissections, except for representatives of those taxa denoted by an asterisk in appendix 3. The latter specimens had been dry mounted, but were rehydrated for dissection by immersion into equal parts of water and concentrated ammonium-hydroxide solution until the pronotum could be easily removed and internal muscles were flexible. The period of immersion varied because muscles detached from the cuticle during dissection if not hydrated sufficiently, but became an amorphous mass if excessively hydrated. All dissections were made in 70% ethanol and remaining parts are in the author's collection. Dissected parts used for scanning electron microscopy (SEM) were dehydrated through 98% ethanol and critical-point dried to avoid shrinkage of muscles. Extraneous internal tissue, such as connective tissue, trachea, and dried haemolymph was removed from dried specimens using pins and commerically available double-sided sticky tape for SEM stubs. Pins were scratched across the surface of the sticky tape to pick up a small amount of adhesive on the tip, and this was then used to pick out the extraneous tissue without disturbing the structures to be viewed. Specimens were gold coated with a sputter coater and photographed with a Cambridge Stereoscan 250 scanning electron microscope.

2.3.2 Classification

The higher classification of Hymenoptera is not stable and various classifications have been proposed in recent years (*cf.* Königsmann 1977, 1978a, b; Krombein *et al.* 1979; Rasnitsyn 1980). Symphyta and Aculeata are classified here following Rasnitsyn (1980), except that Orussoidea is assigned to Symphyta and the superfamily Apoidea is recognized within Aculeata. Proposed classifications of Terebrantes are not used because of existing confusion that is the result of disagreements as to validity and membership of most of the proposed superfamilies. Only four terebrant superfamilies are referred to in this paper, *viz.*, Ichneumonoidea (Paxylommatidae, Braconidae and Ichneumonidae), Cynipoidea and Ceraphronoidea (*sensu* Krombein *et al.* 1979), and Chalcidoidea (*sensu* Peck *et al.* 1964). Other proposed superfamilies, such as Diaprioidea, Evanioidea, Megalyroidea, Pelecinoidea, Proctotrupoidea, and Trigonaloidea are not discussed; rather, the individual families are treated separately. Classification followed is reflected by the taxa listed in appendix 3.

2.3.3 Terms

Selection of terms for external structures is based on hypotheses of homology and on the original meaning of each term. In the interests of stability common usage rather than priority was used to select between competing terms. Accepted terms are printed in bold face where they are first defined or used, and known synonyms are either listed with the accepted term or discussed in the respective section on terms. Terms that are often confused or not commonly used are listed alphabetically and are defined in appendix 1. Abbreviations used for illustrated structures are given in bold face in the text, and listed in appendix 2.

Endoskeletal ridges or plates of the tergum are termed phragmata, whereas those of the pleuron are termed apodemes; designation of mesothoracic muscles follows Daly (1963, 1964); designation of parts of the mesofurca follows Duncan (1939, figs. 88, 92); and the terms "suture", "articulation", "line" and "sulcus" follow Daly (1964). "Suture" is restricted to regions believed to represent the union of formerly separate sclerites; "articulation" is used as a replacement word for suture where a line of flexibility is involved; "line" is used for linear marks that are not invaginated internally as a ridge; and "sulcus" is used for a groove or furrow that is external evidence of an internally invaginated ridge. The latter terms are used more or less interchangeably at present but restricting their definition as proposed by Daly (1964) makes communication of actual structure more precise.

2.4 Character systems

2.4.1 Transscutal articulation and axillae

Most Symphyta have the **mesonotum** composed of a single sclerite that is differentiated into a posterior **scutellum** (scl) and an anterior **mesoscutum** by a variedly prominent **scutoscutellar sulcus** (sss) (Figs. 2.1, 2.2). However, some symphytes also have a transverse line of flexibility across the mesonotum at about the level of the base of the fore wings. This transverse line of flexibility, the **transscutal articulation** (**tsa**, Figs. 2.3, 2.4), divides the mesonotum into two sclerites. Snodgrass (1910) showed through comparative studies that the transscutal articulation subdivides the mesoscutum, as its name implies, so that the sclerite behind the articulation is composed of both the scutellum and a posterior part of the mesoscutum. The mesoscutal regions segregated posterior to the transscutal articulation are the **axillae** (**das** + **las**, Figs. 2.3, 2.5), and the composite structure is the **scutellar-axillar complex**.

There are discrepancies as to which symphytes the transscutal articulation is stated to be present in. Ross (1937) noted that xiphydriids and orussids differ from typical symphytes in having a transscutal articulation (transverse suture *sensu* Ross). He further stated that the mesoscutum of siricids is "divided by diagonal, wide, trench-like sutures into an anterior sclerite and two posterolateral sclerites", which he alternately referred to as the **parascutal lobes** (**psl**, Fig. 2.2) and "lobes of the mesoscutum" (Ross, 1937, p.26). Rasnitsyn (1980) stated that siricids, xiphydriids, and orussids all have a transscutal articulation, and Richards (1956b, fig. 29) illustrated an articulation (scutal suture *sensu* Richards) for *Cephus cultratus* Eversmann, as did Saini (1983, fig.7) for *Cephus cinctus* Norton (Cephidae). Individuals of Cephidae (Fig. 2.1) and Siricidae (Fig. 2.2) do **not** have a transscutal articulation. Xiphydriids and orussids are the only symphytes having a transscutal articulation (**tsa**, Figs. 2.3, 2.4), with the articulation being incomplete laterally in many xiphydriids (Fig. 2.3).

Most Apocrita also have a transscutal articulation. Absence is commonly correlated with aptery (Reid 1941), but otherwise only individuals of Proctotrupidae, some Cynipoidea, and many Ichneumonoidea (Terebrantes) lack or have an incomplete transscutal articulation. However, the articulation is visible at the extreme lateral edges of the mesoscutum in some proctotrupids (**tsa**, Fig. 2.7), and when incomplete is visible laterally in cynipoids and medially in many ichneumonoids.

Orussids and xiphydriids are the only symphytes having axillae, because these are a secondary result of presence of the transscutal articulation. The dorsal axillar surfaces (**das**) are large and contiguous in individuals of both families (Figs. 2.3, 2.4), and they are distinct even in xiphydriids without a complete transscutal articulation because the articulation is extended laterally as a line of finer sculpture (Fig. 2.3). Size and shape of the axillae are extremely varied in Apocrita, and what constitutes conspicuous or well-defined regions is subjective. Apocritans with relatively large axillae are given in the section on phylogenetic implications, as is an hypothesis of correlation between axillar size and presence of muscles originating from the axillae.

2.4.1.1 Phylogenetic implications

Ross (1937) and Rasnitsyn (1969) considered the transscutal articulation and axillae of xiphydriids and orussids to be homologous with the oblique mesoscutal grooves and parascutal lobes, respectively, of siricids. Based on his ideas of evolution of Symphyta, Rasnitsyn (1969) also hypothesized that the mesoscutal structure described above for siricids (Fig. 2.2) was secondarily derived from the mesoscutal structure characteristic of xiphydriids (Fig. 2.3). I consider this unlikely. I also consider it unlikely that the oblique mesoscutal grooves of siricids are an incipient stage in the evolution of a transverse transscutal articulation, *i. e.*, that the articulation was derived by 'straightening' primitively oblique grooves across the mesoscutum (*c.f.* Figs. 2.2, 2.4). I consider it more probable that the two mesoscutal structures are independently derived, and consequently interpret the parascutal lobes, delineated by oblique mesoscutal grooves, as an autapomorphy of Siricidae. This is evidence of monophyly of the family, but not of a relationship with Xiphydriidae or Orussidae.

Ross (1937) considered Braconidae (Ichneumonoidea) to be the most primitive family of Apocrita. Because he also thought braconids lack a transscutal articulation, he concluded the articulation of apocritans evolved independently from that of xiphydriids and orussids. However, numerous braconids have a partial or complete transscutal articulation. According to C. van Achterberg (pers. comm.), species that are considered to belong to basal groups of Braconidae commonly have a transscutal articulation, whereas there is a tendency for the articulation to be absent in species belonging to terminal groups. Some Ichneumonidae also have a partial or complete transscutal articulation, though the articulation is absent from individuals of *Hybrizon* Fallén (Paxylommatidae). I interpret this character-state distribution as evidence that the transscutal articulation is a groundplan (plesiomorphic) character of Ichneumonoidea, and that the articulation is prone to loss in members of this superfamily.

Absence of the transscutal articulation from proctotrupids and some cynipoids is also indicated to be the result of secondary loss, because most cynipoids have a complete articulation and the articulation is present laterally in some proctotrupids. Thus, the most parsimonious explanation for distribution of the transscutal articulation in Hymenoptera is that the articulation was derived in the common ancestor of Xiphydriidae + Orussidae + Apocrita, and that it was secondarily lost in the common ancestor of Proctotrupidae, and an unknown number of independent times in Cynipoidea, Ichneumonoidea, and various apterous apocritans.

The above hypothesis is based on distribution of the transscutal articulation in extant hymenopterans. Studies of fossil hymenopterans may provide supportive evidence. Rasnitsyn (1980) considered that the extinct taxa Karatavitidae and Ephialtitidae represent the most primitive Apocrita. Illustrations of fossils by Rasnitsyn (1975, 1980) show that representatives of both families had a transscutal articulation and distinct axillae. If Rasnitsyn (1980) is correct that karatavitids and ephialtitids represent the ancestors of all extant apocritans, then absence of a transscutal articulation in some of these must be secondary.

The hypotheses made above may also be supported by studies of functional morphology. The transscutal articulation is an important component of the structural basis for flight. The line of flexibility functions like a hinge so that the mesoscutum and scutellar-axillar complex flex relative to one another with alternate contraction of the indirect flight muscles. Flexing produces rocking movements of the anterior and posterior notal wing processes, which are transmitted through the axillary sclerites to the base of the fore wings to produce the correct wings movements necessary for flight (see Pringle 1957, Matsuda 1970). According to Weber (1925), the fourth axillary sclerite is situated closer to the lower end of the first axillary sclerite in individuals with a transscutal articulation, and shape of the first axillary sclerite and articulation of this with the mesonotum differs between individuals with and those without a transscutal articulation. If absence of the transscutal articulation from proctotrupids and various cynipoids and ichneumonoids is secondary, their flight mechanism should be like other apocritans with a transscutal articulation. Similarly, siricids should have a flight mechanism like other symphytes without a transscutal articulation if their mesoscutal structure is not an intermediate stage in the evolution of the mesoscutal structure characteristic of xiphydriids, orussids and most apocritans.

As previously noted, large and contiguous dorsal axillar surfaces (**das**) are characteristic of symphytes with a transscutal articulation [Xiphydriidae (Fig. 2.3) and Orussidae (Fig. 2.4)]. Xiphydriids have a single muscle, **t_2-2ph** (Fig. 2.39), originating from a relatively small part of each axilla. T_2-2ph is absent from orussids, but in other symphytes it originates from the mesoscutum lateral to the scutellum in positions homologous with the axillae. Character-state distribution in Apocrita indicates that a second muscle, **t_2-tr_2** (Fig. 2.39), was partly transferred to the axilla from the mesoscutum in the ancestor of extant apocritans, so that this ancestor had both t_2-tr_2 and t_2-2ph originating from the axilla (see character 5a for justification). Extant terebrants having both t_2-2ph and t_2-tr_2, or those having only t_2-tr_2 as a large muscle from the axilla [Stephanidae (Fig. 2.41), Megalyridae (Fig. 2.44), Ceraphronoidea (Fig. 2.43) and most Chalcidoidea (Fig. 2.45)] have large and typically contiguous dorsal axillar surfaces (**das**, Figs. 2.6, 2.8). Individuals of Diapriidae (except for those of Ismarinae) have both muscles (**t_2-2ph**, **t_2-tr_2**, Fig. 2.42), but are an exception to the above in having typically small and widely separate axillae. At least some Formicidae (Aculeata) also have t_2-tr_2 (Fig. 2.46) and large and contiguous axillae, though size of these is highly varied in members of this family. Monomachidae, Cynipoidea and Vanhorniidae (Terebrantes) have t_2-2ph only, and the axillae are large and contiguous in monomachids and many cynipoids. Other apocritans lack muscles originating from the axillae and these are typically small and widely separate, though the axillae are relatively large in members of a few taxa [*e. g.* Pelecinidae (Terebrantes)].

I interpret the above-described character states as evidence that large and contiguous axillae arose primarily as a consequence of the origin of the transscutal articulation. I further conclude that such axillae are plesiomorphic for Apocrita, and that in the ancestor of extant apocritans the axillae secondarily acquired functional significance as major sites of muscle attachment. I suggest that most extant apocritans with small axillae descended from ancestors that had secondarily lost the axillar muscles, and consequently the selection pressure to retain the axillae as large and well-delineated regions disappeared. I thus consider there to be limited phylogenetic value in size of the axillae. Large and contiguous axillae is the hypothesized plesiomorphic state for Apocrita, and thus not evidence of monophyly or of relationships between taxa sharing this state. Small axillae are considered as apomorphic, but this state is usually correlated with a loss of muscles that likely happened a number of times (see further under character 5).

2.4.1.2 Terms

Synonyms of the transscutal articulation include scutoscutellar suture *sensu* Snodgrass (1910), transverse suture (Ross 1937), scutal suture (Richards 1956b) and notal suture (Pringle 1957). Snodgrass (1910) first used "scutoscutellar suture" in a dual sense. In symphytes without a transscutal articulation he used the term as now interpreted, and for the mesoscutal cuticular bend (Fig. 2.1) that is homologous with the axillar carina (axc, Fig. 2.3) in hymenopterans with a transscutal articulation. He also used the term to designate the transscutal articulation in hymenopterans having this articulation. Snodgrass later clarified scutoscutellar suture by restricting it to the sulcus that separates the scutellum from the mesoscutum, and originating the new term "transscutal suture" for the mesothoracic articulation as now interpreted. Most authors have followed Snodgrass' usage since 1935 and his terms are accepted here, except that they are modified in accordance with Daly (1964) for the reasons given under materials and methods.

"Axillae" was originated by Thomson (1876) for triangular regions lateral to the scutellum in *Pteromalus* Svederus (Chalcidoidea) *sensu* Thomson. Though different terms are used to denote homologous regions in the recent papers of Middlekauff (1983), Saini *et al.* (1982), and Saini (1983), all other modern works employ Thomson's term and it is accepted here. There are, however, numerous synonyms of axilla, plus additional terms for either the lateral surface of the axilla or the homologous region of the mesoscutum in symphytes without a transscutal articulation. These synonyms include mesothoracic parapteron *sensu* MacLeay (1830); proscutellum (Escherich 1906); juxtascutellum (Crampton 1914a); prescutellum and parascutellum (Crampton 1914b); parascutellum *sensu* Bird (1926); postmesoscutum and posterior alar plate (Bucher 1948); parapsides *sensu* Arora (1953), Bracken (1961) and Wong (1963); postalar plate (Grissell 1983); posterior notal wing process *sensu* Ulenberg (1983); and posterolateral lobe (Saini *et al.* 1982). This large number of synonyms is largely the result of confusion as to exact axillar homology. In order to clarify previously proposed terms, and in an attempt to forestall additional terms from being proposed in the future, homology of the axilla and previous use of terms are discussed below.

MacLeay's use of "parapteron" for the axilla of *Polistes billardieri* Fab. [= *P. crinitus* (Felton)] (Vespoidea: Vespidae) has priority over Thomson's term, but as pointed out by Crampton (1914b) it is an incorrect use of a term originated by Audouin (1824). Thomson's term was unknown to Crampton and he (1914b) originated "parascutellum" as a replacement for parapteron *sensu* MacLeay. Crampton failed to realize though that the more vertical axilla of *Polistes* is homologous with the horizontal region he himself termed the "prescutellum" in Formicidae and in Xiphydriidae (Crampton 1914b, fig. 6), and of the region he had earlier (1914a) termed the "juxtascutellum". "Axilla", "juxtascutellum", "prescutellum", and "parascutellum" are thus all synonyms. Unfortunately, some authors subsequent to Crampton also used parascutellum to designate the axilla, or some other mesothoracic region. Salmon (1929) used parascutellum to denote the axilla in a morphological study of *Pepsis elegans* Lepeletier (Pompiloidea: Pompilidae), as did Tulloch (1925) in a comparative study of the thorax of Formicidae, and most recently Middlekauff (1983) in a taxonomic revision of Orussidae. Pratt (1940) used the same term in a study of *Arotes amoenus* Cresson (Ichneumonoidea: Ichneumonidae) to designate a region lateral to the scutellum that is only partly homologous with the axilla, and Grandi (1921), Gordh (1975), and Ulenberg (1983) used parascutellum for a laterally subdelineated region of the scutellum that is not homologous with the axilla. This subdelineated scutellar region was previously termed the **axillula** by Thomson (1876). Finally, Bird (1926) used parascutellum for a region of the mesoscutum in *Hoplocampa halcyon* (Norton) (Symphyta, Tenthredinoidea: Tenthredinidae). In this and other symphytes without a transscutal articulation the mesoscutum is laterally bent posterior to the fore wing base so as to form a more or less declivous region that is obliquely angled from the wing base to the scutellum (Fig. 2.1). It is this posterolateral declivous region that Bird (1926, fig. 19) termed the parascutellum. Ross (1937) alternately termed this region the parascutellum (p. 140) or parascutellar areas (p. 25). More recent studies of symphytes having this mesoscutal structure [*e. g.* Arora 1953 (figs. 8, 10), Bracken 1961 (fig. 16) and Wong 1963 (fig. 11)], term the posterolateral mesoscutal cuticular bend as the "parapsidal furrow" or "suture", and the declivous region lateral to this as the "parapsis" or "parapsides". These are incorrect designations, however, because parapsidal lines are absent from symphytes that lack the transscutal articulation (see further below and under character 2).

The posterolateral declivous mesoscutal region in symphytes without a transscutal articulation, which Bird (1926) called the parascutellum, is homologous with the lateral surface of the axilla in hymenopterans having the transscutal articulation. Origin of the transscutal articulation (**tsa**) between the fore wing bases segregated the posterodorsal horizontal regions of the mesoscutum as the dorsal surfaces of the axillae (**das**), and the posterolateral declivous regions of the mesoscutum as the lateral, vertical sides of the axillae (**las**). The posterolateral cuticular bend in symphytes without a transscutal articulation is thus homologous with the carina (**axc**) that delineates the dorsal and lateral axillar surfaces in most hymenopterans with an articulation (*cf.* Figs. 2.1, 2.3).

Distinct dorsal (**das**) and lateral (**las**) axillar surfaces are evident in xiphydriids (Fig. 2.3), orussids (Fig. 2.4), and apocritans that have the dorsal surfaces large and in a continuous horizontal plane with the scutellum (Figs. 2.6, 2.8). The two axillar surfaces are not conspicuous in many apocritans with small axillae because the dorsal surfaces are not only reduced, they are posteriorly or laterally declined in many taxa. This is illustrated by the axillae of *Polistes* (Vespoidea: Vespidae) (Fig. 2.5). The mesoscutum is convex so that the regions lateral to the parapsidal lines (**pl**), the parapsides (**par**) (see character 2), are highly angled posterolaterally (Fig. 2.5). Though the parapsides are almost vertical, they are a part of the dorsal surface of the mesoscutum because the lateral edge of the mesoscutum is delimited by the **parascutal carina** (psc, Fig. 2.5) *sensu* Tulloch (1935, fig. 1) [= supra alar carina *sensu* Michener (1944, fig. 22)]. Individuals of *Polistes* also have a prominent longitudinal carina on the axilla (**axc**) that is at the same level as the parascutal carina, and which is curved to the posterior notal wing process. This carina undoubtedly represents the lateral extent of the dorsal surface of the axilla so that the region above it represents the true dorsal axillar surface, even though almost entirely vertical (**das**, Fig. 2.5). The axillar structure described by Duncan (1939) for *Vespula pennsylvanica* (Saussure) (Vespoidea: Vespidae) is very similar to that described for *Polistes*, so that the "scutellar pit" *sensu* Duncan (1939, fig. 41: ScuP) is formed by the dorsal axillar surface, which is declined anterior to the "scutellar crest" *sensu* Duncan (figs. 41, 42: ScuSc). Unfortunately, Duncan termed the carina that is continuous from the parascutal carina to the posterior notal wing process, and which represents the division between the dorsal and lateral axillar surfaces, as the "transscutellar carina" (fig. 41: CScu). I reject Duncan's term for the carina because it traverses the axilla and is not part of the scutellum. Other terms that are available to designate the carina are postscutal flange (Bucher 1948, figs. 27, 28), axillary ridge (Tulloch 1935, figs. 1, 3) and axillar carina (Ulenberg 1983, fig. 11a). None of these terms are established in the literature, though Reid (1941) did use Tulloch's term. I suggest **axillar carina** *sensu* Ulenberg (1983) be used for the carina that delineates the dorsal surface of the axilla from the lateral surface. I consider this to be the most appropriate of the available terms because "axillary" should only be used in reference to the axillary sclerites of the wings and "postscutal flange" is not as descriptive.

Dorsal and lateral axillar surfaces are not distinctly delineated if the axillar carina is not developed. However, each surface can be of taxonomic importance if evident. Some authors, particularly those studying Chalcidoidea, have therefore given the lateral axillar surface a separate name. Ulenberg (1983, figs. 3, 11a) most recently termed the lateral surface of the axilla as the "posterior notal wing process", similar to James' (1926, figs. 47, 48) designation of this as the "sclerite of the posterior wing process". The lateral surface of the axilla was also termed the "postalar plate" by Grissell (1983), similar to Bucher's (1948, fig. 27) earlier term of "posterior alar plate". The former three authors used "axilla" for only the dorsal surface of this structure, whereas Bucher (1948) did not use the term and called the dorsal surface of the axilla the "postmesoscutum". Parascutellum *sensu* Bird (1926) has priority of the terms proposed for the lateral axillar surface because the mesoscutal region he designated as this in symphytes is homologous with the lateral axillar surface. However, I reject this term because Crampton (1914b) originated parascutellum for the entire axillar region, even though he undoubtedly did not realize this, and because of the confusion caused by various authors using the same term for different mesoscutal regions. Designation of the lateral axillar surface as the posterior notal wing process by Ulenberg (1983) is also rejected because Snodgrass (1909) originated this term for only the apical process of the plate that articulates with the fourth axillary sclerite, or the third axillary sclerite when the fourth is absent. Consequently, available names for the lateral axillar surface are posterior alar plate *sensu* Bucher (1948) and postalar plate *sensu* G[illegible]ll (1983). These, however, are indifferent terms because they give no indication as to homology or exact position. Furthermore, Bird (1926) first used postalar plate to designate two regions of the mesopostnotum (= postscutellum *sensu* Bird). A special term for the lateral axillar surface, and the posterolateral declivous mesoscutal region of symphytes without a transscutal articulation would be useful for recognition of homology. However, any of the above-proposed terms obscure the fact that the lateral axillar surface is part of the axilla, and if a separate term is used for the lateral axillar surface then one is also required for the dorsal surface so that "axilla" is not used in a dual meaning, *i. e.*, for the entire structure and for only the dorsal surface. To avoid an unnecessary proliferation of terms I consider it better to reject all of the terms proposed for the lateral axillar surface, and propose that the two surfaces simply be called the **dorsal axillar surface** and the **lateral axillar surface**.

2.4.2 Notauli, parapsidal lines and median mesoscutal sulcus

In most Symphyta a triangular region, the **median mesoscutal lobe**, is delineated anteriorly on the mesoscutum by posteriorly convergent **notauli (no)**, and is longitudinally divided by the **median mesoscutal sulcus (mms)** (Fig. 2.1). Both notauli and the median mesoscutal sulcus are external indications of internal phragmata (Wong 1963). The dorsolongitudinal indirect flight muscles originate anteriorly from the **first phragma** *sensu* Michener (1944), and from the median mesoscutal lobe between the notaular phragmata, whereas the dorsoventral indirect flight muscles originate from the **mesoscutal lateral lobes** (= scapulae of some authors) lateral to the notaular phragmata. The spatial relationship between the notauli and the two sets of indirect flight muscles indicates homology of the notauli throughout Hymenoptera. The dorsolongitudinal indirect flight muscles are also segregated into two discrete longitudinal bands by the median mesoscutal phragma.

In Symphyta, the notauli and median mesoscutal sulcus are incomplete or obsolete only in Orussidae (Orussoidea), some Tenthredinoidea [some Nematinae (Tenthredinidae) (Wong 1968), and some Argidae, Pergidae and Cimbicidae (Benson 1938)], and some Siricoidea. Individuals of *Syntexis* Rohwer (Anaxyelidae) and Xiphydriidae (Siricoidea) have the characteristic symphyte structure, except that both notauli (**no**) and the median mesoscutal sulcus (**mms**) extend to the transscutal articulation (**tsa**) in xiphydriids (Fig. 2.3). Siricids lack notauli, and though the median mesoscutal sulcus may be indicated by a line of finer sculpture (Fig. 2.2) the sulcus is developed into a phragma only within the first phragma. Notauli and the median mesoscutal sulcus are also inevident or are indistinct in orussids (Fig. 2.4), but if notauli are present they are largely furrow-like and parallel posteriorly so as to remain widely separate (**no**, Fig. 2.4). Furthermore, the median mesoscutal sulcus is developed only at the anteriormost part of the mesoscutum (**mms**, Fig. 2.4) so that there is only a very short internal phragma.

A longitudinally subdivided median mesoscutal lobe is variously developed in Apocrita. The notauli (**no**) are percurrent (Fig. 2.8) to absent (Fig. 2.7) and convergent to parallel, but in most taxa if the sulci are percurrent they are at least slightly separate at the transscutal articulation. Only individuals of Gasteruptioninae (Gasteruptionidae), some Braconidae and Chalcidoidea (Terebrantes), and some Formicidae (Aculeata) have an entire, triangular, median mesoscutal lobe anterior to the transscutal articulation. Furthermore, a percurrent median mesoscutal sulcus (**mms**), which by definition is invaginated into a phragma, is possessed only by some Stephanidae (Fig. 2.6), Megalyridae, and Ceraphronoidea (Fig. 2.8). Dinapsinae (Megalyridae) have a distinct median mesoscutal sulcus, but Riek (1970) stated that the sulcus is mainly in the large species of *Megalyra* Westwood (Megalyridae: Megalyrinae). Descriptions of Elliott (1922) also indicate that various stephanids lack the median mesoscutal sulcus, as do various ceraphronoids (Dessart 1962). Rasnitsyn (1980) noted that some cynipoids have a median mesoscutal line, but this line is typically developed only towards the posterior of the mesoscutum and is not invaginated into a phragma. In cynipoids such as *Ibalia* Latreille (Ibaliidae), which have a percurrent median groove as deep as the notauli, dissections show the notauli to be invaginated as phragmata, but the median groove to be only a depression. Some chalcidoids (*e. g.* various Eulophidae) have a median mesoscutal line, as do individuals of *Baryconus* Förster and some *Trissolcus* Ashmead (Terebrantes: Scelionidae). Again, these are not invaginated into phragmata. Various aculeates also have a median line that is not invaginated into a phragma. Daly (1964) showed that what superficially appears to be the median mesoscutal sulcus in Apoidea is actually composed of two parallel lines. These **anteroadmedian lines** *sensu* Daly are analogous to parapsidal lines (see below) because they represent initial sites of attachment of muscles in the pharate pupae. The anteroadmedian lines indicate the initial sites of attachment of the dorsolongitudinal flight muscles. The true median mesoscutal sulcus is present only at the anteriormost edge of the mesoscutum and is not clearly defined.

Numerous apocritans also have a second pair of mesoscutal marks, the **parapsidal lines** (**pl**), lateral to the notauli (**no**) (Figs. 2.5, 2.7, 2.8). Parapsidal lines typically extend anteriorly as longitudinal marks from the posterior region of the mesoscutum, and are thus distinguished from notauli (Tulloch 1929). If not so-extended, or if only a single set of mesoscutal marks is present, correct distinction of parapsidal lines from notauli is indicated by the spatial relationship between the marks and the two sets of indirect flight muscles. As previously described, notauli indicate the line of separation between the dorsolongitudinal and dorsoventral indirect flight muscles whether or not they are invaginated as internal phragmata (Michener 1944). Parapsidal lines originate lateral to the median edge of each dorsoventral flight muscle so that they are readily distinguished from notauli if specimens are dissected. Dissections show, for example, that Ritchie and Peters (1981, fig. 11) misinterpreted the mesoscutal lines of *Diplolepis rosae* (L.) (Cynipoidea: Cynipidae). Their "parapsidal furrows" are the notauli, whereas their "notaulix" (*sic*) are the anteroadmedian lines and their "lateral lines" are the parapsidal lines.

Only individuals of Orussidae in Symphyta have linear lateral marks on the mesoscutum that extend anteriorly from the transscutal articulation and are not invaginated as phragmata (**pl**, Fig. 2.4). Crampton (1914b, fig.6) and Tulloch (1929, fig. 1) both stated that indivduals of *Xiphydria* Latreille (Siricoidea: Xiphydriidae) have parapsidal lines, but though there is an elongate region of finer sculpture on each mesoscutal lateral lobe, there is not a 'line' as such (Fig. 2.3). Most genera of Xiphydriinae have variously delineated elongate regions of finer sculpture on the mesoscutal lateral lobes, but the latter are uniformly sculptured in Derecyrtinae (Xiphydriidae). Differentiated regions of finer sculpture are also apparent on the mesoscutal lateral lobes of some Tremecinae (Siricidae).

2.4.2.1 Phylogenetic implications

Notauli are undoubtedly a groundplan character for Hymenoptera and a symplesiomorphic state for Apocrita based on their wide distribution in Apocrita and Symphyta. The same is most likely true for the median mesoscutal sulcus. Though only relatively few extant apocritans have this sulcus (some Stephanidae, Megalyridae and Ceraphronoidea), a median mesoscutal line is evident in fossilized representatives of numerous and diverse Mesozoic apocritan taxa (Rasnitsyn 1975). It can not be proven from fossil impressions that this line was invaginated as a phragma, but if so it indicates that a median mesoscutal sulcus is symplesiomorphic for Apocrita.

Rasnitsyn (1980) hypothesized that Stephanidae repre[illegible] the only extant taxon of the group, Stephanomorpha, which he considers all other Ap[illegible] derived from (excluding Orussoidea by his classification). He also considers Megalyridae to be the most primitive member of a closely related group, Ceraphronoidea *sensu* Rasnitsyn, which also includes Ceraphronoidea (*sensu* present classification) and Trigonalidae. If the median mesoscutal sulcus is a plesiomorphic state for Apocrita, this supports Rasnitsyn's hypothesis that Stephanidae, Megalyridae, and Ceraphronoidea are early apocritan lineages. However, presence is not evidence of monophyly or of relationships between these three taxa. The median mesoscutal sulcus must also have been reduced independently in orussids and most apocritans if this sulcus is a groundplan character of Apocrita, and if Orussidae is the extant sister group of Apocrita as proposed under character 1.

Daly (1964) showed that parapsidal lines of Apoidea represent lines of epidermis to which the dorsoventral indirect flight muscles initially attach to in the pharate pupa. These initial sites remain as vestiges in the adult cuticle even though the muscles have enlarged areas of attachment. He later stated that the various external marks on the mesothorax of apocritans, including parapsidal lines, "are associated with the attachment of fibrillar muscles to the epidermis during metamorphosis" and that "absence of all marks of this kind in most

Chalastogastra (= Symphyta), even though fibrillar muscles are present, must indicate a different kind of morphogenetic relationship between the muscles and the epidermis" (Daly 1965, p. 151). The dorsoventral indirect flight muscles of Siricidae and Cephidae studied by Daly were close-packed, whereas those of the other symphytes studied were fibrillar. Orussids do not have dorsoventral indirect flight muscles, though they do have massive mesotergal-trochanteral muscles (character 5a, Fig. 2.40: t_2-tr_2) that occupy the same region and are anteriorly separated from the dorsolongitudinal indirect flight muscles by notaular phragmata. Unfortunately, these muscles were not examined by Daly (1963) to determine whether they are close-packed or fibrillar. Daly (1963) also did not study the muscles of xiphydriids. Morphogenetic studies are required to determine if the mesoscutal marks of those xiphydriids and siricids that have these, and particularly the mesoscutal lines of orussids develop in the same manner as the parapsidal lines of apocritans. A more comprehensive study of the parapsidal lines is also necessary to determine why these lines are evident in some apocritans and not in others, even in the same family.

2.4.2.2 Terms

Tulloch (1929) clarified use of "parapsidal lines" and "notauli", but recent literature still shows discrepancies in how they are used. Hence, proper use of the terms is again reviewed below.

The term "parapsides" was originated for lateral regions of the mesoscutum by MacLeay (1830). The lines which MacLeay illustrated as mesally delineating the parapsides are thus the "parapsidal lines", though this was not explicitly stated by him. According to Tulloch (1929), "notauli" was originated by Kokouyew (1898) in the sense used in this paper, and is a synonym of "convergent furrows" *sensu* Mayr (1861). Mayr's term never became established in the literature and most subsequent authors used "notauli" for one set of mesoscutal marks and "parapsidal furrows", "sutures", or "lines" for the other set. Exceptions include Arora (1953) and Saini (1983) who used "convergent sutures" for notauli, though Saini used the former term only for the notauli of Symphyta, and used "convergent ridges" and "anterolateral scutal sutures" for the homolgous sulci of various Apocrita. Saini also termed the parapsidal lines of Apocrita as the "posterolateral scutal sulci". Richards (1956b) was a further exception in that he called the notauli the "prescutal sutures". Other authors realized that there was a problem in correct designation of the marks, but attempted to avoid the problem by giving both sets of marks approximately the same name. For example, Weber (1925) called the notauli the "parapsidal grooves" and the parapsidal lines the "secondary parapsidal grooves", and Matsuda (1970) called the notauli the "parapsidal sutures" and the parapsidal lines the "parapsidal furrows".

Though convergent sulci *sensu* Mayr (1861) has priority over notauli *sensu* Kokouyew (1898), and notauli and parapsidal lines have often been confused in the past, the latter two terms are well established in the literature. For this reason I consider that both notauli and parapsidal lines should be retained and used in their original meaning, as established by MacLeay (1830) and Kokouyew (1898), and as distinguished by their spatial relationship with the two sets of indirect flight muscles.

There has also been some confusion as to whether "notaulus" as the singular and "notauli" as the pleural is correct, or whether "notaulix" and "notaulices" respectively are correct. Forbes (1940) discussed the Greek derivation of the term and stated that there is "some slight justification for *notaulus*, none at all for *notaulix*" (p. 137). Hopper (1959) also considered that notaulus and notauli are correct.

2.4.3 Pronotal lobe

A posterolateral region of the pronotum that extends over the anterior of the mesepisternum so as to cover the mesothoracic spiracle, or a **pronotal lobe** (= pronotal tubercle of some authors), is generally regarded to be characteristic of Aculeata. Aculeates have the spiracle at least covered by the pronotal edge, though not by a distinct lobe in all taxa (Brothers

1975, character 21, fig. 13). A pronotal lobe also is possessed by some terebrants, however, as noted by Richards (1971). Individuals of Stephanidae and Gasteruptioninae (Gasteruptionidae) have a pronotal lobe, as do some Aulacinae (Gasteruptionidae) (*e. g.* *Aulacus* Jurine) and Evaniidae. A pronotal lobe also covers the mesothoracic spiracle in all Trigonalidae except *Nomadina* Westwood. Individuals of this latter genus and aulacines without a pronotal lobe (*e. g.* *Pristaulacus* Kieffer) have the spiracle exposed between the pronotum and mesepisternum, whereas evaniids without a pronotal lobe have the spiracle covered by the posterolateral edge of the pronotum. A small lobe of the pronotum also overlies the mesothoracic spiracle in some Ichneumonoidea (**prl?**, Fig. 2.27), but in such instances the lobe is raised so that the spiracle is visible in posterior view.

Most Symphyta have the posterolateral edge of the pronotum straight, or only slightly sinuate so that the spiracle or sclerite covering the spiracular fossa is visible between the pronotum and mesepisternum in at least a posterolateral view (**sp**, Figs. 2.9, 2.11-2.13). Only members of Orussidae have a pronotal lobe. The posteroventral edge of the pronotum is straight and is attached to the anterior mesepisternal edge, but dorsally the pronotum is distinctly protruded as a large lobe (**prl**, Fig. 2.36) that overlies and conceals both the mesothoracic spiracle and anterior mesepisternal edge.

2.4.3.1 Phylogenetic implications

Function of the pronotal lobe is undoubtedly to help regulate gaseous movement, in particular water loss, as well as to prevent foreign material from entering the atrium. Richards (1971) noted that even in symphytes with an exposed spiracle there is a tendency for the posterior edge of the pronotum to be raised so as to partly conceal the spiracle, most conspicuously so in some Tenthredinoidea.

Distribution of the pronotal lobe in Aculeata and Terebrantes indicates that this is a symplesiomorphic state for Apocrita. Because only Orussidae have a definite pronotal lobe in Symphyta, this can be interpreted as a further possible synapomorphy for Orussidae +

Apocrita. I do not know why the pronotal lobe is retained in all aculeates, but was apparently reduced a number of times in terebrants so that in most taxa the spiracle is secondarily reexposed.

2.4.4 Intersegmentalia and mechanism of pronotal-mesepisternal attachment

Crampton (1909) originated **intersegmentalia** as a general term for sclerites positioned in the membrane between segments. There is considerable discrepancy in the literature about Hymenoptera as to homology of the intersegmentalia between the pro- and mesothoracic segments, in what phylogenetic inferences can be derived from their various states, and in what terms are used to designate them. This paper attempts to clarify the discrepancies by describing the structure of the lateral pro- and mesothoracic junction of hymenopterans at the family or superfamily level. The various intersegmentalia or regions discussed include the basalare, postspiracular sclerite, prepectus, netrion and epicnemium. Type of pronotal-mesepisternal attachment and position of the mesothoracic spiracle and spiracular occlusor muscle are also [illegible] in order to justify hypothesized transformation of the sclerites during evolution of the order.

Xyelidae (Symphyta: Xyeloidea) have the mesothoracic spiracle (sp) situated in the membrane between the pro- and mesothoracic segments below the **basalare** (**ba**) and the exposed lateral edge of the mesocutum (Fig. 2.9). The basalare is present in all macropterous hymenopterans and should be considered as present though not described below for all taxa. The mesopleural-basalare muscle inserts into the basalare, and contraction of this muscle pronates the fore wing (Weber 1925). Location of the mesopleural-basalare muscle indicates homology of the basalare in different hymenopterans. A large subtriangular to rectangular sclerite, the **prepectus** (**pre**, Fig. 2.9), is partly inserted into the excised anterior margin of the mesepisternum below the mesothoracic spiracle. The **spiracular occlusor muscle** (*cf.* **om**, Fig. 2.33) originates from the prepectus in most hymenopterans, if the prepectus is present, and inserts into the peritreme of the spiracle. Location of the spiracular occlusor muscle indicates homology of the prepectus in hymenopterans, and probable fate of the prepectus in those that lack the sclerite. Unfortunately, I was unable to confirm presence of a spiracular occlusor muscle in xyelids from the material available for dissection. Unique to xyelids is a depigmented line of weakness on the mesepisternum that is extended posteroventrally from the indentation for the prepectus (Fig. 2.9). This line incompletely segregates the mesepisternum into a smaller dorsal and a larger ventral region.

The intersegmentalia of Megalodonotoidea differ in members of the two extant families. Pamphiliidae lack a prepectus and the spiracular occlusor muscle originates from the anterior margin of the mesepisternum immediately below the ventral margin of the pronotum. There is, however, a small independent sclerite, the **postspiracular sclerite** (*cf.* pss, Fig. 2.10), behind the spiracle and between this and the basalare. Homology of the postspiracular sclerite in hymenopterans is indicated only by its position relative to the spiracle and basalare. Megalodontidae lack the postspiracular sclerite, but they have a tiny, linear prepectus that is externally visible in dried specimens if the posterolateral edge of the pronotum is slightly displaced from the mesepisternum.

Most Tenthredinoidea have a postspiracular sclerite (pss), and many have a prepectus (pre) below the mesothoracic spiracle (sp) (Fig. 2.11). The postspiracular sclerite is typically subtriangular and relatively large, except in most Pergidae. Some pergids have a large postspiracular sclerite (*e. g. Philomastix* Froggatt and *Eurys* Newman), but most either lack this sclerite or have it markedly reduced. The prepectus is extremely varied in tenthredinoids. It is always much smaller than the postspiracular sclerite and is typically exposed and subtriangular when present, but it is absent from some taxa, or may appear to be absent because it is reduced and concealed beneath the posterolateral edge of the pronotum. Many tenthredinoids have the spiracular occlusor muscle originating from a spine-like apodeme, the **occlusor muscle apodeme**, which projects internally from the prepectus. Because of this insertion, the spiracular occlusor muscle typically originates from the prepectus even if it is highly reduced. The muscle originates from both the prepectus and the pronotum in a few taxa, or from only the pronotum if the prepectus is absent. Individuals of Nematinae (Tenthredinidae) have an independent prepectus, or one that is variously fused to the mesepisternum. In the latter instances the spiracular occlusor muscle superficially appears to originate from an apodeme on the anterior margin of the mesepisternum.

Cephoidea have both a postspiracular sclerite and a prepectus. The prepectus (**pre**) is considerably larger than the postspiracular sclerite (**pss**) so as to be conspicuous externally, and it is subtriangular to rhomboidal with the edges attenuate beneath the fore coxae (Fig. 2.10).

The intersegmentalia of *Syntexis* Rohwer (Siricoidea: Anaxyelidae) (Fig. 2.12) are very similar to those described for cephoids. Other Siricoidea (Xiphydriidae and Siricidae) have the prepectus (**pre**) as an elongate and slender sclerite hidden beneath the posterolateral edge of the pronotum (*cf.* Figs. 2.13, 2.14). The spiracular occlusor muscle originates from the prepectus, and not from the mesepisternum as described by Tonapi (1958). Except for members of Tremecinae (Siricidae), xiphydriids and siricids also have an oval to subtriangular postspiracular sclerite (**pss**, Fig. 2.13). Tiny sclerotized regions additionally surround or cover the spiracular atrium in xiphydriids and siricids (Fig. 2.13).

Orussidae (Orussoidea) differ from other symphytes in having the posterolateral edge of the pronotum overlapping the mesepisternum so that the mesothoracic spiracle is not visible. Though the pronotum superficially appears to be rigidly attached to the mesothorax, the two are still quite flexibly united. The only intersegmentalia visible in undissected individuals is the dorsalmost portion of a single sclerite near the base of the fore wing. Removal of the pronotum from specimens of *Orussus* Latreille reveals this sclerite to be an unusually massive, elongate-triangular basalare (**ba**) that is extended from the wing base to the prepectus (**pre**) (Fig. 2.14). Shcherbakov (1981) mistook the former sclerite for the postspiracular sclerite (= basalare 1 *sensu* Shcherbakov), but insertion of the mesopleural-basalare muscle shows it to be the basalare, as does the characteristically shaped pincer-like dorsal edge that articulates with the wing base. I do not know what sclerite Shcherbakov (1981, fig. 8) illustrated as the basalare (= basalare 2 *sensu* Shcherbakov). Individuals of *Orussus* lack a postspiracular sclerite, but the prepectus (pre, Fig. 2.14) is elongate-triangular and is concealed beneath the posterolateral edge of the pronotum. The mesothoracic spiracle (sp, Fig. 2.14) lies anterior to the juncture between the basalare and the prepectus, and the spiracular occlusor muscle arises from the latter sclerite.

The basalare and prepectus are the only intersegmentalia present in Apocrita, and relatively few apocritans have the latter sclerite. Brothers (1975) described the various states of the prepectus found in aculeates. When present, the prepectus is concealed beneath the posterolateral edge of the pronotum, or at least dorsally concealed by the pronotal lobe. Dissections I made revealed an independent prepectus in representatives of Chrysidoidea (Bethylidae, Chrysididae, Dryinidae and Plumariidae) and some Scolioidea (Sierolomorphidae and Tiphiidae). Size, shape, and position of the prepectus relative to the mesothoracic spiracle was extremely varied. In most aculeates the prepectus is extended to the lateral edge of the mesoscutum behind the mesothoracic spiracle (pre, Fig. 2.35), but the prepectus is expanded dorsally in chrysidids so that the spiracle lies in its dorsally concave edge (Brothers 1975, fig. 19, state 29).

Brothers (1975) considered that the prepectus was reduced and hidden beneath the pronotum in Vespoidea [= vespid group *sensu* classification of Brothers (1975, fig. 19, state 29.1.1.1)]. However, I did not find an independent prepectus in representatives of Eumenidae, Vespidae, and Masaridae that I dissected. Brothers (1975) did not state so, but I suspect he interpreted as the prepectus a slender sclerotic strip that is attached to the pronotum behind and above the spiracle (Fig. 2.33). This strip is attached to the pronotum by membrane in some vespoids (*e. g. Polistes* Latreille), but is fused to the pronotum in others (*e. g. Vespula* Thomson) (Fig. 2.33) [see also Duncan (1939, fig. 65)]. The sclerotic strip is an extension of a linear thickening along the posterolateral edge of the pronotum, the **posterior pronotal**

inflection (ppi) *sensu* Duncan (1939) (= intersegmental ridge *sensu* Maki 1938). The spiracular occlusor muscle (**om**) originates from the occlusor muscle apodeme (**oma**) (= attachment peg *sensu* Duncan 1939), which extends from the posterior pronotal inflection below the spiracle (**sp**) (Fig. 2.33), as previously described for *Vespula pennsylvanica* (Saussure) by Duncan (1939). Because the plesiomorphic site of origin of the spiracular occlusor muscle and occlusor muscle apodeme is from the prepectus, I interpret the apodeme, posterior pronotal inflection, and dorsal sclerotic strip to be all remnants of an extremely reduced prepectus that is fused along the posterolateral edge of the pronotum. Condition of the prepectus relative to the pronotum and spiracle in many Tiphiidae supports such an hypothesis. In tiphiids, the internal prepectus is closely associated with the pronotum and is often reduced to a narrow sclerite that is extended to the lateral edge of the mesoscutum behind the spiracle (**pre**, Fig. 2.35). Further reduction and fusion of the prepectus to the inner edge of the pronotum would result in a state similar to that of vespoids. An hypothesis of reduction and fusion of the prepectus to the pronotum is also supported by analagous structures of the pronotum in many terebrants (see below).

The posterior pronotal inflection serves a function in pronotal-mesepisternal attachment in vespoids. Members of this superfamily have the pronotum immoveably associated with the mesothorax. In part this is simply because the pronotal and mesepisternal edges rigidly abut, but also because a rim along the anterior mesepisternal edge fits into the groove formed between the posterior pronotal inflection and the outer posterolateral edge of the pronotum (Fig. 2.33). This tongue-and-groove interlocking mechanism is described in considerably more detail by Duncan (1939).

If the region interpreted as the prepectus in vespoids is truly the degenerate prepectus, then these are the only aculeates to have this sclerite fused to the pronotum. Brothers recorded absence of the prepectus from representatives of Formicidae, Mutillidae, Pompilidae, Scoliidae, and Sphecoidea *sensu* Brothers. He hypothesized that in these the prepectus was fused to the mesepisternum. I dissected representatives of the above taxa to determine site of origin of the spiracular occlusor muscle. Few specimens were dissected for groups as large as encompassed above, but in all instances the occlusor muscle originated from an apodeme (**oma**) on the anterior margin of the mesepisternum below the spiracle (**sp**) (Fig. 2.34a). This was previously reported for *Apis mellifera* L. (Apidae) by Snodgrass (1942), and for *Formica polyctena* Förster (Formicidae) by Märkl (1966). The mesepisternal site of origin for the spiracular occlusor muscle indicates that Brothers' (1975) hypothesis is correct, and that the prepectus is fused with the mesepisternum in the aculeates listed above.

Scoliids are similar to vespoids in having the pronotum immoveably associated with the mesothorax. The pronotal and mesepisternal edges rigidly abut, and individuals of *Scolia bicincta* Fabricius and *Proscolia spectator* Day have an inner groove along the posterolateral pronotal edge, though there is no sclerotic strip behind the spiracle (Fig. 2.34b) as there is in vespoids. The pronotum is ungrooved in specimens of *Campsomeris plumipes confluenta* Say, so that there is no pronotal-mesepisternal interlocking mechanism.

Only members of Chalcidoidea were thought to have an independent prepectus (**pre**, Figs. 2.17, 2.18) in Terebrantes until Rasnitsyn (1980) discovered this sclerite concealed beneath the posterolateral edge of the pronotum in Stephanidae (Fig. 2.16) and Monomachidae (Fig. 2.15). I also found an independent prepectus in individuals of *Ropronia garmani* Ashmead (Roproniidae) and *Austronia nitida* Riek (Austroniidae).

The intersegmentalia of stephanids are very similar to those described for orussids (Symphyta) (*cf.* Figs. 2.14, 2.16). The pronotum is flexibly attached to the mesothorax and the pronotal lobe covers the mesothoracic spiracle and intersegmentalia. The basalare (**ba**) is unusually long and extends from the fore wing base to the mesothoracic spiracle (**sp**), which lies anterior to the junction between the basalare and ventral prepectus (**pre**) (Fig. 2.16). The prepectus is similar to that of orussids except the spiracular occlusor muscle arises on an occlusor muscle apodeme, which is indicated externally on the prepectus by a tiny pit (**inv**, Fig.

2.16).

Individuals of *Monomachus* Klug (Monomachidae) have a considerably smaller basalare than do orussids and stephanids (*cf.* **ba**, Figs. 2.14-2.16). It does not to extend to the spiracle; rather, the prepectus is elongate and extends behind and above the spiracle to the lateral edge of the mesoscutum (**pre**, Fig. 2.15). The ventral edges of the two prepecti approach the midline of the thorax in monomachids and stephanids, but the prepecti remain as independent lateral sclerites.

Size and shape of the prepectus is extremely varied ~~in~~ Chalcidoidea, and in many there is a single semiannular sclerite (**pre**, Fig. 2.18) rather than two separate lateral sclerites. A ventral fusion of the two lateral prepecti otherwise occurs only in some Bethylidae (Aculeata: Chrysidoidea). Chalcidoids are the only apocritans with an independent and externally visible prepectus, at least dorsally adjacent to the lateral edge of the mesoscutum (Fig. 2.17). Eucharitinae (Eucharitidae), most Perilampidae and a few Mymaridae lack an independent prepectus, but this is the result of secondary fusion with the pronotum (as will be justified in a subsequent paper). Position of the mesothoracic spiracle is unique for chalcidoids in Hymenoptera. The spiracle (**sp**) is at the lateral edge of the mesoscutum, at or somewhat anterior to the anterodorsal angle of the prepectus (**pre**) (Fig. 2.17), though this is not always externally evident.

Individuals of *Austronia nitida* Riek (Austroniidae) have the pronotum closely appressed to the mesepisternum, but what appears to be a small prepectus is visible behind and slightly above the mesothoracic spiracle. Unlike chalcidoids, the apparent prepectus is not externally extended to the lateral edge of the mesoscutum because the posterodorsal angle of the pronotum is interposed between the two. Exact state of the prepectus could not be determined because specimens were unavailable for dissection. However, undissected individuals of *A. nitida* are similar in appearance to those of *Ropronia garmani* (Roproniidae), and dissection of specimens of this latter species revealed a small triangular prepectus behind the spiracle (**pre**,

Fig. 2.19). The prepectus is flexibly joined to both the pronotum and mesepisternum, and it is internally extended beneath the posterolateral angle of the pronotum to the lateral edge of the mesoscutum.

The site of origin of the spiracular occlusor muscle and apodeme, and different structures of the pronotum indicate that the prepectus is reduced and fused to the pronotum in most other terebrants. Rasnitsyn (1980) proposed that the prepectus was fused to the pronotum in Proctotrupidae, Pelecinidae, Vanhorniidae, Scelionidae and Platygastridae. Members of these families have an annular pronotum, *i. e.*, a pronotum that is ventrally continuous behind the procoxae to form a complete ring (Figs. 2.22, 2.24). Rasnitsyn hypothesized that this structure resulted from the two lateral prepecti fusing to the pronotum, and to each other along the ventral midline. He also considered external regions of the pronotum to represent additional vestiges of the prepectus in Pelecinidae, Proctotrupidae and Scelionidae

Many scelionids have a row of foveae, or a linear or foveolate sulcus delineating a typically spindle-shaped region on the pronotum below the spiracle (**net**, Fig. 2.23). Rasnitsyn (1980) hypothesized that this region was the fused prepectus, though Masner (1979, figs. 1-32) considered it to be a secondarily delineated region of the pronotum, which he termed the **netrion**. Some Platygastridae also have a posterolateral region of the pronotum delineated by a sulcus below the spiracle (L. Masner, pers. comm.), and Vanhorniidae have a spindle-shaped region delineated by a row of foveae. The row of foveae or sulcus on the pronotum of such individuals indicates an invaginated apodeme along the inner pronotal surface (Fig. 2.24). I do not consider the netrion apodeme as a line of fusion between the pronotum and prepectus; rather, I consider it to be a secondary development that most probably is correlated with an annular pronotum (see section on phylogenetic implications for justification). Consequently, I concur with Masner (1979) that the netrion is not the prepectus fused with the pronotum.

The mesothoracic spiracle (sp) originates from the pronotum in Proctotrupidae (Fig. 2.21) and Pelecinidae, rather than apparently between the pronotum and the mesepisternum as in most other terebrants (Fig. 2.23). Rasnitsyn (1980) concluded that this resulted from fusion of the prepectus with the pronotum behind the spiracle. However, all terebrants except gasteruptionids have the spiracle surrounded by pronotal cuticle, though this is not externally evident in most because of how the pronotum and mesepisternum attach. Megalyridae (Fig. 2.32) and Ceraphronoidea (Figs. 2.29-2.31) are most similar to proctotrupids and pelecinids because the spiracle originates from the pronotum, though inconspicuously so in most Ceraphronidae (Fig. 2.31). Cynipoidea, Diapriidae (Fig. 2.25), Heloridae (Fig. 2.20), Evaniidae, Trigonalidae (Fig. 2.26), Pelecinidae, Proctotrupidae (Fig. 2.22), Vanhorniidae, Scelionidae (Fig. 2.24) and Platygastridae all have the mesothoracic spiracle surrounded internally by pronotal cuticle. The mesothoracic spiracle (sp) is below the lateral edge of the mesoscutum and an internal ridge along the posterolateral edge of the pronotum, the posterior pronotal inflection, extends behind and above the spiracle so that this is entirely surrounded by cuticle (**ppi**, Figs. 2.20, 2.22, 2.24-2.26).

The posterior pronotal inflection and outer posterolateral edge of the pronotum form between them a relatively deep groove, and the anterior edge of the mesepisternum fits into this groove in a rigid tongue-and-groove interlocking mechanism. The spiracular occlusor muscle either originates near the posterolateral edge of the pronotum below the spiracle, or from an apodeme (**oma**, Figs. 2.20b, 2.22, 2.25b) in this same location, except in vanhorniids and many scelionids (see below). A tiny pit (**inv**, Figs. 2.21, 2.22) is externally visible near the posterolateral edge of the pronotum in many taxa, and indicates the invagination for the occlusor muscle apodeme. I did not observe an apodeme for the occlusor muscle in the platygastrids, trigonalids (Fig. 2.26b), or evaniids that I dissected. However, very few representatives of the latter two families were examined. Absence of an occulsor muscle apodeme in platygastrids is more probably because of the very small size of individuals. Absence of the apodeme from small individuals of various terebrant taxa is apparently common. Vanhorniids, and scelionids having both a netrion and an occlusor muscle apodeme are exceptional in having the latter originating from, or anterior to the netrion apodeme (Fig. 2.24), rather than from, or near the posterior pronotal inflection as in other terebrants (Figs. 2.20b, 2.22, 2.25b).

Ichneumonoidea do not have a distinct posterior pronotal inflection. However, the posterolateral edge of the pronotum is somewhat expanded and inflected into the body (Fig. 2.28), and the anterior edge of the mesepisternum abuts against this (*cf.* Figs. 2.27, 2.28a). The posterolateral pronotal edge is also projected into a lobe beneath the mesothoracic spiracle (**sp**) so that this lies in the fork formed between the lobe and the posterodorsal angle of the pronotum (**prl?**) (Figs. 2.27, 2.28a). The lobe is posterodorsally angled behind the spiracle in many ichneumonoids (Fig. 2.28), but the spiracle is not entirely surrounded by pronotal cuticle. The spiracular occlusor muscle originates from either a spine-like apodeme (**oma**, Fig. 2.28b) or a ridge extended from the posterolateral edge of the pronotum. A small pit (**inv**) within or near the suture between the pronotum and mesepisternum is external evidence of this apodeme or ridge (*cf.* Figs. 2.27, 2.28a, b).

Megalyridae and Ceraphronoidea have yet a different pronotal structure from those described above. The mesothoracic spiracle is conspicuous on the pronotum in megalyrids (**sp**, Fig. 2.32a) and dissection of an individual of *Megalyra* Westwood shows that the posterolateral pronotal edge is not modified into a groove (*cf.* Figs. 2.32a, b). Though connected only by membrane, the posterolateral pronotal and anterior mesepisternal edges rigidly abut against each other. I did not find a spiracular occlusor muscle, and there definitely was no apodeme on the inner surface of the pronotum for this muscle (Fig. 2.32b). Alate representatives of Megaspilidae (Ceraphronoidea) have a similar pronotal structure to that described for megalyrids. The mesothoracic spiracle originates from a posterolaterally differentiated region of the pronotum (Figs. 2.29, 2.30a), the posterolateral edge of the pronotum is unmodified, and the pronotal and mesepisternal edges rigidly abut, but are connected only by membrane (*cf.*

Figs. 2.29, 2.30a, b). Alate individuals of Ceraphronidae have this same pronotal structure, except that the pronotal region behind the spiracle is extremely narrow (Fig. 2.31a), and in many taxa is below the plane of the pronotum so that the pronotum and mesepisternum appear to be separated by a very slender groove. Many apterous ceraphronoids differ in having the pronotum laterally fused to the mesepisternum, without a differentiated pronotal region behind the mesothoracic spiracle. The spiracular occlusor muscle originates from either a spine-like or a tubercle-like invagination near the posteroventral edge of the pronotum (**oma**, Figs. 2.30b, 2.31b). This differs from the more medial location of the apodeme in other terebrants (**oma**, Figs. 2.20b, 2.22, 2.24, 2.25b, 2.28b).

Finally, individuals of Gasteruptionidae (Aulacinae and Gasteruptioninae) have neither an independent prepectus or a pronotal region behind the mesothoracic spiracle. The edges of the pronotum and mesepisternum rigidly abut, and the spiracle lies freely between them. The spiracular occlusor muscle originates from the pronotum below the spiracle without the aid of an apodeme.

2.4.4.1 Phylogenetic implications

Shcherbakov (1980, 1981) stated that structure of the pterothoracic pleurosternal region of Xyelidae (Xyeloidea) could be considered as the groundplan model for Hymenoptera. Most hymenopterists would probably agree that extant xyelids retain more plesiomorphic states than other hymenopterans, based on present hypotheses of origin and evolution of the order. However, it can not be proven that all other hymenopterans were derived from an ancestor that had all the character states of modern xyelids. The states described by Shcherbakov (1980, 1981), and those described here for members of Xyelidae can not be considered as groundplan characters of Hymenoptera, *a priori*; rather, each state must be independently justified as a groundplan character.

In Symphyta, a postspiracular sclerite is absent from representatives of Xyelidae (Xyeloidea), Megalodontidae (Megalodontoidea), Orussidae (Orussoidea), and some Pergidae

(Tenthredinoidea) and Siricidae (Siricoidea). Shcherbakov (1980) considered that the dorsal mesepisternal region of xyelids, which is delineated ventrally by the line of weakness extending from the indentation for the prepectus, represents the postspiracular sclerite (= basalar 1 *sensu* Shcherbakov) of other symphytes (*cf.* Figs. 2.9, 2.10). An independent postspiracular sclerite is not a groundplan character of Hymenoptera if he is correct, but could be a synapomorphy for hymenopterans excluding xyelids.

Rasnitsyn (1969, 1980) hypothesized a diphyletic origin from Xyelidae for other Hymenoptera, with the nearest common ancestor of Tenthredinoidea within Macroxyelinae and the nearest common ancestor of all other Hymenoptera within Madygellinae (extinct) or Xyelinae. This hypothesis requires independent origin of the postspiracular sclerite within each lineage if he and Shcherbakov (1980) are both correct. Alternatively, if a postspiracular sclerite is a groundplan character of Hymenoptera and absence is the result of secondary loss in extant xyelids, then loss must have occurred independently in both lineages of Xyelidae for Rasnitsyn's hypothesis to be true. Secondary loss of the postspiracular sclerite is hypothesized below for other taxa, but whether absence from xyelids is primary or secondary it does not support a diphyletic theory of origin of Hymenoptera from Xyelidae.

The number of times loss of the postspiracular sclerite must be hypothesized from Hymenoptera depends on the relationships between the higher taxa. Independent loss from Megalodontidae (Megalodontoidea), Pergidae (Tenthredinoidea) and Tremecinae (Siricoidea: Siricidae) must be minimally hypothesized. A single loss also must be hypothesized for the common ancestor of Orussidae and Apocrita if these are sister taxa, or two independent losses if Cephoidea and Apocrita are sister taxa, as maintained by Königsmann (1977).

Michener (1944) and Shcherbakov (1981) both hypothesized absence of the postspiracular sclerite from apocritans to be the result of fusion of this sclerite with the anterior margin of the mesepisternum. Shcherbakov (1981) additionally interpreted a carina on the mesepisternum of individuals of *Pelecinus* Latreille as evidence of this fusion. However, there is no compelling evidence that the carina represents a line of fusion between two sclerites; rather, absence of the carina from most other apocritans indicates that it is of seco[illegible]rigin in *Pelecinus*. An alternate hypothesis is that the postspiracular sclerite was fuse[illegible]asalare in the common ancestor of Orussidae + Apocrita. This is suggested by the unusually massive and elongate basalare (**ba**) of individuals of *Orussus* (Fig. 2.14), and the elongate basalare of stephanids (Fig. 2.16). Secondary reduction of the fused postspiracular sclerite-basalare would be necessary to explain the smaller basalare of other apocritans (see further below). Another hypothesis for absence of the postspiracular sclerite in orussids and apocritans, other than simple loss, is fusion of the sclerite to the pronotum as the pronotal lobe. None of these hypotheses can be proven at this time.

All symphytes have an independent prepectus, except for pamphiliids (Megalodontoidea) and some tenthredinoids. Because some aculeates and terebrants also have a prepectus, this is indicated to be both a groundplan character of Hymenoptera and a symplesiomorphic state of Apocrita. Members of Xyelidae (Xyeloidea), Cephidae (Cephoidea), and Anaxyelidae (Siricoidea) have the prepectus as a large, flat, rectangular to rhomboidal sclerite that is fully exposed between the pronotum and mesepisternum (**pre**, Figs. 2.9, 2.10, 2.12). I interpret this as the plesiomorphic state for Hymenoptera because it is shared by members of taxa assigned to three different symphyte superfamilies. At least two independent transformation series are required to explain states of the prepectus in other symphytes. Members of Tenthredinoidea and Megalodontoidea lack the prepectus, or have it as a small sclerite. If analysis is based only on this single character, then the minimal hypothesis required is reduction of the prepectus to a tiny sclerite in a common ancestor of both taxa, and further independent reduction in both lineages so that the sclerite is lost in some members of each. A single event is also required to explain states of the prepectus in Siricidae, Xiphyiidridae (Siricoidea), and Orussidae (Orussoidea). The prepectus is relatively large and thick in members of these three taxa, but it is concealed under the posterolateral edge of the pronotum. Except for chalcidoids, all apocritans with an independent prepectus also have this concealed under the pronotum. Some chrysidoids (Aculeata) have the prepectus largely exposed ventrally, but in all instances it is dorsally concealed because the pronotum is extended to the mesepisternum. A concealed prepectus is thus a possible synapomorphy for Siricidae + Xiphydriidae + Orussidae + Apocrita. This hypothesis requires that the prepectus was secondarily reexposed in the common ancestor of Chalcidoidea.

Rasnitsyn (1980) hypothesized that Orussomorpha and Stephanomorpha *sensu* Rasnitsyn (of which only Orussidae and Stephanidae remain extant) are sister taxa, and that all other Apocrita were derived from Stephanomorpha. The similar structure of the intersegmentalia in orussids and stephanids supports an hypothesis that Orussidae is the extant sister group of Apocrita, and that Stephanidae is a basal apocritan lineage, though not necessarily the sister group of all other apocritans. Symphytes with a postspiracular sclerite (**pss**) have this positioned between the basalare (**ba**) and the prepectus (**pre**), with the mesothoracic spiracle (**sp**) at the anterodorsal angle of the prepectus, somewhat below the lateral edge of the mesoscutum (Figs. 2.9-2.12). Individuals of *Orussus* lack the postspiracular sclerite and the elongate basalare extends to the dorsal edge of the prepectus in its place, but relative positions of the other intersegmentalia are unchanged (Fig. 2.14). Stephanids have the same structure of the intersegmentalia as do individuals of *Orussus* (*cf.* Figs. 2.14, 2.16), but other apocritans differ in having the basalare small and in having different states of the prepectus, or different positions of the mesothoracic spiracle, prepectus, or both, relative to the lateral edge of the mesoscutum.

If the intersegmentalia of stephanids represent the plesiomorphic condition of these for apocritans, then the small basalare of other apocritans must be the result of secondary reduction. Alternatively, the similarly elongate basalare of orussids and stephanids could be independently derived. Whichever is true, the common ancestor of Apocrita is indicated to have had an independent prepectus, with the mesothoracic spiracle at the anterodorsal angle of the prepectus, somewhat below and separate from the lateral edge of the mesoscutum. This condition is common to Symphyta (Figs. 2.9-2.14) and Stephanidae (Apocrita) (Fig. 2.16). Different structures of the pronotum, as well as different postions of the prepectus and mesothoracic spiracle relative to the lateral edge of the mesoscutum indicate at least three separate transformation series from this plesiomorphic condition during evolution of Terebrantes. These three transformation series are described below.

The first proposed transformation series is indicated by the autapomorphic pronotal structure of ichneumonoids. I interpret the pronotal lobe beneath the mesothoracic spiracle as the dorsal edge of a degenerate prepectus that is fused to the posterolateral edge of the pronotum as the narrow-inflexed margin (Fig. 2.28). I interpret location of the occlusor muscle apodeme between the inflexed pronotal margin and outer pronotal surface as evidence for this hypothesis (*cf.* **inv**, Fig. 2.28a and **oma**, Fig. 2.28b). Because the spiracle is separated from the lateral edge of the mesoscutum by the posterodorsal angle of the pronotum (**prl?**, Fig. 2.27), in this hypothesized transformation series the prepectus was merely reduced and fused to the pronotum below the mesothoracic spiracle so that this retains its plesiomorphic position relative to both the prepectus (at anterodorsal angle) and mesoscutum (below exposed lateral edge).

The autapomorphic structure described for chalcidoids indicates a second, independent transformation series from the hypothesized plesiomorphic condition of the apocritan intersegmentalia. In this proposed transformation series the prepectus (**pre**) was secondarily exposed, and with the mesothoracic spiracle (**sp**) extended to the lateral edge of the mesoscutum so that the spiracle retains its plesiomorphic position relative to the prepectus, but occupies an apomorphic position relative to the mesoscutum (at the exposed lateral edge) (Fig. 2.17).

Monomachids, roproniids, and austroniids are the only other terebrants with an independent prepectus. Exact state of the prepectus is unknown for austroniids, but in the other two families the prepectus (**pre**) is concealed and extends to the lateral edge of the mesoscutum behind the mesothoracic spiracle (**sp**), which lies below the lateral edge of the mesoscutum (Figs. 2.15, 2.19). Furthermore, Cynipoidea, Diapriidae, Heloridae, Evaniidae, Trigonalidae, Pelecinidae, Proctotrupidae, Vanhorniidae, Scelionidae and Platygastridae have a posterior pronotal inflection behind and above the spiracle to the lateral edge of the mesoscutum (**ppi**, Figs. 2.20a, 2.22, 2.24, 2.25a, 2.26a). I consider that the above taxa represent a third independent transformation series from the hypothesized plesiomorphic condition of the apocritan intersegmentalia. In this proposed transformation series the prepectus was extended behind and above the mesothoracic spiracle to the lateral edge of the mesoscutum, and the prepectus later further reduced and fused along the inner pronotal edge as the posterior pronotal inflection. The mesothoracic spiracle thus retains its plesiomorphic position relative to the mesoscutum, but occupies an apomorphic position relative to the prepectus (below the dorsal edge).

It is probable that megalyrids and ceraphronoids should also be included in the above-hypothesized transformation series. They likewise have the mesothoracic spiracle entirely surrounded by pronotal cuticle (Figs. 2.29-2.32), but differ in having the spiracle externally apparent on the pronotum and lacking a prepectus or posterior pronotal inflection. However, there is a differentiated pronotal region behind the spiracle in ceraphronoids (Figs. 2.29-2.31). I interpret the pronotal structure of megalyrids and ceraphronoids as evidence that a reduced prepectus was subsequently fused to the pronotum after being extended to the lateral edge of the mesoscutum behind the spiracle. The differentiated pronotal region behind the spiracle in ceraphronoids (Figs. 2.29-2.31) may indicate that the prepectus was secondarily exposed prior to fusion with the pronotum. If so, fusion was independent from that in the ten terebrant taxa listed with a posterior pronotal inflection. Alternatively, it is possible that the posteriorly differentiated region of the pronotum in ceraphronoids may have been derived by 'flattening' an ancestral posterior pronotal inflection behind the spiracle. If so, the pronotal structure of ceraphronids (Fig. 2.31) could represent an intermediate stage between the pronotal structure of terebrants with a posterior pronotal inflection (**ppi**, Fig. 2.25), and the pronotal structures of megaspilids (Figs. 2.29, 2.30) and megalyrids (Fig. 2.32). Dissections of other megalyrids are required to confirm absence of a spiracular occlusor muscle apodeme. Absence of this apodeme could indicate that the prepectus was lost without fusion to the pronotum in megalyrids, and the spiracle only secondarily surrounded by pronotal cuticle.

The exact evolutionary sequence that resulted in the pronotal structure of gasteruptionids is likewise uncertain. Gasteruptionids lack both a prepectus and a posterior pronotal inflection. The mesothoracic spiracle lies between the pronotum and mesepisternum below and separate from the lateral edge of the mesoscutum. This structure indicates that the ancestor of gasteruptionids had an independent prepectus, which was subsequently lost without fusion to the pronotum. This could represent an additional independent transformation series from the hypothesized plesiomorphic condition of the apocritan intersegmentalia, or be a part of the proposed transformation series including monomachids, roproniids, and austroniids prior to fusion of the prepectus with the pronotum.

The above-hypothesized transformation series and homology of the prepectus in Terebrantes differs significantly from those proposed by Rasnitsyn (1980). As previously noted, he hypothesized that the annular pronota of Pelecinidae, Proctotrupidae, Vanhorniidae, Scelionidae and Platygastridae were derived through ventral fusion of the two lateral prepecti, and fusion of this with the pronotum. He interpreted the independent prepecti of Monomachidae (**pre**, Fig. 2.15) to represent the plesiomorphic unfused condition; the pronotal structure of *Vanhornia* Crawford (Vanhorniidae), and some Scelionidae such as Caloteleini [Calliscelionini *sensu* Masner (1979)] that have a distinctly delineated netrion (**net**, Fig. 2.23) to represent the primitively fused prepectus; and the pronotal structure Proctotrupidae (Fig. 2.21), Pelecinidae, Platygastridae and most Scelionidae to represent the most apomorphic condition because there is no distinctly defined region on the pronotum that is reminiscent of an independent sclerite.

Rasnitsyn's hypothesis of the netrion being the prepectus fused to the pronotum [illegible] without support. The netrion (**net**) is always below the mesothoracic spiracle (**sp**) (Fi[illegible] except in individuals of *Nixonia* Masner (Scelionidae) (see below). Furthermore, in vanhorniids, and in scelionids with a netrion the spiracular occlusor muscle originates from an apodeme (oma; Fig. 2.24) extending from, or slightly anterior to the netrion apodeme, *i. e.*, the line of fusion hypothesized by Rasnitsyn between the prepectus and pronotum. This is the position that the occlusor muscle apodeme should occupy if the netrion is the fused prepectus. However, it is also the position that might be expected on functional criteria if the netrion is only a secondarily subdelineated region of the pronotum. The mesothoracic spiracle (sp, Fig. 2.24) is anterodorsal to the netrion apodeme, and if the spiracular occlusor muscle is to be unimpeded in action it must also arise on or anterior to the apodeme.

Distribution of states of the netrion in Pelecinidae, Proctotrupidae, Vanhorniidae, Scelionidae and Platygastridae do not support Rasnitsyn's hypothesis. Only a few platygastrids (L. Masner, pers. comm.) and some scelionids have a netrion that is defined by a foveolate or linear sulcus. If this represents the primitively fused state of the prepectus, as proposed by Rasnitsyn (1980), then the line of fusion has been independently obscured in some members of both taxa, and at least once in the remaining three families if they are sister taxa. In Scelionidae, a netrion that is delineated by a linear or foveolate sulcus is present in members of only four of 17 tribes of Scelioninae defined by Masner (1979) (Nixonini, Baryconini, Calliscelionini and Psilanteridini), and though a sulcus, or more rarely a line of foveae delineates the netrion in Teleasinae, the netrion is not distinguished in Telenominae, or is defined only by a row of foveae. Masner (1968) considered the most "plesiomorphic" scelionids to be *Sparasion* Latreille, *Sceliomorpha* Ashmead, *Archaeoteleia* Masner, and *Nixonia* Masner. Individuals of the former three genera have the netrion delineated only by a row of foveae, though those of "the living fossil" *Nixonia* (Masner 1968, p. 632) have the netrion delineated by a sulcus. This sulcus is dorsally extended anterior to the mesothoracic spiracle (Masner 1979, fig. 1), however, and must therefore be secondary feature and not a line of fusion between the prepectus and the pronotum.

Though I agree with Rasnitsyn (1980) that there is a correlation between an annular pronotum and a netrion, I do not consider the netrion or the ventrally continuous part of the pronotum as the fused prepectus. I interpret only the posterior pronotal inflection as vestiges of the degenerate prepectus as hypothesized above. I consider the ventrally continuous pronotum of pelecinids, proctotrupids, vanhorniids, scelionids and platygastrids to be the result of secondary ventral extension and fusion of the pronotum after reduction and fusion of the prepectus with the pronotum as the posterior pronotal inflection. Consequently, I polarize states of the netrion differently than does Rasnitsyn. I consider as plesiomorphic, rather than apomorphic, the pronotum of pelecinids and many proctotrupids that have a short line of foveae delineating a very narrow posteroventral region on the pronotum (Fig. 2.21). I interpret the delineation of a broader, spindle-shape netrion by a row of foveae, by a foveolate sulcus, and by a linear sulcus to be increasingly more apomorphic states.

Daly (1964, p. 67) noted that sulci are lines of support and strength, and appropriately cautions that "sulci may not represent relics of true sutures and should be only cautiously used as boundaries for hypothetical sclerites". Masner (1979) suggested that the netrion apodeme might serve for attachment of muscles, but dissections show this to be inaccurate. I suspect that origin and function of the netrion is somehow related to the ventrally continuous, *i. e.*, annular pronotum, and may simply serve to strengthen the lateral wall of the pronotum.

Brothers (1975, state 29) hypothesized transformation series of the prepectus within Aculeata. I did not study structure of the intersegmentalia in this infraorder comprehensively enough to do likewise. However, except for chrysidids (Chrysidoidea), aculeates with an independent prepectus (pre) have this extended behind and above the mesothoracic spiracle (sp) (Fig. 2.35). More comprehensive studies of the intersegmentalia of aculeates are required to determine if this indicates a relationship with the terebrant taxa having this state, or whether the similar states were independently derived. Similarity between the pronotal structures of vespoids and terebrants with a posterior pronotal inflection is certainly convergent.

Dissections of scoliids and vespoids for state of the intersegmentalia do indicate that Brothers (1975) is incorrect in his hypothesis that an inflexible pronotal-mesothoracic association is a synapomorphy for these two taxa. Rasnitsyn (1980) also questioned Brothers' analysis and considered that the similarities were the result of independent development. Apparent fusion of the prepectus with the pronotum in vespoids, but with the mesepisternum in scoliids supports Rasnitsyn's (1980) view because there appears to be a correlation in Apocrita between presence or absence of an independent prepectus, degree of pronotal mobility relative to the thorax, and shape of the pronotum.

In Terebrantes, members of Stephanidae, Monomachidae, Roproniidae, Austroniidae, and most Chalcidoidea have an independent prepectus. The prepectus (pre) is large and external in most chalcidoids (Figs. 2.17, 2.18), and relatively large though concealed by the pronotum in stephanids (Fig. 2.16) and monomachids (Fig. 2.15). Individuals also have the pronotum relatively long in dorsal view so as to be more or less saddle-like in lateral view (Fig. 2.17), and loosely connected to the mesepisternum so as to be variedly mobile relative to the mesothorax. However, terebrants that lack an independent prepectus have the pronotum dorsally reduced so that in lateral view the pronotum is subtriangular with the posterodorsal angle extended to the tegula (Figs. 2.21, 2.23, 2.27, 2.29). Furthermore, the posterolateral edge of the pronotum is rigidly united to the anterior edge of the mesepisternum, whether or not there is a tongue-and-groove interlocking mechanism, so that the pronotum and thorax are immoveably associated. Roproniids have an independent, small prepectus, and their pronotum is intermediate in both shape and degree of mobility between the two extremes described above.

The correlation between pronotal shape, degree of pronotal mobility, and presence or absence of a prepectus is well-illustrated by different groups of Chalcidoidea. Chalcidoids with an independent prepectus have a more or less saddle-like and mobile pronotum. Eucharitines (Eucharitidae), individuals of *Ptilomymar* Annecke and Doutt (Mymaridae), and most perilampids lack an independent prepectus. They also have the pronotum rigidly associated with the mesepisternum, and individuals of the former two taxa have pronota of the same shape as described for other terebrants lacking a prepectus. The pronotum of perilampids is more saddle-like.

Shape and relative mobility of the pronotum thus appear to be of little value for phylogenetic analysis of Terebrantes. A dorsally elongate (saddle-like) pronotum that is loosely connected to the mesepisternum is correlated with an independent prepectus, whereas a dorsally reduced (triangular in profile) pronotum that is rigidly connected to the mesepisternum is correlated with absence of a prepectus. Because an independent prepectus is symplesiomorpic for Terebrantes, the correlated pronotal structure is undoubtedly also symplesiomorphic and not evidence of monophyly or of relationships between taxa. The dorsally reduced pronotum and rigid pronotal-mesepisternal attachment are apomorphic states in Terebrantes, but similarity in structure is homoplasous in some instances because an independent prepectus was probably lost at least four times during the evolution of the infraorder (loss in gasteruptionids and independent fusion with the pronotum in ichneumonoids, terebrants with a posterior pronotal inflection, and megalyrids and ceraphronoids). Furthermore, it is likely that the prepectus was independently fused to the pronotum more than the three times indicated above.

The pronotum is also more or less saddle-like and mobile in aculeates with an independent prepectus, *i. e.*, known chrysidoids (Bethylidae, Chrysididae, Dryinidae, Plumaridae) and some scolioids (Sierolomorphidae and Tiphiidae). An independent prepectus is absent from other known aculeates, but is indicated to be fused to either the pronotum (Vespoidea) or the mesepisternum (Apoidea, Formicoidea, Pompiloidea, Sphecoidea and some Scoliidae) based on position of the apodeme for the spiracular occlusor muscle. In vespoids, the pronotum is dorsally reduced so that it is triangular in lateral view, and rigidly associated with the mesepisternum, *i. e*, of the same structure as the pronota of terebrants lacking a prepectus. Shape and degree of pronotal mobility is highly varied in aculeates having the prepectus fused with the mesepisternum. For example, pompilids and some formicids have the pronotum saddle-like and mobile, whereas scoliids and other formicids have a pronotal structure similar to vespoids.

Variation in shape and in degree of pronotal mobility in aculeates having the prepectus fused with the mesepisternum does not affect the conclusion that the common ancestor of Vespoidea [vespid group *sensu* Brothers (1975)] and Scoliidae must have had a saddle-like and mobile pronotum if they are sister groups. Because the prepectus is apparently fused to the pronotum in vespoids, but to the mesepisternum in scoliids, any common ancestor must have had an independent prepectus. Consequently, a mobile pronotum must be assumed for the common ancestor, because all extant aculeates with an independent prepectus have a mobile pronotum. The immoveably associated pronotum and mesothorax of vespoids and scoliids must therefore be the result of convergence, and can not be considered as a synapomorphy for the two taxa.

I suspect that pronotal shape and rigid attachment of the pronotum to the mesepisternum in vespoids is a functional consequence of fusion of the prepectus with the pronotum. This is indicated by the similar pronotal structure of terebrants having the prepectus fused with the pronotum. I do not know why scoliids, which have the prepectus fused to the mesepisternum, have a similarly structured pronotum. It is possible that this is a secondary modification related to fossorial habits because many ants have a similar pronotal structure, or an adaptation for searching for prey in concealed situations. Greater structural thoracic strength imparted by a rigid association of the pronotum and mesepisternum may be beneficial for these habits.

2.4.4.2 Terms

There is possibly more discrepancy in terms used for the intersegmentalia between the pro- and mesothoracic segments than for any other body region. These discrepancies are partly because of inaccurate recognition of homology and partly because different authors use different terms for the same structures.

Snodgrass (1910) originated "prepectus", but initially used the term to designate two different structures. He termed as the prepectus the independent sclerite between the pronotum and mesepisternum in chalcidoids, and an anterior region of the mesepisternum in various ichneumonoids that is delineated by a carina or sulcus. Snodgrass considered the independent sclerite of chalcidoids to be derived from the anterior parts of both the mesepisternum and mesosternum (mesopectus *sensu* Snodgrass). He interpreted the anterior mesepisternal region of ichneumonoids as the primitive precursor of the independent sclerite of chalcidoids, and thus homologous. The same mesepisternal region that Snodgrass termed the prepectus in ichneumonoids was previously termed the **epicnemium** by Thomson (1873, fig. 15). Enslin (1913, fig. 6) later termed a similar region in various symphytes as ~~the~~ "praesternum", and Shcherbakov (1981) considered the region to be the "anepisternum" in various hymenopterans. Shcherbakov based his term on presumed homology of the sclerite within the subcoxal theory of the origin of the pleuron in insects.

Snodgrass (1909) further designated the basalare as the "second parapterum", and the postspiracular sclerite as the "first parapterum". "Parapteron" was originated by Audouin (1824), but he initially used the term to denote two different structures, as indicated by Crampton (1914b). Audouin used the term to designate an anteriorly delineated region of the mesepisternum in *Dytiscus* L. (Coleoptera: Dytiscidae), as well as to designate the sclerite at the base of the fore wing that Kirby and Spence (1826) gave the now generally accepted term, **tegula** [see especially Grandi (1929) for a detailed discussion of improper use of Audouin's terms]. Because Snodgrass' (1909) use of parapterum was in neither of Audouin's original meanings, Crampton (1914b) originated the term "basalare" and used "posterior basalare" to replace "second parapterum" (= basalare) and "anterior basalare" to replace "first parapterum" (= postspiracular sclerite).

Michener (1944) also objected to the term "first parapterum", ~~but because~~ the sclerite was nonmusculated and is "clearly not associated with wing movement" (p. 174). He therefore proposed the new term "postspiracular sclerite", because of the sclerites position relative to the mesothoracic spiracle in Symphyta. He further suggested that the prepectus of chalcidoids "appears to be the greatly enlarged postspiracular sclerite" (p. 174). Prior to Michener, Reeks (1937) had termed the same sclerite as the "epipleurite", using a term originated by Snodgrass (1927) as a collective term for all the small sclerites beneath the wings. The postspiracular sclerite more recently has been termed the "anepisternum" by Arora (1953), and by Bracken (1961).

Richards (1956b) considered "prepectus" and "epicnemium" to be synonymous because he thought that the intersegmental sclerite below the spiracle in some symphytes was homologous with an anteriorly delineated region of the mesepisternum in others. Both a ventral intersegmental sclerite and an anteriorly delineated region of the mesepisternum were described for individuals of *Pristiphora erichsonii* (Hartig) (Symphyta: Tenthredinidae) by Wong (1963). He used "epicnemium" for the intersegmental sclerite, and "prepectus" for the mesepisternal region (Wong 1963, fig. 15). Richards (1956a) further considered the independent sclerite of chalcidoids to be composed of the postspiracular sclerite dorsally and the epicnemium ventrally. Domenichini (1969) also considered the sclerite in chalcidoids to be of composite structure, but of the epicnemium dorsally and the spinasternum (of intersegmental origin) ventrally (Domenichini 1969, Table VII-XI). Finally, Shcherbakov (1980) followed Rasnitsyn (1969) and used "basalare sclerite 2" for the basalare, "basalare sclerite 1" for the postspiracular sclerite, and "postspiracular sclerite" for the prepectus.

In summary, "prepectus" and "postspiracular sclerite" are both used to designate the same independent sclerite in chalcidoids. "Prepectus" is further used for an anteriorly delineated region of the mesepisternum in various symphytes, aculeates and ichneumonoids, and "postspiracular sclerite" is used for two different sclerites in symphytes. "Epicnemium" is generally regarded as a synonym of "prepectus" in literature on Apocrita (see for example Brothers 1975 and Bohart and Menke 1976), but the two terms are used to designate separate structures in literature on Symphyta.

It is evident that a set of terms for use throughout the order depends on correct homology of the various sclerites and regions. However, stablity in terms also requires agreement as to which terms should be used because different terms have been proposed for the same structures. Reasons for the way terms are used in this paper are given below.

Second parapterum and first parapterum *sensu* Snodgrass (1909) are rejected for designation of the basalare and postspiracular sclerite respectively, because of incorrect application of Audouin's (1824) term. Thus, posterior basalare and anterior basalare *sensu* Crampton (1914b) have priority for the respective sclerites. Though Rasnitsyn (1969) and Shcherbakov (1980, 1981) use the similar terms basalare sclerite 2, and basalare sclerite 1 for the two sclerites, they are alone in this among recent workers. Basalare is now generally restricted to designate the single sclerites that articulate with and pronate each fore- and hind wing, and a separate term is used for the sclerite found in symphytes between the mesothoracic spiracle and basalare. The most commonly used term for this latter sclerite is postspiracular sclerite *sensu* Michener (1944). I also use this term, rather than anterior basalare, because I consider the former term to be more appropriate. Firstly, the postspiracular sclerite is a modification of the mesothorax alone and no such sclerite is associated with the basalare of the metathorax. Secondly, the terms posterior basalare and anterior basalare imply a similar if not equal function. Shcherbakov (1981) stated that pull of the mesopleural-basalare muscle is transmitted to the two sclerites "via the pedicel of a cup-shaped apodeme which emerges on the surface between these sclerites" (p. 210), but my dissections do not confirm this. The postspiracular sclerite is connected by membrane to the dorsal surface of the basalare disc, but the tendon-like pedicel of the disc is inserted directly into the basalare. Though the postspiracular sclerite articulates dorsally with the basalare, pronation of the fore wing by contraction of the mesopleural-basalare muscle is apparently effected through the basalare alone. I also prefer postspiracular sclerite because it is the most descriptive term of those available, the most commonly used term, and the only one that was specifically established for the sclerite in Symphyta. Use of "postspiracular sclerite" for the prepectus of chalcidoids is incorrect because of incorrect homology, as is Shcherbakov's (1980, 1981) use of the term for the same reason.

Because Snodgrass (1910) initially used prepectus to designate two structural regions, correct application of the term depends on homology and on choice of how to apply the term. Described pronotal structures and sites of origin of the spiracular occlusor muscle for chalcidoids and ichneumonoids indicate that the two regions designated by Snodgrass as the prepectus in these taxa are non-homologous. The independent sclerite of chalcidoids that was termed the prepectus by Snodgrass appears to be highly reduced and fused to the posterolateral edge of the pronotum in ichneumonoids, rather than to the mesepisternum as believed by Snodgrass. I propose restricting "prepectus" to designate the sclerite of chalcidoids and homologous regions of other hymenopterans, because an earlier term, "epicnemium" *sensu* Thomson (1873), is available for the mesepisternal region of ichneumonoids.

Some authors also have termed anterior mesepisternal regions of various symphytes and aculeates as the prepectus. However, there is little evidence to support these designations. Symphytes have an independent prepectus, except for pamphiliids (Megalodontoidea) and some tenthredinoids. The spiracular occlusor muscle arises from the inner surface of the pronotum in tenthredinoids without a prepectus, except for numerous nematines (Tenthredinidae). In these, the spiracular occlusor muscle appears to arise from the anterior margin of the mesepisternum. Many nematines, like many other tenthredinoids, also have an anteriorly delineated region of the mesepisternum that is commonly termed the "prepectus". However, presence of both the delineated mesepisternal region (epc) and an independent prepectus (pre) in some symphytes (Fig. 2.11) shows that the mesepisternal region is not the prepectus. Furthermore, all degrees of fusion of the prepectus with the mesepisternum are evident in different nematines, and the prepectus is often clearly distinguished as a small region at the anterior edge of the mesepisternal region, even though fused with it.

The spiracular occlusor muscle also originates from an apodeme on the anterior edge of the mesepisternum in Pamphiliidae, but presence of only a very tiny prepectus in Megalodontidae (Megalodontoidea) indicates that the prepectus is probably absent from pamphiliids because of loss rather than fusion. Consequently, present use of "epicnemium" and "prepectus" in literature on Symphyta should be reversed (*cf.* Fig. 2.11 and Wong 1963, fig. 15).

Though "prepectus" is also used by some authors to designate variously delineated anterior mesepisternal regions in different aculeates, there is equally little evidence that the sulci defining the regions represent the line of fusion between the prepectus and mesepisternum. Except for vespoids, aculeates without an independent prepectus have the spiracular occlusor muscle originating from an apodeme on the anterior edge of the mesepisternum, indicating that the prepectus is fused to the mesepisternum. I dissected various sphecids, pompilids, halictids, and colletids that had a more or less vertical sulcus on the mesepisternum. This showed that the sulcus is invaginated as an apodeme, which separates the sites of origin of different sets of direct flight muscles in the different taxa. Furthermore, dissections of aculeates without a sulcus showed that the sites of origin of the different direct flight muscles do not differ between those with and those without the vertical mesepisternal sulcus and apodeme. I conclude from this that the sulci defining anterior mesepisternal regions in various aculeates are secondarily derived, and most probably are independently derived in the taxa in which different sets of muscles are segregated.

The sulci or carinae delineating anterior mesepisternal regions are undoubtedly independently derived in Symphyta, Ichneumonoidea, and Aculeata, and probably were derived a number of times in each group. The regions are thus analogous rather than homologous. Use of the same term for structures implies homology and relationship through common ancestry, so that analogous regions, which are the result of convergence rather than inheritance, should not be given the same term. However, there is equally little value in a proliferation of terms required to designate similar structures that were independently derived in different taxa. For this reason I believe that some terms should be recognized as general terms, indicating relative structure and position but not homology. I suggest that "epicnemium" and "epicnemial carina" or "sulcus" be accepted as such general terms, and that they be used to designate the similar mesepisternal structures of various symphytes, aculeates, and terebrants.

2.4.5 Mesothoracic musculature

Matsuda (1970) listed the taxa examined and publications about mesothoracic musculature in Hymenoptera. The musculature of only two terebrant species have been studied in detail, *viz., Stenobracon deesae* Cameron (Braconidae) (Alam 1951), and *Philopsyche sauteri* Cushman (Ichneumonidae) (Maki 1938). Furthermore, the only comparative studies are those of Märkl (1966), who studied the musculature of three different aculeates, and Maki (1938) who studied a single member each of Symphyta, Aculeata and Terebrantes. Daly (1963) conducted a more comprehensive survey, but primarily to determine what the histological types were of some selected mesothoracic muscles. Distribution of two of the muscles studied by Daly indicated that they might be [illegible]ble for phylogenetic analysis of Hymenoptera, and particularly of Terebrantes.

2.4.5.1 Mesotrochanteral depressor

One of the mesothoracic muscles studied by Daly (1963) was the mesotrochanteral depressor. He reported this muscle from representatives of Xyelidae, Siricidae, and Cephidae in Symphyta, but only from Chalcidoidea (Terebrantes) in Apocrita. The muscle was described as being tubular, originating from the posterior part of the mesoscutum, and inserting into an expanded pedicel of the mesotrochanter (*c.f.* Fig. 2.37). My dissections indicate that all hymenopterans probably have the mesotrochanteral depressor, but that this muscle is extremely varied in shape, number of components, and sites of origin. Daly (1963) apparently did not realize that the mesotrochanteral depressor was composed of two thoracic components in all symphytes except tenthredinoids. Non-tenthredinoid symphytes have the tubular tergal component (**mesotergal-trochanteral depressor: t_2-tr_2**) described by Daly, and a much smaller muscle that originates from the vertical plate of the mesofurca where the furca diverges as the lateral mesofurcal arms (**mesofurcal-trochanteral depressor: fu_2-tr_2**) (Figs. 2.39, 2.40). Both tergal and furcal components insert ventrally into a golf tee-like pedicel (*cf.* Fig. 2.37) that is tendon-like extended through the coxa to insert into the trochanter. Additional muscle originates and inserts into the tendon of the depressor within the coxa, but this is not described below because I could not accurately determine presence or absence in many terebrants.

I found a mesotrochanteral depressor composed of the two mesothoracic components in representatives of Pamphiliidae, Anaxyelidae, Xiphydriidae (Fig. 2.39) and Orussidae (Fig. 2.40), in addition to the non-tenthredinoid symphytes [illegible] by Daly (1963). Relative size of t_2-tr_2 differed considerably, but the muscle originated posteriorly from the mesoscutum in all individuals, *i. e.*, anterior to the transscutal articulation in xiphydriids and orussids (Figs. 2.39, 2.40). Specimens of *Orussus sayi* (Westwood), the only orussid dissected, differ from other symphytes in having massive t_2-tr_2 muscles, but no dorsoventral indirect flight muscles (Fig. 2.40)! Tenthredinoids also differ from other symphytes in lacking t_2-tr_2. The mesotrochanteral depressor consists only of fu_2-tr_2, which is fan-like, originates from the mesofurcal arm, and is tendon-like extended through the coxa (*cf.* Figs. 2.47, 2.48) (Weber 1927, Maki 1938, Tait 1962, Dhillon 1966, Rasnitsyn 1969).

Almost all aculeates also have a mesotrochanteral depressor consisting of only fu_2-tr_2. The muscle is typically quite large in such aculeates, and originates from the mesofurcal arm, or from this and an anterior process of the mesofurcal bridge so as to appear to be two-parted in some individuals. This was described for *Vespula pennsylvanica* (Saussure) by Duncan (1939, fig. 77, III3a and III3b). The muscle is conical or fan-like so as to converge to a linear tendon that extends through the coxa and inserts into the trochanter.

Formicids are the only aculeates known to have the mesotrochanteral depressor composed of both fu_2-tr_2 and t_2-tr_2. Lubbock (1879, p. 149) stated that the mesotrochanteral depressor of *Lasius flavus* (Fab.) workers was two-parted, originating "partly from the upper lateral wall of the mesonotum immediately under the spiracle, partly from the medifurca [= mesofurca], and passing downwards contracts into a tendon which is continued into the leg". I did not observe fu_2-tr_2 in [illegible] dissections of *Lasius* sp. workers, most likely because of the small size of specimens, but did substantiate a fan-like muscle originating from the mesopleuron. A few fibers also originated on the tergum and inserted with the mesopleural portion into the trochanter. Dissections show that the mesotrochanteral depressor is two-parted in queens of this species with fu_2-tr_2 as the major component, but with one or two muscle fibers originating from the axilla. I also discovered tergal and furcal components of the mesotrochanteral depressor in queens of *Myrmica* sp., *Crematogaster* sp. and *Camponotus* sp. Queens of the latter taxon have the tergal component fan-like and originating from the mesoscutum anterior to the transscutal articulation. They also have the furcal component extended onto the mesopleuron adjacent to the dorsal edge of the mesofurcal arm (Fig. 2.46). Illustrations by Saini *et al.* (1982) indicate that the muscles labelled by them as "31" and "26" for winged and non-winged individuals of *Camponotus camelinus* (Smith) are not muscles inserted into the rim of the mesocoxa, but respectively the furcal and tergal components of the mesotrochanteral depressor. Daly (1963) did not indicate presence of a tergal component of the mesotrochanteral depressor in the formicids he studied, nor did Märkl (1966) for *Formica polyctena* Förster workers. Hence, more comprehensive surveys of the musculature of workers, queens, and males are required to determine exact states of the mesotrochanteral depressor in formicids.

States of the mesotrochanteral depressor are most varied in Terebrantes. Megalyridae, Stephanidae, and Diapriidae except for Ismarinae have both fu_2-tr_2 and t_2-tr_2. Stephanids (Fig. 2.41) and non-ismarine diapriids (Fig. 2.42) have t_2-tr_2 tubular, fu_2-tr_2 fan-like, and both inserted ventrally into an expanded trochanteral pedicel (*cf.* Fig. 2.37). Fu_2-tr_2 originates dorsally from the vertical plate of the mesofurca where this diverges as the mesofurcal arms, and is thus between t_2-tr_2 and the mesofurca (Figs. 2.41, 2.42). T_2-tr_2 originates almost entirely from the axilla (Figs. 2.41, 2.42), though a few anterior fibers originate from the posterior of the mesoscutum in stephanids. Only specimens of *Ismarus flavicornis* (Thomson) were dissected as representative of Ismarinae (Diapriidae), but these did not have t_2-tr_2. I was unable to conclusively determine which, if any of the muscles of the coxal region is the depressor of the mesotrochanter.

Dissection of a single specimen shows that the mesotrochanteral depressor of [illegible] Westwood (Megalyridae) also is composed of fu_2-tr_2 and t_2-tr_2. However, t_2-tr_2 originates [illegible] almost equally from the axilla and from the tergum anterior [illegible]sscutal articulation (Fig. 2.44), unlike stephanids and non-ismarine diapriids. [illegible]ore, fu_2-tr_2 originates from the mesofurcal arm so that it is behind t_2-tr_2 rather than between it and the vertical plate of the mesofur[illegible]g. 2.44).

The mesotrochanteral depressor of ceraphronoids also has an equally large component of t_2-tr_2 originating anterior and posterior of the transscutal articulation, but each component is relatively slender so that they converge to a linear tendon that is extended through the mesocoxa (Fig. 2.43). Fu_2-tr_2 is also absent.

Chalcidoids have only t_2-tr_2 composing the mesotrochanteral depressor. It is tubular (Fig. 2.45) and inserts ventrally into an expanded pedicel (Fig. 2.37), but unlike other terebrants originates both from the axilla and a horizontal axillar phragma that projects anteriorly beneath the mesoscutum (axp, Figs. 2.38, 2.45). Axillar phragmata [= "apodeme of posterior plate of mesonotum" *sensu* James (1926) and "pseudophragma of postscutellum" *sensu* Bucher (1948)] are absent from females of Eupelminae (Eupelmidae), but this is the result of secondary modification (to be described in a subsequent paper). T_2-tr_2 usually appears to be two-parted if the axillar phragma is large (Fig. 2.45), and thus is superficially similar to the muscle of megalyrids (Fig. 2.44).

Other known terebrants lack t_2-tr_2, and the mesotrochanteral depressor consists of only fu_2-tr_2, a pleural component (pl_2-tr_2), or both. Monomachidae, Trigonalidae, Aulacidae (Fig. 2.48), Gasteruptionidae (Fig. 2.49), Roproniidae, Heloridae (Fig. 2.47), Cynipoidea, and Ichneumonoidea have fu_2-tr_2 as a conical or fan-shape muscle originating from the mesofurcal lateral arm; Proctotrupidae, Pelecinidae, Evaniidae (Fig. 2.50), and Vanhorniidae have fu_2-tr_2 originating from the mesofurcal lateral arm and extended onto the mesopleuron as pl_2-tr_2; and Scelionidae have only pl_2-tr_2 adjacent to the mesofurcal lateral arm (Fig. 2.51). The muscle(s) always converge to pass through the mesocoxa as a linear trochanteral tendon (Figs. 2.47-2.51). Dissections of Platygastridae show that these lack t_2-tr_2, but because of the small size of specimens I was unable to conclusively determine which, if any of the muscles of the coxal region is the mesotrochanteral depressor.

Phylogenetic implications:

The plesiomorphic state of the mesotrochanteral depressor for Hymenoptera is indicated by non-tenthredinoid Symphyta. Other than tenthredinoids, all symphytes have both a tergal (t_2-tr_2) and furcal (fu_2-tr_2) component, in addition to muscle originating within the mesocoxa. The major component is t_2-tr_2, which is tubular and originates from the posterior of the mesoscutum. The smaller thoracic component, fu_2-tr_2, originates near the dorsal edge of the vertical plate of the mesofurca where this diverges as the lateral mesofurcal arms. Consequently, it is between t_2-tr_2 and the vertical plate of the mesofurca (Figs. 2.39, 2.40). The single fan-like fu_2-tr_2 mesotrochanteral depressor of tenthredinoids is undoubtedly apomorphic through loss of t_2-tr_2, and a synapomorphy for members of this superfamily.

States of the mesotrochanteral depressor in Apocrita indicate that the plesiomorphic condition for this suborder was the same as that described for non-tenthredinoid symphytes, except that t_2-tr_2 had two sites of origin. T_2-tr_2 originates from the mesoscutum anterior to the transscutal articulation in xiphydriids and orussids (Figs. 2.39, 2.40), the only symphytes with a transscutal articulation (Figs. 2.3, 2.4), but in apocritans either from the axilla, which is posterior to the transscutal articulation, (Stephanidae and non-Ismarine Diapriidae: Figs. 2.41, 2.42), or equally from the axilla and mesoscutum anterior to the transscutal articulation (Megalyridae and Ceraphronoidea: Figs. 2.43, 2.44). I interpret this character-state distribution as evidence that part of t_2-tr_2 was expanded from the mesoscutum to the axilla in the common ancestor of Apocrita.

No modern apocritan is known to have the hypothesized plesiomorphic condition of the mesotrochanteral depressor, but all known states can be readily derived from the hypothesized condition. Furthermore, the mesotrochanteral depressor of megalyrids is very similar to that hypothesized as plesiomorphic for apocritans, except that fu_2-tr_2 originates from each lateral mesofurcal arm rather than from the vertical plate of the mesofurca. The muscle is thus positioned posterior to t_2-tr_2 (Fig. 2.44), rather than between t_2-tr_2 and the vertical plate of the mesofurca (Figs. 2.41, 2.42). Ceraphronoids are the only other apocritans with equal portions of t_2-tr_2 originating anterior and pos[illegible] to the transscutal articulation (Fig. 2.43). As a hypothesized symplesiomorphy this is not evidence that ceraphronoids and megalyrids are sister taxa. However, it probably indicates a close relationship because they are the only apocritans having this state, and because the mesotrochanteral depressor of ceraphronoids can be derived [illegible]at of megalyrids by loss of fu_2-tr_2 and reduction in size of t_2-tr_2.

Stephanids and non-ismarine diapriids also have a mesotrochanteral depressor that is similar to the hypothesized plesiomorphic state for apocritans, except that t_2-tr_2 originates entirely or almost so from each axilla (Figs. 2.41, 2.42). Because fu_2-tr_2 occupies the hypothesized plesiomorphic position between t_2-tr_2 and the vertical plate of the mesofurca, this indicates that stephanids and non-ismarine diapriids evolved from an ancestor(s) with the hypothesized plesiomorphic condition of the mesotrochanteral depressor, independently from that of megalyrids. I presently consider absence of t_2-tr_2 in ismarines to be the result of secondary loss, but analysis of the exact relationships between the four recognized subfamilies of Diapriidae, and between diapriids and other terebrants is required to substantiate this.

T_2-tr_2 superfically appears to originate partly from the axilla and partly from the mesoscutum anterior to the transscutal articulation in chalcidoids (Fig. 2.45), as in megalyriids (Fig. 2.44) and ceraphronoids (Fig. 2.43). However, the muscle originates only from the axilla because the anterior section originates from a phragma extended from the anterior edge of the axilla (axp, Fig. 2.38). I interpret this as evidence that the ancestor of chalcidoids had t_2-tr_2 originating only from the axilla, but that this muscle was secondarily increased in size in the common ancestor of Chalcidoidea by development of axillar phragmata for muscle attachment. Riek (1970) stated that orussids are agile leapers, and their jumping ability and very large t_2-tr_2 muscles are undoubtedly correlated. T_2-tr_2 is apparently the major muscle for jumping in chalcidoids, and I suspect that the axillar phragmata and resultantly large t_2-tr_2 muscles were secondarily derived for increased jumping ability.

T_2-tr_2 is absent from other apocritans, except for at least some formicids (Aculeata). I presently consider presence as secondary in formicids because other aculeates only have fu_2-tr_2. The t_2-tr_2 muscle of formicids is also fan-like rather than tubular as in other hymenopterans. This may indicate that it was secondarily reacquired.

T_2-tr_2 was lost in tenthredinoids (Symphyta), and most probably was lost more than once during the evolution of Apocrita. I do not consider loss of t_2-tr_2 to be a reliable indicator of relationship for those apocritans that have only fu_2-tr_2. In a similar study of the possible phylogenetic significance of the mesotrochanteral depressor in Diptera, Smart (1958) concluded that loss of the muscle must have occurred again and again during the evolution of that order. It is probable that the same is true for Apocrita, though relationships are insufficiently known to hypothesize number of times independent loss might have happened.

Evaniidae, Pelecinidae, Proctotrupidae, and Vanhorniidae do have a hypothesized apomorphic state of the mesotrochanteral depressor among apocritans lacking t_2-tr_2. Fu_2-tr_2 not only originates from the lateral arm of the mesofurca, but extends onto the mesopleuron adjacent to the lateral arm as pl_2-tr_2 (Fig. 2.50). Presence of pl_2-tr_2 may be a synapomorphy for the above taxa, but independent expansion of fu_2-tr_2 onto the mesopleuron is also possible.

Scelionidae only have pl_2-tr_2 (Fig. 2.51). I consider this to represent the terminal state in a transformation series in which the mesotrochanteral depressors of evaniids, pelecinids, proctotrupids and vanhorniids represent intermediate states. One, or some combination of the above families is thus indicated as the sister group of Scelionidae. Unfortunately, I did not determine state of the mesotrochanteral depressor for platygastrids, other than that t_2-tr_2 is absent. Königsmann (1978a) hypothesized that Platygastridae is the sister group of Scelionidae. If Königsmann and my analysis are both correct, then platygastrids should either have fu_2-tr_2 and pl_2-tr_2, or only pl_2-tr_2.

2.4.5.2 Second-phragmal flexor

An oblique lateral muscle from the tergum to a lateral process of the second phragma (t_2-2ph) is the second muscle that was indicated to have potential significance for phylogenetic analysis of Terebrantes. Daly (1963) reported this muscle from all Symphyta studied, but only from Cynipoidea (Terebrantes) in Aculeata.

My dissections show t_2-2ph as a tubular muscle in Pamphiliidae, Anaxyelidae, and Xiphydriidae (Fig. 2.39), in addition to Xyelidae, Diprionidae, Tenthredinidae, Siricidae, and Cephidae (Daly 1963). T_2-2ph is absent from *Orussus sayii* (Westwood) (Fig. 2.40), the only orussid dissected. In *Xiphydria mellipes* Harris, t_2-2ph originates primarily from the axilla, though a few fibers also originate from the mesoscutum anterior to the transscutal articulation. In Siricidae, t_2-2ph originates from the mesoscutal region anterolateral to the scutellum that is designated as the parascutal lobe. It also originates from the mesoscutum in a position anterolateral to the scutellum in other symphytes.

Aculeates lack t_2-2ph, as documented by Daly (1963) and other studies of aculeate musculature listed by Matsuda (1970). However, not only do Cynipoidea have t_2-tr_2 in Terebrantes, but so do Ceraphronoidea (Fig. 2.43), Diapriidae (Fig. 2.42), Monomachidae, and Vanhorniidae. The muscle originates entirely from the axilla.

Phylogenetic implications:

Site of origin t_2-2ph is additional evidence that axillae are morphologically the posterolateral angles of the mesoscutum that became segregated with origin of the transscutal articulation. The muscles originate from the mesoscutum lateral to the scutellum in symphytes without a transscutal articulation, but from the axilla in xiphydriids and terebrants. Site of origin of t_2-2ph also indicates that the parascutal lobes of siricids are at least analagous to the axillae of other hymenopterans. Furthermore, presence of t_2-2ph in all symphytes except orussids indicates that this muscle is a groundplan character of Hymenoptera. Presence in cynipoids, ceraphronoids, vanhorniids, diapriids, and monomachids further indicates that t_2-2ph is symplesiomorphc for Apocrita and not evidence of relationship. I do not co[illegible] absence of the muscle from other apocritans to be a reliable indicator of relationship because it can not be determined how many independent times loss occurred. Loss of t_2-2ph from orussids must be independent of loss from most apocritans if Orussidae is the extant sister group of Apocrita, as previously hypothesized.

2.5 Discussion

2.5.1 Relationships of Apocrita and Symphyta

Origin of Apocrita and its relationship to Symphyta are much discussed topics, but they have yet to be resolved. Königsmann (1977) hypothesized that Cephidae is the sister group of Apocrita and that this monophyletic assemblage is the sister group of the monophyletic taxon, Symphyta *s. s.* (Symphyta excluding Cephidae). Other hymenopterists have usually considered Apocrita as monophyletic, but Symphyta (including Cephidae) as paraphyletic, with either

Cephidae or Orussidae hypothesized as the extant sister group of Apocrita. The most recent analysis of Rasnitsyn (1980) proposed that Orussidae is the sister group of Apocrita, that Cephidae is the sister group of Orussidae + Apocrita, and that Siricoidea (Anaxyelidae, Siricidae, Xiphydriidae) is the sister group of Cephidae + Orussidae + Apocrita. In a previous analysis Rasnitsyn (1969) proposed that Cephidae was the sister group of Siricoidea + Orussidae + Apocrita, and tentatively proposed that Siricoidea was paraphyletic because Xiphydriidae was the extant sister group of Apocrita, and Orussidae was the sister group of Xiphydriidae + Apocrita.

Distribution of character states of the thoracic structures described in this paper do not support a sister group, or even a close relationship between Cephidae and Apocrita. Rather; relationship of Apocrita with a siricoid-orussid lineage is supported. Relationship of Siricidae, Xiphydriidae, Orussidae, and Apocrita is indicated by a single character state that is hypothesized to be a synapomorphy for members, a prepectus that is concealed beneath the posterolateral edge of the pronotum. Presence of the transscutal articulation plus resultant axillae further indicate a relationship of Xiphydriidae, Orussidae and Apocrita, and presence of linear parapsidal marks (parapsidal lines), a pronotal lobe, an elongate basalare, and absence of a postspiracular sclerite indicate that Orussidae is the probable sister group of Apocrita. The latter two character states may be correlated, however, and not independent evidence of relationship. Furthermore, absence of the second-phragmal flexor (t_2-2ph) and reduced notauli and median mesoscutal sulcus described for orussids and many apocritans must be the result of independent reductions and losses if Orussidae is the extant sister group of Apocrita.

2.5.2 Classification of Symphyta

Present classifications of Hymenoptera either recognize Anaxyelidae, Siricidae, Xiphydriidae and Orussidae as the superfamily Siricoidea (*s. l.*) in Symphyta (Riek 1970, Königsmann 1977, Smith 1979), or Orussidae is excluded from Siricoidea (*s. s.*) and either accorded superfamilial status in Symphyta (Rasnitsyn 1969), subordinal status in Hymenoptera

(Idiogastra *sensu* Rowher 1918), or infraordinal status in Apocrita (Orussomorpha *sensu* Rasnitsyn 1980). Relationships indicated by character-state distribution of the thoracic structures studied supports none of these classifications. No putative synapomorphies were found to support monophyly of Siricoidea *s. l.* exclusive of Apocrita, though possible synapomorphies were found that indicate Orussidae is more closely related to Apocrita than are the three families assigned to Siricoidea *s. s.* Consequently, this analysis supports excluding Orussidae from Siricoidea. However, no character states were found to support monophyly of Siricoidea *s. s.* exclusive of Orussidae + Apocrita. Removal of Orussidae from Siricoidea *s. l.* probably makes Siricoidea *s. s.* paraphyletic relative to orussids and apocritans. Distribution of the character states proposed previously as possible synapomorphies indicates a nested pattern of relationships, that is, [Siricidae + (Xiphydriidae + [Orussidae + Apocrita])]. If these relationships are valid, siricids and xiphydriids should minimally each be accorded the same status as orussids.

Rasnitsyn (1980) realized that classifying orussids in Symphyta made this latter taxon paraphyletic, so that he proposed recognizing orussids as an infraorder within Apocrita. However, my analysis of thoracic structures indicates that Rasnitsyn's solution only makes Symphyta paraphyletic at another level. The traditional classification of Hymenoptera, which recognizes the monophyletic suborder Apocrita primarily on the basis of fusion of the first abdominal segment with the thorax as the propodeum, is useful, even though Symphyta is an acknowledged paraphyletic taxon. I concur with Rasnitsyn (1980) that Orussidae is the probable extant sister group of Apocrita and that it should not be classified in Siricoidea, but I consider it better to recognize orussids as a superfamily in Symphyta.

New classifications can always be proposed on the basis of one or a few character systems, as for example the classification of Symphyta by Togashi (1970) that was based on the internal reproductive organs of males and females. However, I believe that a stabile classification of Hymenoptera, which reflects the evolutionary history of this order, will only result after a detailed analysis of as many characters as possible. My analysis of relationships indicates that Orussidae + Siricidae + Xiphydriidae is not a monophyletic group if Apocrita is excluded, and that all three families should be accorded superfamilial status in Symphyta. However, Ross (1937) proposed that Siricoidea *s. l.* is a monophyletic group based on character states of the head, though he did state that this group is "undoubtedly the most heterogenous group of sawflies" (p. 33). Benson (1955) stated that the shared states were correlated with the wood-boring habitat of larvae. It is obvious that more detailed studies are required to determine what character states, if any, shared by Anaxyelidae, Xiphydriidae, Siricidae, and Orussidae define monophyly of all or part of this group, and which states are due to symplesiomorphy, homoplasy, or are intermediate states in transformation series which may include Apocrita. Similar studies are also required to reexamine proposed synapomorphic states for Cephidae and Apocrita.

2.5.3 Relationships and classification of Apocrita

Most of the hypothesized apomorphic states of the thoracic characters studied in Apocrita are either reductions and fusions, or losses. Losses as indicators of relationship generally are considered to be the least reliable of all transformations because it can not be determined whether common absence is the result of a single or multiple losses. Unfortunately, most analyses of character-state distribution of Apocrita will probably result in a high percent of the proposed apomorphic states being reductions or losses. This is because the body size of apocritans, and particularly terebrants, is generally much smaller than that of most symphytes, and simplification of the body through reductions and losses is correlated with small size. Though losses and reductions must be used in phylogenetic analyses of Apocrita out of necessity, this limitation emphasizes the necessity of analyzing as many characters as possible so that hypotheses of relationship are based on congruence of unrelated character transformations. This study of thoracic structure analyzes only a few characters so it is not surprising that it is insufficient to clarify most questions concerning relationships of Apocrita.


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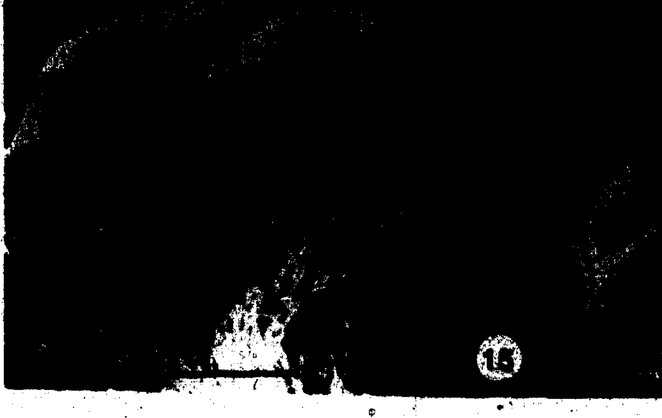
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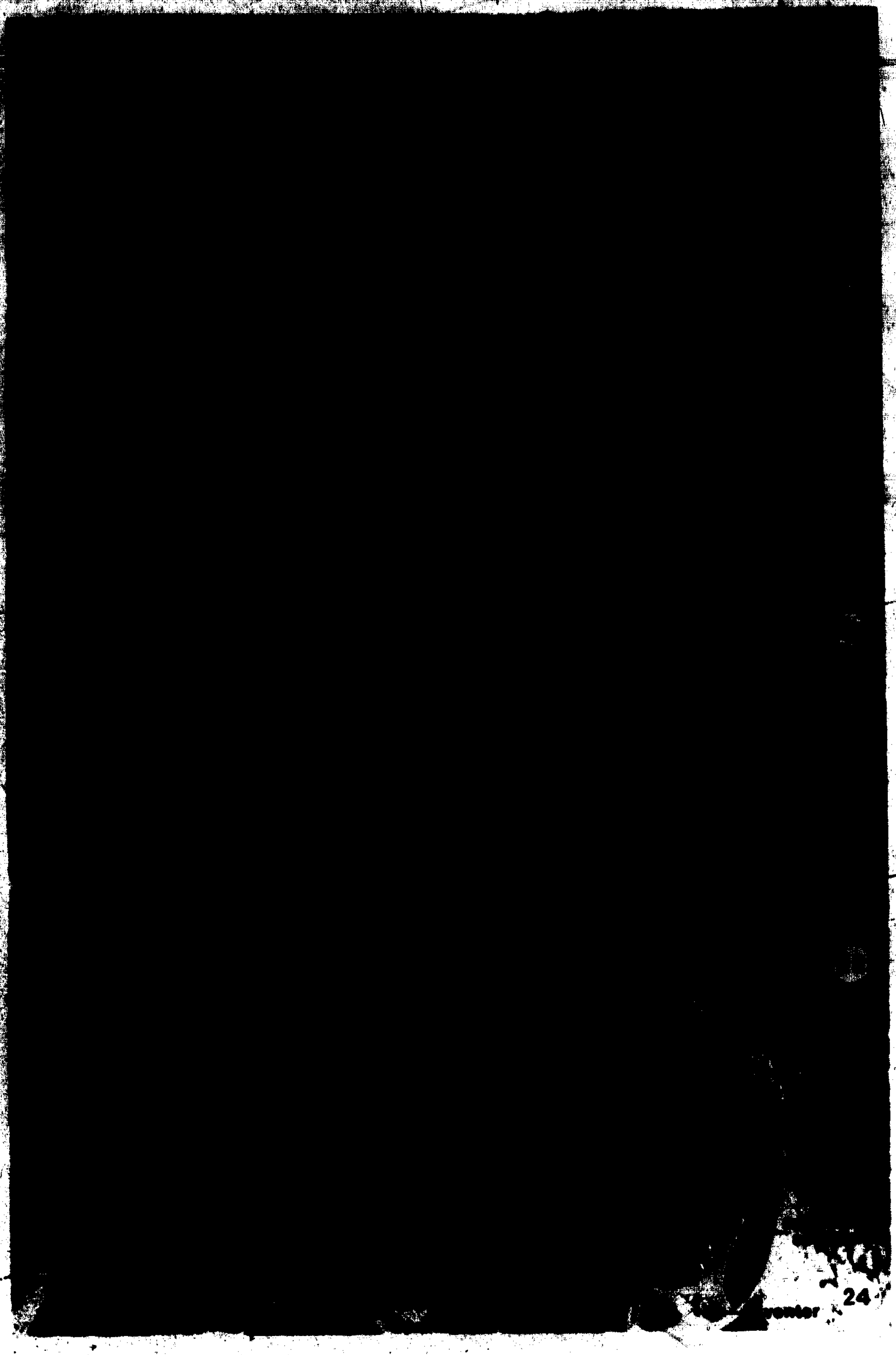

However, some states appear to be useful for testing previous hypotheses of relationship and classification.

The suborder Apocrita has traditionally been divided into two infraorders, Aculeata and Terebrantes, though Rasnitsyn (1980) hypothesized that extant apocritans (excluding orussids by his classification) form four main groups, which he recognized as infraorders. Aculeata was accepted as the infraorder Vespomorpha, but Terebrantes was not recognized and three separate infraorders were proposed, *viz.*, Stephanomorpha, Evaniomorpha, and Ichneumonomorpha. Neither the traditional classification, nor that of Rasnitsyn (1980) is supported by this study of thoracic structures because no tenable synapomorphies were found to support monophyly of any of the proposed taxa. However, if Aculeata and Terebrantes are monophyletic sister taxa, then absence of a median mesoscutal sulcus, the second-phragmal flexor (t_2-2ph), and tergal portions of the mesotrochanteral depressor (t_2-tr_2) in aculeates and various terebrants must be the result of independent reductions and losses. Furthermore, Stephanidae has the hypothesized plesiomorphic condition of the intersegmentalia for Apocrita, whereas the intersegmentalia of Aculeata are considered as apomorphic and could be included in a transformation series that indicates a possible relationship with the majority of Terebrantes.

Riek (1970) classified Stephanidae and Megalyridae as the superfamily Megalyroidea. This classification is not supported by the present study because all thoracic states shared by members of these two families are hypothesized to be symplesiomorphic states (median mesoscutal sulcus, large axillae, tergal portion of mesotrochanteral depressor), except for absence of the second-phragmal flexor (t_2-2ph), which is absent from most Apocrita. Classification of Stephanidae in Ichneumonoidea by Krombein *et al.* (1979) is likewise not supported. Monophyly of Paxylommatidae, Braconidae and Ichneumonidae is supported by their unique structure of the pronotum, which indicates that these three families alone should be classified as the superfamily Ichneumonoidea. Rasnitsyn (1980) classified Stephanidae as the only extant member of his infraorder Stephanomorpha, but also included the extinct families

Ephialtitidae and Karatavitidae. Rasnitsyn considered that extant Apocrita were derived from Ephialtitidae and that stephanids are the apocritans that are least modified from ephialtitids. The thoracic structures studied support Rasnitsyn's hypothesis that stephanids are a basal apocritan lineage, even if not the sister group of the rest of Apocrita, based on the number of plesiomorphic features they retain. Stephanidae have the hypothesized plesiomorphic condition of the intersegmentalia, a saddle-like and mobile pronotum (correlated with an independent prepectus), a pronotal lobe, a median mesoscutal sulcus, both tergal and furcal portions of the mesotrochanteral depressor (though not the hypothesized plesiomorphic condition for Apocrita), and large and contiguous axillae (correlated with presence of t_2-tr_2). The only hypothesized apomorphic states found for stephanids were absence of t_2-2ph and loss of the mesoscutal portion of t_2-tr_2. Because no derived states were found to indicate exact relationships of stephanids with other apocritans I agree with Rasnitsyn (1980) that Stephanidae is best classified as its own superfamily, the Stephanoidea.

Rasnitsyn (1980) included two superfamilies in Evaniomorpha, Ceraphronoidea and Evaniodea (Aulacidae [= Gasteruptionidae] and Evaniidae). Most hymenopterists consider gasteruptionids and evaniids as sister taxa, or at least closely related, though Townes (1950) considered that the major apomorphic state shared, a high attachment of the metasomal petiole, was independently derived in the two taxa. Character-state distribution of the thoracic structures studied supports Townes' (1950) hypothesis. No character states were found to indicate monophyly of gasteruptionids and evaniids, and two states were found to differ that would require an hypothesis of convergence with other terebrants if the two are sister groups. The pronotum of evaniids has a posterolateral inflection so that the pronotum and mesepisternum have a tongue-and-groove interlocking mechanism, whereas the pronotum of gasteruptionids is ungrooved and merely abuts against the mesepisternum. The pronotal state of gasteruptionids is hypothesized to be the result of loss of the prepectus without fusion to the pronotum, whereas the pronotal state of evaniids is hypothesized to be the result of fusion of the prepectus to the inner posterolateral edge of the pronotum. If evaniids and gasteruptionids are sister taxa, then the common ancestor must have had an independent prepectus, which was lost in gasteruptionids and fused to the pronotum in evaniids, convergently to Cynipoidea, Diapriidae, Heloridae, Pelecinidae, Proctotrupidae, Vanhorniidae, Scelionidae, Platygastridae and Trigonalidae. Furthermore, gasteruptionids have only fu_2-tr_2, whereas evaniids have fu_2-tr_2 and pl_2-tr_2. If gasteruptionids and evaniids are sister taxa then fu_2-tr_2 must have been extended onto the mesopleuron as pl_2-tr_2 in evaniids, convergently to Proctotrupidae, Pelecinidae and Vanhorniidae.

Rasnitsyn (1980) included Ceraphronidae, Megaspilidae, Megalyridae and Trigonalidae in Ceraphronoidea. Riek (1970), Königsmann (1978a) and Krombein *et al.* (1979) included only Ceraphronidae and Megaspilidae in Ceraphronoidea. Riek (1970) also recognized Megalyroidea, composed of Megalyridae and Stephanidae, and Trigonaloidea, whereas Königsmann (1978a) did not assign trigonalids, megalyrids or stephanids to superfamily, and Krombein *et al.* (1979) recognized Trigonaloidea, included stephanids in Ichneumonoidea and did not discuss megalyrids. Character-state distribution of the thoracic characters studied indicates that Ceraphronidae and Megaspilidae are minimally monophyletic based on state of the mesotrochanteral depressor (composed of t_2-tr_2 only, with equal portions arising anterior and posterior to the transscutal articulation, and converging to a linear tendon) and on location of the occlusor muscle apodeme (near the posteroventral angle of the pronotum). Analysis revealed no derived states to support classifying trigonalids or stephanids with ceraphronids and megaspilids. However, two states indicate that megalyrids are probably closely related to ceraphronids and megaspilids so that these three taxa could be classified together as a single superfamily. Megalyrids, ceraphronids and megaspilids have the mesotergal-trochanteral muscle arising equally anterior and posterior to the transscutal articulation. Though this is the hypothesized plesiomorphic condition for Apocrita, only these three families retain this state and the mesotrochanteral depressor characteristic of ceraphronids and megaspilids can be derived from that of megalyrids by reduction of t_2-tr_2 and loss of fu_2-tr_2. Furthermore, megalyrids, ceraphronids, and megaspilids are the only apocritans with the mesothoracic spiracle surrounded by pronotal cuticle, but without a distinct groove formed between the outer and an inner posterolateral edges of the pronotum.

Rasnitsyn (1980) recognized five superfamilies in Ichneumonomorpha, *viz.*, Ichneumonoidea, Chalcidoidea, Cynipoidea, Diaprioidea, and Proctotrupoidea. Diaprioidea was newly established for Mymaridae, Scelionidae, Platygastridae, Diapriidae, Austroniidae, and Monomachidae. These families are assigned to Proctotrupoidea in other classifications of Hymenoptera, except for Mymaridae, which is included in Chalcidoidea. Rasnitsyn erected Diaprioidea because he considered that Cynipoidea are more closely related to the taxa he included in Diaprioidea than to the taxa he included in Proctotrupoidea (Proctotrupidae, Vanhorniidae, Pelecinidae, Roproniidae and Heloridae). Though the present study revealed no apomorphic states for Proctotrupoidea *s. l.* (Proctotrupoidea plus Diaprioidea *sensu* Rasnitsyn) excluding Cynipoidea, no synapomorphies were found either to support monophyly of Cynipoidea + Diaprioidea. Furthermore, apomorphic states were found that indicate Diaprioidea and Proctotrupoidea *sensu* Rasnitsyn are not monophyletic taxa.

Proctotrupoidea, Diaprioidea and Cynipoidea, plus Evaniidae and Trigonalidae, either have an independent prepectus or a posterior pronotal inflection extended behind and above the mesothoracic spiracle. Austroniidae and Monomachidae (Diaprioidea *sensu* Rasnitsyn), and Roproniidae (Proctotrupoidea *sensu* Rasnitsyn) have an independent prepectus, whereas other members of the above taxa have a posterior pronotal inflection and a rigid tongue-and-groove pronotal and mesepisternal interlocking mechanism. If Diaprioidea and Proctotrupoidea *sensu* Rasnitsyn are each monophyletic, then loss of the prepectus through fusion with the pronotum as the posterior pronotal inflection must have occurred independently within each group. Furthermore, two independent character state transformation series indicate that Proctotrupidae, Pelecinidae and Vanhorniidae (Proctotrupoidea *sensu* Rasnitsyn) plus Scelionidae and Platygastridae (Diaprioidea *sensu* Rasnitsyn) constitute a monophyletic group. Members of these five families have an annular pronotum, *i. e.*, a pronotum that is continuous ventrally behind the procoxae. The mesotrochanteral depressor of evaniids, proctotrupids, pelecinids, and vanhorniids is also composed of both fu$_2$-tr$_2$ and pl$_2$-tr$_2$. State of the mesotrochanteral depressor is unknown for platygastrids, other than t$_2$-tr$_2$ is absent, but scelionids have pl$_2$-tr$_2$ only. I hypothesized that a mesotrochanteral depressor composed only of pl$_2$-tr$_2$ is the terminal state in a transformation series in which presence of fu$_2$-tr$_2$ and pl$_2$-tr$_2$ is an intermediate state from an hypothesized ancestral state of fu$_2$-tr$_2$ only. This transformation series is congruent with that of the annular pronotum if Evaniidae is the sister group of Proctotrupidae + Pelecinidae + Vanhorniidae + Scelionidae + Platygastridae, or if expansion of fu$_2$-tr$_2$ onto the mesopleuron was independent in Evaniidae, and if it is shown that Platygastridae either have fu$_2$-tr$_2$ and pl$_2$-tr$_2$, or pl$_2$-tr$_2$ only.

Of the five families listed above as a possible monophyletic group, Proctotrupidae and Pelecinidae are additionally similar and indicated as sister taxa on the basis of the mesothoracic spiracle being exposed on the pronotum. It is also possible that Vanhorniidae is the sister group of Proctotrupidae + Pelecinidae + Scelionidae + Platygastridae, based on absence of t$_2$-2ph from members of the latter four families. However, I do not consider this to be a reliable indicator of relationship because t$_2$-2ph appears to have been lost a number of times within Apocrita. Additional study of a posteriorly delineated region of the pronotum (netrion) in the above five families may provide character states to further clarify the relationships.

Taxa assigned to Cynipoidea, Diaprioidea, and Proctotrupoidea *sensu* Rasnitsyn have a mesotrochanteral depressor composed of fu$_2$-tr$_2$ only, except for most Diapriidae. Of the four recognized subfamilies of Diapriidae, Ismarinae have only fu$_2$-tr$_2$, but Ambositrinae, Belytinae and Diapriinae have fu$_2$-tr$_2$ and t$_2$-tr$_2$. I presently consider that both a furcal and tergal component of the mesotrochanteral depressor is the plesiomorphic condition for Diapriidae, and that absence of t$_2$-tr$_2$ in Ismarinae is the result of secondary loss. However, diapriids are unlike other terebrants with a tergal component to the mesotrochanteral depressor because they typically have small and widely spaced axillae. This might indicate that t$_2$-tr$_2$ was absent from the ancestor of diapriids, but that this muscle was secondarily reacquired in the ancestor of Ambositrinae, Belytinae, and Diapriinae. Clarification of the relationships of the subfamilies of Diapriidae, and of diapriids with other terebrants is required to determine which transformations series is accurate.

The present analysis revealed little of value for testing classification of Aculeata, partly because the survey of character-state distribution was insufficient in this infraorder. A more detailed analysis of states of the prepectus is at least warranted. Apparent fusion of the prepectus with the pronotum does support classifying eumenids, masarids and vespids as a higher taxon, but an apparent correlation between pronotal mobility and presence or absence of an independent prepectus indicates that Brothers (1975) is incorrect in his hypothesis that a rigid pronotal and mesepisternal attachment is a synapomorphy for Vespoidea + Scoliidae (*sensu* present classification). However, falsification of this state as a synapomorphy does not falsify the hypothesis that Vespoidea and Scoliidae are sister taxa.

The recent phylogenetic analyses of Hymenoptera by Königsmann (1977, 1978a, b) and Rasnitsyn (1980) will hopefully stimulate additional research into the evolutionary history of this order. Some of the discrepancies in their conclusions resulted from different interpretations of the same states, but also from differences in knowledge of character-state distribution. Accuracy of phylogenetic reconstruction depends on accurate knowledge of structure and interpretation of homology. Consequently, clarification of the intraordinal relationships of Hymenoptera, and establishment of a stabile classification for the order will not be possible without comparative studies of structure. As mentioned in the introduction, I hope that this paper will not result in acceptance of inadequately proven generalizations or hypotheses based on only a very few characters, but will stimulate additional studies of comparative morphology of Hymenoptera.

Figure 2.1. *Janus abbreviatus* (Say), dorsolateral view of thorax.

Figure 2.2. *Urocerus albicornis* (Fab.), dorsal view of thorax.

Figure 2.3. *Xiphydria mellipes* Harris, dorsolateral view of thorax.

Figure 2.4. *Orussus sayii* (Westwood), dorsal view of thorax.

Figure 2.5. *Polistes* sp., posterolateral oblique view of thorax.

Figure 2.6. *Megischus texanus* Cresson, dorsal view of thorax.

Figure 2.7. *Codrus* sp., dorsolateral view of thorax.

Figure 2.8. *Megaspilus* sp., dorsal view of thorax.

Scale bar = 200 μm.

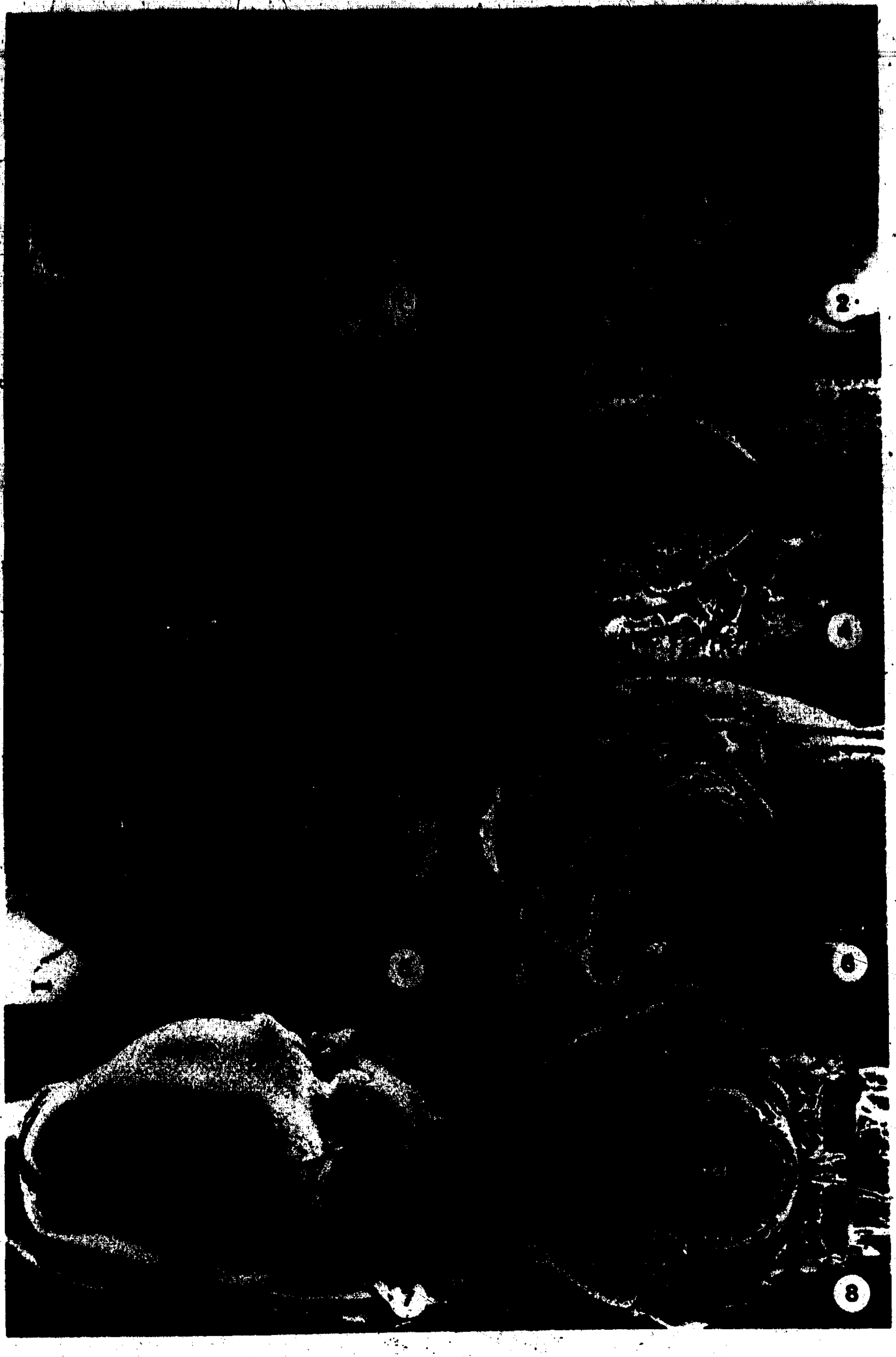
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Figure 2.9. *Xyelecia nearctica* Ross, lateral view of intersegmentalia between pro- and mesothorax.

Figure 2.10. *Janus abbreviatus* (Say), lateral view of intersegmentalia between pro- and mesothorax, pronotum removed.

Figure 2.11. *Pteronidea* sp., frontolateral view of intersegmentalia between pro- and mesothorax.

Figure 2.12. *Syntexis libocedrii* Rohwer, lateral view of intersegmentalia between pro- and mesothorax.

Figure 2.13. *Xiphydria mellipes* Harris, lateral view of intersegmentalia between pro- and mesothorax.

Figure 2.14. *Orussus sayii* (Westwood), frontal view of intersegmentalia between pro- and mesothorax, pronotum removed.

Figure 2.15. *Monomachus* sp., lateral view of intersegmentalia between pro- and mesothorax, pronotum and spiracle removed.

Figure 2.16. *Megischus texanus* Cresson, lateral view of intersegmentalia between pro- and mesothorax, pronotum and spiracle removed.

Scale bar = 200 μm.

Figure 2.17. *Torymus* sp., lateral pronotum-mesothorax.

Figure 2.18. *Hemiptarsenus* sp., ventral view of prepectus, prothorax removed.

Figure 2.19. *Ropronia garmani* Ashmead, posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.20. *Helorus anomalipes* (Panzer), posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.21. *Proctotrupes* sp., lateral pronotum-mesothorax.

Figure 2.22. *Proctotrupes* sp., posterolateral view of isolated pronotum.

Figure 2.23. *Calliscelio* sp., lateral pronotum-mesothorax.

Figure 2.24. *Paridris* sp., posterolateral view of isolated pronotum.

Scale bar = 100 μm.

Figure 2.25. *Propsilomma* sp., posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.26. *Orthogonalys pulchella* (Cresson), posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.27. *Lissonota montana* (Cresson), lateral pronotum-mesothorax.

Figure 2.28. *Diphyus ormenus* (Cresson), posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.29. *Megaspilus* sp., lateral pronotum-mesothorax.

Figure 2.30. Megaspilus sp., posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.31. *Ceraphron* sp., posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.32. *Megalyra* sp., posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Scale bar = 100 μm.

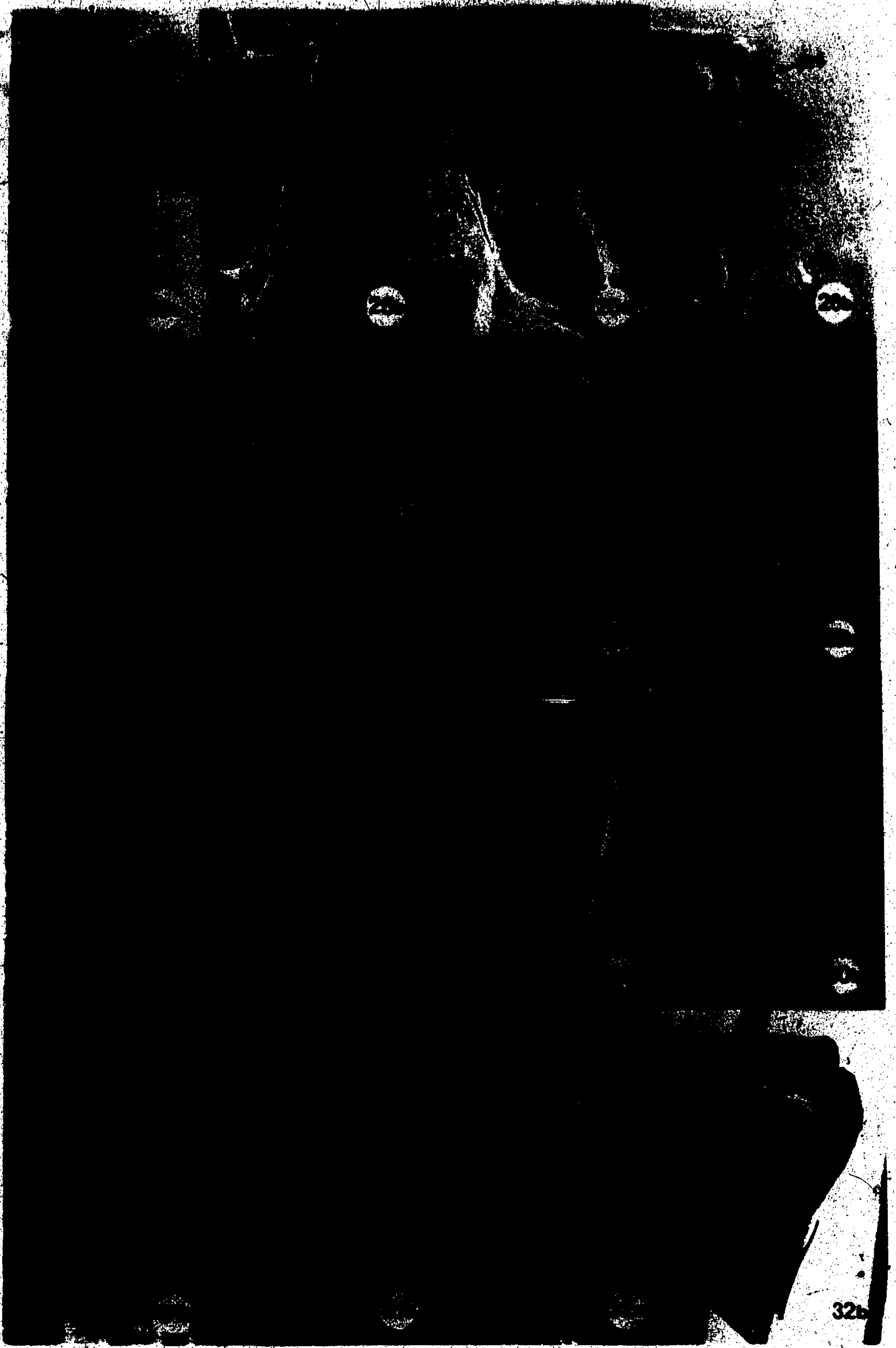

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Figure 2.33. *Vespula arenaria* (Fab.), inner view of posterolateral pronotal edge.

Figure 2.34. *Scolia bicincta* Fab.

a. frontal view of mesepisternal edge, pronotum removed.

b. inner view of posterolateral edge of pronotum.

Figure 2.35. *Myzinum* sp., prepectus and posterolateral pronotal edge.

a. posterior view.

b. inner view.

Figure 2.36. *Orussus sayii* (Westwood), posterolateral edge of isolated pronotum.

a. outer.

b. inner.

Figure 2.37. *Perilampus* sp., t_2-tr_2 pedicel.

Figure 2.38. *Gonatocerus* sp., dorsolateral view of isolated scutellar-axillar complex.

Scale bar = 200 μm.

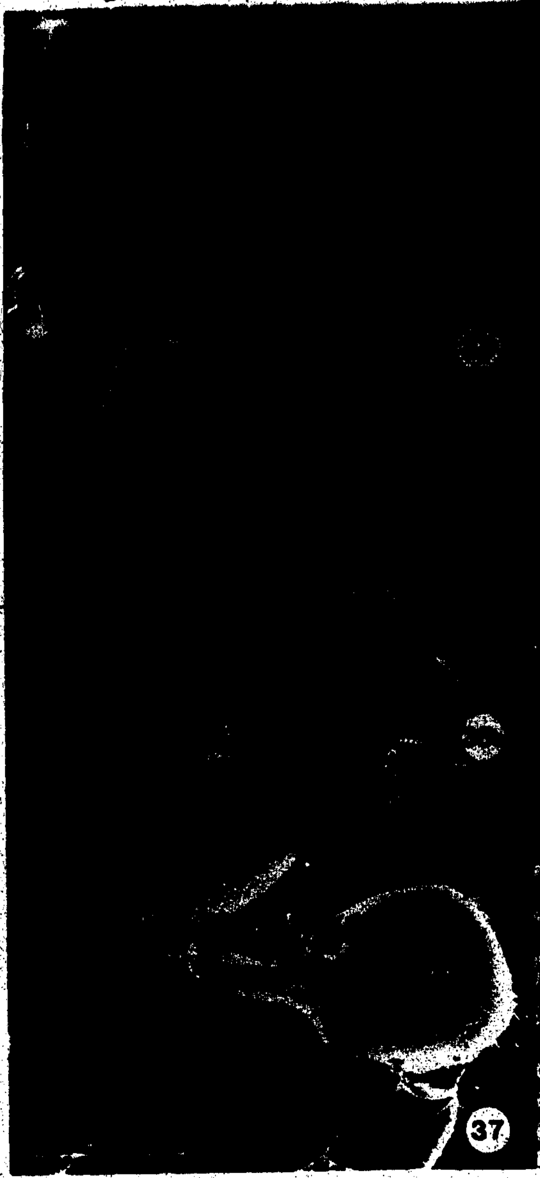

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Figure 2.39. *Xiphydria mellipes* Harris, sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.40. *Orussus sayii* (Westwood), sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.41. *Megischus texanus* Cresson, sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.42. *Psilus* sp., sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.43. *Megaspilus* sp., sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.44. *Megalyra* sp., sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.45. *Tanaostigmodes* sp., sagittal section of thorax, various muscles and mesofurca removed.

Figure 2.46. *Camponotus* sp., sagittal section of thorax, various muscles and mesofurca removed.

Scale bar = 200 μm.

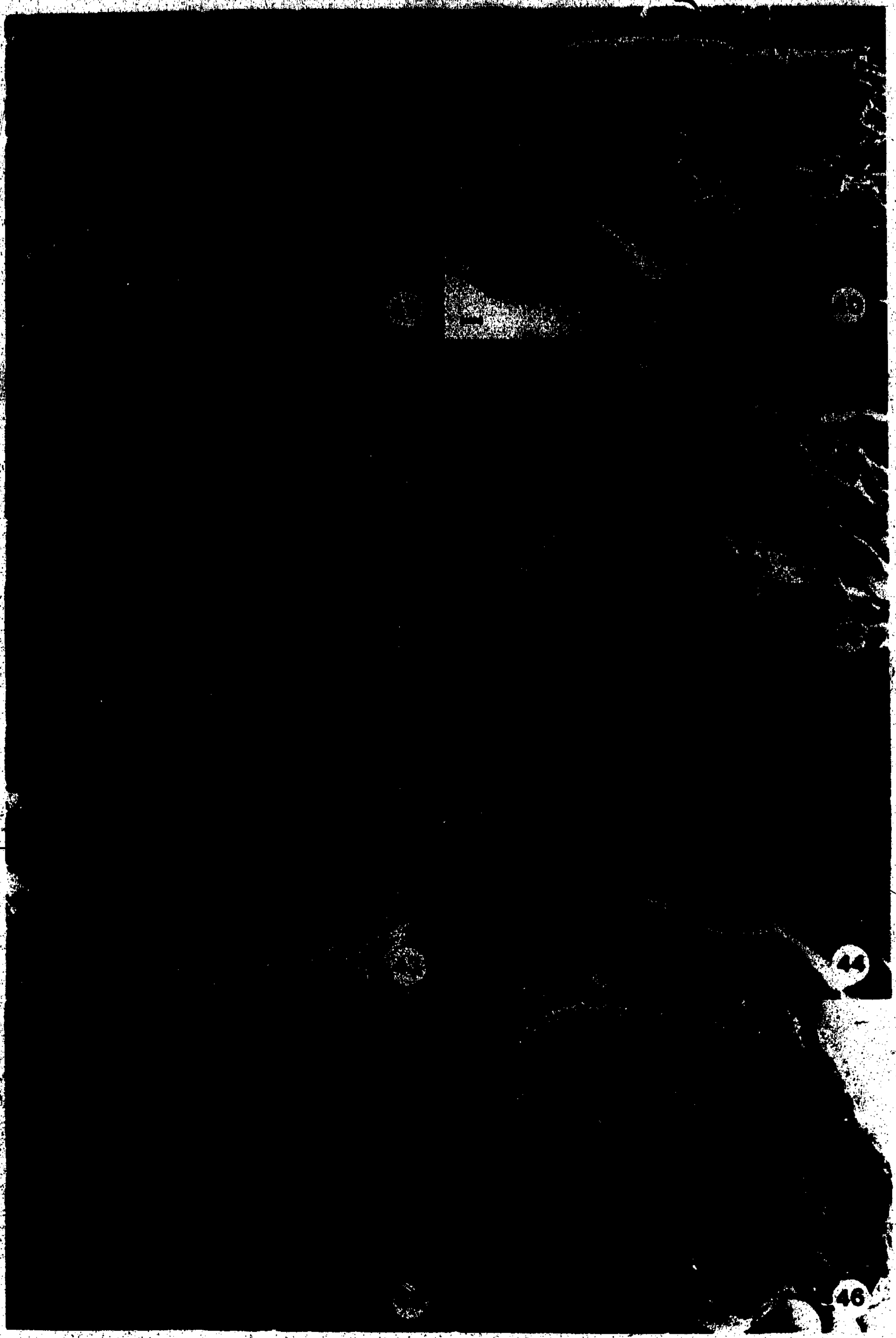

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Figure 2.47. *Helorus anomalipes* (Panzer), cross section of thorax between meso- and metathorax.

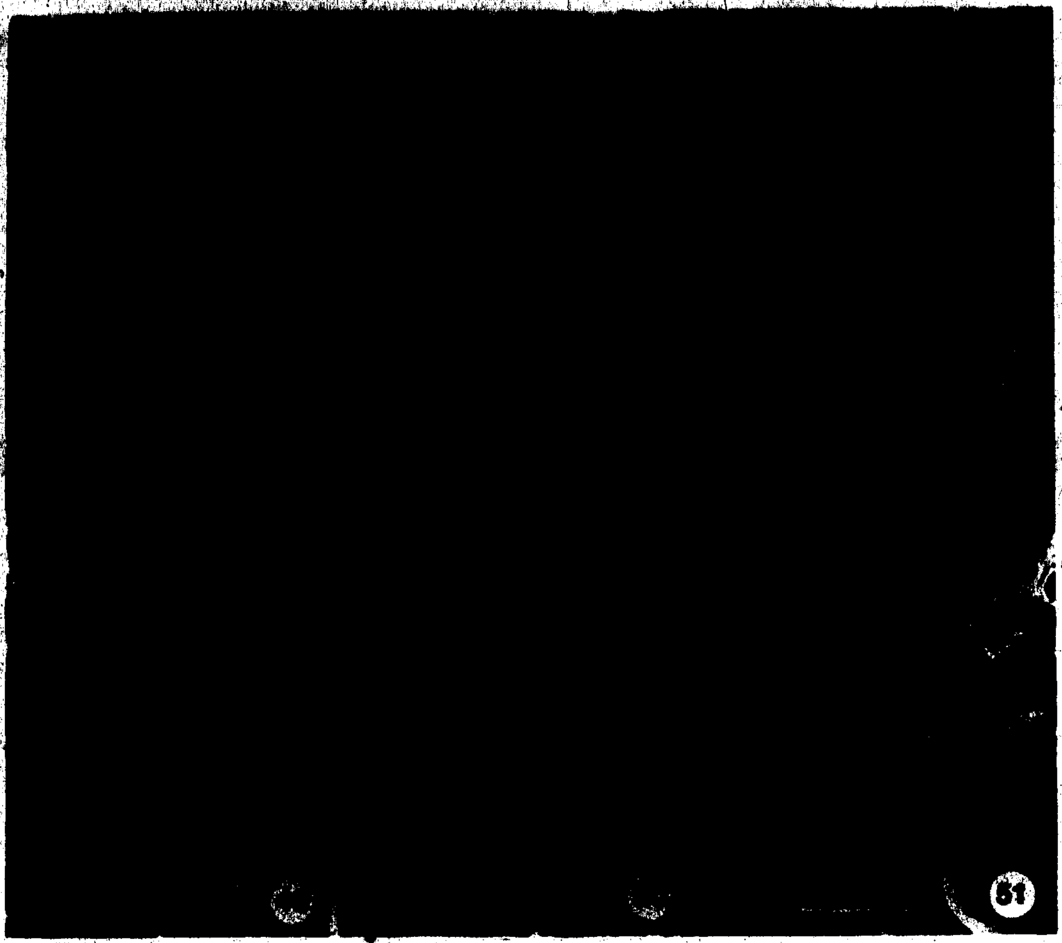
Figure 2.48. *Pristaulacus* sp., cross section of thorax between meso- and metathorax.

Figure 2.49. *Gasteruption* sp., cross section of thorax between meso- and metathorax, left side.

Figure 2.50. *Hyptia* sp., cross section of thorax between meso- and metathorax, left side.

Figure 2.51. *Sparasion* sp., cross section of thorax between meso- and metathorax, left side.

Scale bar = 200 μm.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2.7 Appendix 1: Definition of terms used for structural features

Anteroadmedian lines: anterior paramedial lines of the mesoscutum that represent the initial sites of attachment of the dorsolongitudinal indirect flight muscles in the pharate pupa.

Axillae (Figs. 2.3-2.6, 2.8): posterolateral regions of the mesoscutum that are segregated by the transscutal articulation.

Axillar carina (**axc**, Figs. 2.3, 2.5, 2.7): carina of the axilla that delineates the dorsal axillar surface from the lateral surface, and which is homologous with the posterolateral cuticular bend of the mesoscutum in symphytes without a transscutal articulation.

Axillula: lateral subdelineated region of scutellum that is demarked medially by a longitudinal line, and laterally by the scutoscutellar sulcus.

Basalare (**ba**, Figs. 2.9, 2.10, 2.12-2.16): sclerite that articulates with the base of each fore- and hind wing, into which insets the mesopleural-basalare muscle.

Dorsal axillar surface (**das**, Figs. 2.3-2.6, 2.8, 2.38): region of the axilla that is median to the axillar carina, and which is homologous with the horizontal region of the mesoscutum that is segregated by the transscutal articulation.

Epicnemium (**epc**, Fig. 2.11): general term for any anterior region of the mesopleuron that is delineated by a more or less vertical carina or sulcus.

First phragma: phragma from the anterior margin of the mesoscutum that is projected beneath the pronotum and is the anterior site of origin of the dorsolongitudinal indirect flight muscles.

Intersegmentalia: independent sclerites positioned in the membrane between segments.

Lateral axillar surface (**las**, Figs. 2.3, 2.5, 2.38): region of the axilla that is lateral to the axillar carina, and which is homologous with the posterolateral declivous mesoscutal region in symphytes without a transscutal articulation.

Lateral mesoscutal lobe: region of the mesoscutum lateral to the notauli.

Median mesoscutal lobe: region of the mesoscutum median to the notauli.

Median mesoscutal sulcus (**mms**, Figs. 2.1, 2.3, 2.4, 2.6, 2.8): median sulcus of the mesoscutum that is invaginated as a phragma and separates the dorsolongitudinal indirect flight muscles into two discrete bands.

Netrion (**net**, Figs. 2.23, 2.24): posterolateral region of the pronotum that is delineated externally by a row of foveae or a linear or foveolate sulcus, and internally by an apodeme.

Notauli (**no**, Figs. 2.1, 2.3, 2.4, 2.6, 2.8): sulci or lines of the mesoscutum that delineate the line of separation between the dorsoventral and dorsolongitudinal indirect flight muscles.

Occlusor muscle apodeme (**oma**, Figs. 2.20b, 2.22, 2.24, 2.25b, 2.28b, 2.30b, 2.31b): apodeme or ridge that is the site of origin of the mesothoracic spiracular occlusor muscle.

Parapsidal lines (**pl**, Figs. 2.4, 2.5, 2.7, 2.8): punctiform to elongate linear marks of the mesoscutum that represent the initial sites of attachment of the dorsovental indirect flight muscles in the pharate pupa.

Parapside (**par**, Figs. 2.4, 2.5): region of the mesoscutum delineated medially by the parapsidal line and laterally by the parascutal carina.

Parascutal carina (**psc**, Figs. 2.3, 2.5): lateral carina of the mesoscutum that segregates the dorsal, more or less horizontal mesocutal surface from the lateral, more or less vertical mesoscutal surface.

Parascutal lobe (**psl**, Fig. 2.2): region of the mesoscutum in Siricidae (Symphyta: Siricoidea) that is delineated by an oblique furrow anterolateral to the scutellum.

Posterolateral pronotal inflection (**ppi**, Figs. 2.20a, 2.22, 2.24, 2.25a, 2.26a, 2.33): internal ridge along the posterolateral edge of the pronotum that is hypothesized to be the degenerate prepectus fused to the pronotum.

Postspiracular sclerite (**pss**, Figs. 2.10-2.13): sclerite in most symphytes that is positioned between the pronotum and mesepisternum and between the mesothoracic spiracle and basalare.

Prepectus (**pre**, Figs. 2.9-2.12, 2.14-2.19): sclerite between the pronotum and mesepisternum that is the site of origin of the spiracular occlusor muscle.

Pronotal lobe (**prl**, Figs. 2.26, 2.27, 2.33, 2.34b, 2.36): posterolateral region of the pronotum that extends over the anterior edge of the mesepisternum so as to cover the mesothoracic spiracle.

Scutoscutellar sulcus (sss, Figs. 2.1-2.3): sulcus that delineates the scutellum from the mesoscutum.

Transscutal articulation (tsa, Figs. 2.3-2.8): transverse line of flexibility between the fore wing bases that subdivides the mesoscutum in some Hymenoptera.

2.8 Appendix 2: List of abbreviations used for figures

axc: axillar carina

axp: axillar phragma

ba: basalare

das: dorsal axillar surface

epc: epicnemium

fu$_2$-tr$_2$: mesofurcal-mesotrochanteral muscle

inv: invagination of occlusor muscle apodeme

las: lateral axillar surface

mss: median mesoscutal sulcus

net: netrion

no: notaulus

om: occlusor muscle

oma: occlusor muscle apodeme

par: parapside

pl: parapsidal line

pl$_2$-tr$_2$: mesopleural-mesotrochanteral muscle

ppi: posterolateral pronotal inflection

pre: prepectus

prl: pronotal lobe

psc: parascutal carina

psl: parascutal lobe

pss: postspiracular sclerite

scl: scutellum

sp: mesothoracic spiracle

sss: scutoscutellar sulcus

tg: tegula

tsa: transscutal articulation

t$_2$-2ph: mesotergal-second phragmal flexor

t$_2$-tr$_2$: mesotergal-mesotrochanteral muscle

2.9 Appendix 3

Taxa examined for presence and state of the mesotrochanteral depressor and second phragmal flexor: asterisk denotes dry mounted specimens which were rehydrated for dissection.

Symphyta

Xyeloidea:

Xyelidae: Xyela sp.; *Xyelecia nearctica Ross

Megalodontoidea:

Pamphiliidae: Acantholyda sp.; Pamphilius sp.

Tenthredinoidea:

Argidae: Arge sp.; Ptenus sp.

Diprionidae: Neodiprion sp.

Pergidae: Acordulecera sp.

Tenthredinidae: Dolerus sp.; Empria sp.; Hemitaxonus sp.; Hoplocampa sp.; Pachynematus sp.; Phymatocera sp.; Pteronidea sp.; Strongylogaster sp.; Taxonus sp.; Tenthredo sp.

Cephoidea:

Cephidae: Cephus cinctus Norton; Janus abbreviatus (Say)

Siricoidea:

Anaxyelidae: *Syntexis libocedrii Rohwer

Siricidae: Tremex columba (L.); Urocerus gigas flavicornis (Fab.)

Xiphydriidae: Xiphydria mellipes Harris

Orussoidea:

Orussidae: Orussus sayii (Westwood)

Apocrita: Aculeata

Chrysidoidea:

Bethylidae: Epyris sp.; Goniozus sp.; Pristocera (Acrepyris) sp.

Chrysididae: Chrysis sp.; Cleptes (Cleptes) semiauratus (L.); Hedychrum sp.

Plumariidae: *Plumarius sp.

Pompiloidea:

Pompilidae: Ceropales sp.; Dipogon sp.; Episyron sp.

Sphecoidea:

Sphecidae: Bembix sp.; Cerceris sp.; Ectemnius sp.; Isodontia sp.; Rhopalum sp.; Tachyspex sp.

Apoidea:

Andrenidae: Andrena sp.

Anthophoridae: Melissodes sp.; Nomada sp.

Colletidae: Hyaleus (Hyaleus) sp.

Halictidae: Agapostemon sp.; Dialictus sp.; Halictus sp.; Lasioglossum sp.

Megachilidae: Heriades sp.; Megachile sp.; Osmia sp.

Scolioidea:

Mutillidae: Timulla sp.

Sapygidae: Sapyga sp.

Scoliidae: Campsomeris (Dielis) plumipes confluenta (Say); Proscolia spectator Day; *Scolia (Discolia) bicincta Fab.

Sierolomorphidae: Sierolomorpha sp.

Tiphiidae: Brachycistis sp.; Myzinum sp.; Tiphia (Tiphia) sp.

Formicoidea:

Formicidae: Camponotus sp.; Crematogaster sp.; Lasius sp.; Myrmica sp.

Vespoidea:

Eumenidae: Ancistrocerus sp.; Parancistrocerus sp.; Symmorphus cristatus (Saussure)

Masaridae: Pseudomasaris sp.

Vespidae: Polistes fuscatus aurifer Saussure; Vespula arenaria (Fabricius)

Apocrita: Terebrantes

Ceraphronoidea:

Ceraphronidae: Ceraphron sp.

Megaspilidae: Conostigmus sp.; Megaspilus sp.; Lagynodes sp.

Chalcidoidea:

Aphelinidae: Coccobius sp.; Coccophagus sp.

Chalcididae: Brachymeria sp.; Chalcis sp.; Haltichella sp.; Spilochalcis sp.

Elasmidae: Elasmus sp.

Encyrtidae: Charitopus sp.; Cheiloneurus sp.; Encyrtus sp.; Leptomastix sp.; Ooencyrtus sp.

Eucharitidae: Eucharis sp.; Kapala sp.; Pseudometaga sp.

Eulophidae: Achrysocharella sp.; Dicladocerus sp.; Diglyphus sp.; Euplectrus sp.; Hemiptarsenus sp.; Tetrastichus sp.

Eupelmidae: Anastatus sp.; Calosota sp; Eupelmus sp.; Eusandalum sp.; Macroneura sp.; Metapelma sp.; Tanaostigmodes sp.

Eurytomidae: Eudecatoma sp.; Eurytoma sp.; Harmolita sp.

Leucospidae: Leucospis sp.

Mymaridae: Acmopolynema sp.; Anagrus sp.; Anaphes sp.; Gonatocerus sp.; Mymar sp.; Ooctonus sp.

Ormyridae: Ormyrus sp.

Perilampidae: Euperilampus sp.; Perilampus sp.; Steffanolampus sp.

Pteromalidae: Chalcidectus sp.; Epistenia sp.; Halticoptera sp.; Heydenia sp.; Nasonia sp.; Pteromalus sp.; Spalangia sp.; Trigonoderus sp.

Torymidae: Megastigmus sp.; Monodontomerus sp.; Podagrion sp.; Torymus sp.

Cynipoidea:

Cynipidae: Callirhytis sp.; Diplolepis sp.

Eucoilidae: Pseudeucoila sp.

Figitidae: Anacharis sp.; Figites sp.; Neralsia sp.; Paraspicera sp.; Prosaspicera sp.

Ibaliidae: *Ibalia sp.

Ichneumonoidea:

Braconidae: Agathus sp.; Apanteles sp.; Bracon sp.; Chelonus sp.; Doryctes sp.; Macrocentrus sp.; Meteorus sp.; Opius sp.; Spathius sp.

Ichneumonidae: Coccygomimus sp.; Diphyus sp.; Exetastes sp.; Glyphicnemis sp.; Lissonota sp.; Mesochorus sp.; Ophion sp.; Rhyssa sp.; Scambus sp.

Paxylommatidae: Hybrizon sp.

Terebrants not assigned to superfamily:

Diapriidae: Aclista sp.; Belyta sp.; Coptera sp.; Dissoxylabis sp.; Ismarus flavicornis (Thomson); Oxylabis sp.; Propsilomma columbianum (Ashmead); Psilus sp.; Trichopria sp.

Evaniidae: Hyptia sp.; Prosevania sp.

Gasteruptionidae: Aulacus sp.; Gasteruption sp.; Pristaulacus sp.

Heloridae: Helorus anomalipes (Panzer)

Megalyridae: Megalyra sp.

Monomachidae: Monomachus sp.

Pelecinidae: Pelecinus polyturator (Drury)

Platygastridae: Leptacis sp.

Proctotrupidae: Exallonyx sp.; Phaenoserphus vistor (Haliday); Proctotrupes sp.

Roproniidae: *Ropronia garmani Ashmead

Scelionidae: Calliscelio sp.; Holoteleia sp.; Scelio sp.; Sparasion sp.; Trimorus sp.

Stephanidae: Megischus texanus Cresson; Schletterèrius cinctipes (Cresson)

Trigonalidae: *Orthogonalys pulchella (Cresson)

Vanhorniidae: Vanhornia eucnemidarum Crawford

3. EVIDENCE FOR MONOPHYLY AND RELATIONSHIPS OF CHALCIDOIDEA, MYMARIDAE, AND MYMAROMMATIDAE (HYMENOPTERA: TEREBRANTES)[1]

3.1 Synopsis

Twenty-three characters or character systems of adults and larvae of Terebrantes are analyzed for evidence of monophyly and phyletic relationships of Chalcidoidea, Mymaridae, and Mymarommatidae. The taxa are considered to be a monophyletic group based on three hypothesized synapomorphies: mesotrochanteral depressor without fu_2-tr_2 or mesoscutal portion of t_2-tr_2; axillar phragma as site of origin for all or part of t_2-tr_2 muscle; and independent basal ring absent from male genitalia. The family Mymaridae is considered to be monophyletic based on at least three apomorphies: fore wing with hypochaeta; head with frontal, median and supraorbital sulci; and toruli distinctly closer to inner margin of eye than to each other. Chalcidoidea, including Mymaridae, is considered to be a monophyletic taxon based on three apomorphies: prepectus externally visible, at least dorsally adjacent to lateral edge of mesoscutum; mesothoracic spiracle positioned at exposed lateral edge of mesoscutum; and multiporous plate sensilla of antenna with unique structure, as described in text. Mymarommatidae is considered to be the monophyletic sister group of Chalcidoidea based on several apomorphies, including four autapomorphies: head composed of frontal and occipital sclerites, which are connected by pleated membrane along hyperoccipital region; hind wing stalk-like, without membrane and terminated in bifurcation that clasps fore wing; fore wing with reticulate pattern formed by raised lineations of membrane; and axillar portion of t_2-tr_2 muscle absent. Phyletic relationship of Serphitidae with Mymarommatidae is deemed inconclusive because relevant internal character states of amber fossil serphitids can not be determined. It is suggested that mymarommatids be accorded family status, but not be assigned to superfamily until phyletic relationships are more accurately determined in Terebrantes. A matrix summarizes character-state distribution of most characters analyzed for Terebrantes,

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[1] A version of this chapter has been accepted for publication in The Canadian Entomologist.

and a cladogram illustrates hypotheses of character-state evolution and proposed relationships.

3.2 Introduction

Authors disagree about relationships and formal classification of mymarids and mymarommatids in parasitic Hymenoptera (Terebrantes). Mymarids initially were considered as members of the superfamily Proctotrupoidea by Förster (1856) and by Dalla Torre (1898), until Ashmead (1904) proposed the superfamily Chalcidoidea and included Mymaridae as one of 14 families. A separate superfamily, Mymaroidea, was proposed for Mymaridae and Signiphoridae by Ghesquière (1942), but most workers since Ashmead have continued to include both taxa in Chalcidoidea. However, Kozlov and Rasnitsyn (1979) hypothesized mymarids originated from the same clade as the extinct family Serphitidae, and thus should be classified in Proctotrupoidea as originally placed by Förster. Rasnitsyn (1980) altered this hypothesis slightly by proposing both serphitids and mymarids were derived from within Scelionidae, but independently and probably at different times. All three families were transferred by him to his newly proposed superfamily, Diaprioidea.

Though the first described mymarommatid was misidentified as a species of *Proctotrupes* Latreille (Proctotrupidae) by Duisburg (1868), placement of mymarommatids in Chalcidoidea was generally accepted until recently. Disagreement centered upon whether mymarommatids are merely aberrant mymarids, and should be accorded some infrafamilial rank in Mymaridae (Annecke and Doutt 1961, Yoshimoto 1975), or whether they are sufficiently distinct to warrant separate familial status[3] (Debauche 1948, Königsmann 1978a, Yoshimoto 1984). Kozlov and Rasnitsyn (1979) proposed the radically new hypothesis that mymarommatids are not related to chalcidoids, but to serphitids. They classified mymarommatids as a monobasic subfamily in the otherwise extinct family Serphitidae.

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[3] The family name Mymarommidae as originated by Debauche (1948) was corrected to Mymarommatidae by Brues, Melander and Carpenter (1954).

Königsmann (1978a) considered monophyly of Chalcidoidea to be highly probable based on wing venation, metallic luster, and antennal, pronotal, and male genitalic structure. He classified Mymaridae in Chalcidoidea, and stated that though mymarids possess none of the synapomorphic states elaborated for the superfamily, all of their states either could be derived from those of chalcidoids or else correspond to them. He further considered mymarommatids to share three synapomorphies with mymarids: profile of the fore wings, absence of anelli, and overall habitus. He accorded mymarommatids family status, but stated that a more detailed study was required to determine whether they should be included in Mymaridae, or should be considered as the sister group of Mymaridae.

Schauff (1984) also classified mymarids as a family of Chalcidoidea, uniting members on the basis of three proposed synapomorphies: presence of an exposed prepectus; elongate sensory ridges (multiporous plate sensilla) on the antennae; and a particular ovipositor structure (though polarity of this latter character was questioned). Mymarommatids were recognized as a separate family, but placement to superfamily was said to be problematic.

I (Gibson in press) previously described transformation series for states of 13 characters of the pro- and mesothorax in Hymenoptera, and discussed what phylogenetic inferences could be made from the different states. Of 30 hypothesized derived states shared among members of different higher taxa, two were considered unique (autapomorphic) for Chalcidoidea in Apocrita: position of mesothoracic spiracle at exposed lateral edge of mesoscutum, and presence of axillar phragma as partial site of origin for mesotergal-mesotrochanteral (t_2-tr_2) muscle. Mymarids were included in the above analysis, but mymarommatids were not.

Shared derived character states can be homologous and the result of inheritance from a common ancestor (synapomorphy), or non-homologous and due to convergence (homoplasy). Because hypotheses of synapomorphy and homoplasy are made partly on the basis of parsimony and congruence of different character-state transformations, hypotheses of monophyly, and of phyletic relationships, should ideally be made only after a detailed analysis of as many characters as possible. This paper analyzes character states that were used previously to define or to suggest relationships of Chalcidoidea, Mymaridae, and Mymarommatidae, and attempts to determine which shared states are synapomorphic and valid indicators of monophyly or relationships, and which states are symplesiomorphic or homoplasous.

3.3 Materials and Methods

3.3.1 Materials

Taxa examined for internal structures include those listed in Appendix III of Gibson (in press) and additional taxa listed below. Character-state distribution in Mymaridae is based on specimens in the Canadian National Collection (CNC), including slide-mounted individuals representing 32 genera or subgenera. Character-state distribution in Mymarommatidae is based on specimens representing the seven described extant species - *Palaeomymar anomalum* (Blood and Kryger 1922), [= *P. succini* Meunier 1901, *vide* Doutt 1973; nec *P. duisburgi* (Stein 1877)], *P. goethei* (Girault 1920), *P. mirum* (Girault 1931), *P. mirissimum* (Girault 1935), *P. buyckxi* (Mathot 1966), *P. insulare* (Valentine 1971), and *P. cyclopterus* Fidalgo and De Santis (1982); amber inclusions representing five of the seven described extinct species - *Archaeromma minutissimum* (Brues 1910), *A. nearcticum* Yoshimoto (1975), and *P. agapa*, *P. mandibulatum* and *P. senonicum* Kozlov and Rasnitsyn (1979); and additional specimens in the CNC, Museum of Comparative Zoology, Harvard University (MCZ), and Zoologisk Museum, Copenhagen, representing undescribed extant and extinct species. Character-state distribution in Serphitidae is based on study of amber fossil inclusions in the CNC and on the type specimen of *Microserphites parvulus* Kozlov and Rasnitsyn (1979).

3.3.2 Specimen preparation and illustration

Figures 14 and 31 are photographs of slide mounts using a Carl Zeiss Ultraphot II microscope. Other illustrations are SEM photomicrographs, with methods of specimen preparation as described in Gibson (in press). Abbreviations used for figures are explained in the Appendix.

3.3.3 Phylogenetic methods

The philosophical approach used here to determine probable relationships is phylogenetic *sensu* Hennig, *i. e.*, relationship as defined by common ancestry is determined by shared, derived, homologous character states (synapomorphies), but not by shared primitive character states (symplesiomorphies), nor by independently derived and thus non-homologous character states (homoplasies). Accurate phylogenetic reconstruction requires that similarity due to synapomorphy be distinguished from similarity resulting from the latter two causes.

Hypotheses of apomorphy relative to plesiomorphy depend on polarity, or the direction of character-state evolution. Jong (1980) reviewed various methods proposed to distinguish derived (apomorphic) from primitive (plesiomorphic) states. Ideally, a sister group is proposed and out-group comparisons are made. Though the works of Königsmann (1978a, b) and Rasnitsyn (1980) attempted to analyze phyletic relationships of Apocrita, discrepancies in their conclusions illustrate how uncertain is our knowledge of the evolution of Apocrita. Monophyly of Terebrantes is questionable, and most hypotheses of sister-group relationships in Terebrantes are tenuous. Consequently, polarity of character states in this analysis is based partly on the criterion of commonality, *i. e.*, the most widely distributed state in Apocrita is considered to be plesiomorphic. However, when possible, polarity was hypothesized for character states after comparison of the respective states in Symphyta, hypotheses made of the groundplan (plesiomorphic) state of the character for Apocrita, and transformation series of states hypothesized in Apocrita. Study of character-state distribution is based on extant Hymenoptera, plus fossil serphitids and mymarommatids.

Hypotheses of synapomorphy relative to homoplasy are based on congruence or non-congruence of character-state transformations and judgements as to which transformation series are most reliable as phylogenetic indicators. In accordance with a system developed by Hecht (1976), apomorphic states that are the result of loss are considered to be least reliable because it is not possible to determine whether common absence is the result of a single or multiple losses. Apomorphic states that are the result of reductions, those that are part of a functional complex, and those that are both innovative and unique are considered to be increasingly more reliable as indicators of synapomorphy.

3.4 Phylogenetic analysis of structural features

Twenty-three characters or character systems of adults and larvae are analyzed below. Structural features of adults are discussed first, in morphological sequence beginning with appendages of the head, followed by features of the larvae. Character-state distribution and hypotheses of character-state transformation for 20 of the 23 analyzed character systems are summarized for Terebrantes in Table 3.1. Characters 12 (fore wing venation) and 23 (structure of larvae) are not included in Table 3.1 because they detail habitus, not specific character states. Character 22 (metallic luster of adults) is not included in the table because of insufficient analysis to be meaningful.

3.4.1 Number of antennal articles

One of three character states of the antenna considered by Königsmann (1978a) to indicate probable monophyly of Chalcidoidea was possession of 13 articles by most members. Nikolskaya (1952), Gordh (1979), and Rasnitsyn (1980) also used this as one state to define Chalcidoidea.

Number of antennal articles possessed by terebrants is listed in Table 3.1, character 1. Chalcidoids have from 4 to 26, but the maximum number for most is 13. The only chalcidoids to have more than 13 articles are individuals of *Diglochis* Förster (Pteromalidae), which have 14 (Dzhanokmen 1979), and members of some genera of Eucharitidae. Numerous and diverse chalcidoids have less than 13 articles, including known Aphelinidae, Elasmidae, Encyrtidae, Eulophidae, Signiphoridae, Tetracampidae and Trichogrammatidae. The most parsimonious explanation for this distribution is that 13 articles is the groundplan number of antennal articles for Chalcidoidea, and that this number was secondarily increased in at least 2 clades, and decreased independently an unknown number of times in other clades.

Proctotrupidae, Vanhorniidae and Evaniidae also have 13 antennal articles (Table 3.1). Relationships between these three families are unknown, as are relationships between them and Chalcidoidea. Consequently, the common number of antennal articles could be due to inheritance from a common ancestor, or the result of convergence, making this state unreliable as an indicator of monophyly for Chalcidoidea.

Number of antennal articles is also of little value for determining relationships of mymarids and mymarommatids. The plesiomorphic number of articles for mymarommatids is most probably 13. Females and males known from the Cretaceous had 13 articles, though the terminal four were partly fused and differentiated as a club in females (Yoshimoto 1975). Extant male mymarommatids also have 13 antennal articles, but females have only 9 to 11, and the ultimate article is differentiated as a club (Yoshimoto 1984, figs. 89, 90). The club of females apparently is the result of complete fusion of the terminal four articles in all species except *P. insulare* (Valentine). The club is subdivided by a suture in females of this latter species. Many male mymarids have 13-articled antennae, but females have less than 13 articles and a differentiated club. The antennal club and lesser number of articles in females is probably the result of fusion of some of the apical articles, but reduction in number of articles in many females and males is probably also simply the result of loss.

Königsmann (1978a) is correct in stating that the number of antennal articles of mymarids and mymarommatids either corresponds to the number characteristic of chalcidoids, or can be derived from it, but this no more indicates a close relationship with chalcidoids than does the fewer number of articles characteristic of scelionids, serphitids, platygastrids, or ceraphronoids (Table 3.1).

3.4.2 Anellus

The second antennal character state considered by Königsmann (1978a) to indicate probable monophyly of Chalcidoidea was presence of one or more ring-like antennal articles, anelli, between the pedicel and flagellum. He assumed secondary loss for those chalcidoids lacking an anellus. Kozlov and Rasnitsyn (1979), and Rasnitsyn (1980), interpreted absence of an anellus from mymarids and mymarommatids as evidence that these are not related to chalcidoids. Schauff (1984) stated that presence of an anellus might be a synapomorphy for Chalcidoidea exclusive of Mymaridae, but absence of an anellus was not evidence that mymarids are unrelated to chalcidoids.

Table 3.1, character 2, lists distribution of an anellus in Terebrantes. Only chalcidoids and helorids have an anellus. Reference to anelli in Diapriidae (Ambositrinae) and Ichneumonidae by Königsmann (1978a) and Rasnitsyn (1980) is incorrect. Naumann (1982) determined that the basal region of the first flagellomere in ambositrines, which Masner (1961) called the anellus, is only an annular thickening and not an independent antennal article. The same is true for the anellus-like basal region of the first flagellomere of some ichneumonids (W. R. M. Mason, pers. comm.).

Exact phyletic relationships between Heloridae and Chalcidoidea are unknown, so that presence of an anellus is lessened as a reliable indicator of monophyly for Chalcidoidea. Distribution of an anellus in Chalcidoidea makes this state even more unreliable for phylogenetic inference. Anelli are apparently nothing more than reduced flagellomeres, and designation of one or more basal flagellomeres as anelli in many chalcidoids is subjective. Some members of most chalcidoid families lack anelli, as do known Leucospidae and Eucharitinae

(Eucharitidae). Königsmann (1978a) may be correct in stating that the wide distribution of an anellus indicates this as a groundplan character of Chalcidoidea, but if so, the anellus is prone to loss.

Mymarommatids and mymarids lack an anellus, though the first flagellomere of some mymarids is quite small (Schauff 1984). As stated by Schauff, absence of anelli in mymarids and mymarommatids does not prove that these are unrelated to chalcidoids, nor that they are related to scelionids and serphitids. If absence of an anellus in mymarids and mymarommatids is plesiomorphic, either taxon could still be the sister group of Chalcidoidea. Furthermore, if absence is plesiomorphic, this state can not be used as evidence that mymarids and mymarommatids are related to serphitids, or to any other taxon whose members lack an anellus.

3.4.3 Geniculate antennae

The third antennal character state considered by Königsmann (1978a) to indicate probable monophyly of Chalcidoidea was geniculate antennae. Terebrantes with geniculate (abruptly bent) antennae have the pedicel markedly narrowed basally, with only a relatively small area of articulation with the scape, and the pedicel and flagellum are held at an abrupt angle to the scape (Fig. 3.3).

Table 3.1, character 3, lists distribution of geniculate antennae in Terebrantes. Chalcidoids have geniculate antennae, except for most eucharitines (Eucharitidae, Eucharitinae), which have straight antennae. Eucharitines without geniculate antennae are also unusual in Chalcidoidea because the scape is quite short, which illustrates a general correlation between scape length and geniculate or non-geniculate antennae in Terebrantes. Relative scape length is admittedly subjective, but terebrants in Table 3.1 listed with geniculate antennae also have a relatively long and slender scape, whereas those listed with non-geniculate antennae have a relatively short and stubby scape. Monomachids have non-geniculate antennae, with a scape of intermediate length. Most mymarids have geniculate antennae, but a scape of varied shape, from long and slender to short and stubby, even in different sexes of the same species (*cf.* sc, Figs. 3.2, 3.3). However, if the scape is short and stubby, or there is not a distinct bend in the antenna between the scape and pedicel, the pedicel is still markedly narrowed, with only a very small area of articulation with the scape. A short scape in some mymarids is thus indicated to be due to secondary modification.

Rasnitsyn (1980) hypothesized a long scape as one synapomorphy that united members of his new superfamily, Diaprioidea, but Austroniidae, which he included in Diaprioidea, have a relatively short scape. Even if Rasnitsyn's hypothesis of synapomorphy is correct for the other taxa he included in Diaprioidea, the long scape of members would be convergent with that possessed by chalcidoids and ceraphronoids. Consequently, the typically long scape and associated geniculate antenna of chalcidoids, mymarids, and mymarommatids, could be the result of synapomorphy, symplesiomorphy, or homoplasy.

3.4.4 Multiporous plate sensilla of antenna

Presence of multiporous plate sensilla (= rhinaria, longitudinal ridges or sensilla) on some flagellomeres of mymarids, but not mymarommatids, was one reason Debauche (1948) separated Mymarommatidae as a family distinct from Mymaridae. Kozlov and Rasnitsyn (1979) considered absence of antennal sensilla from mymarommatids to not only differentiate them from mymarids, but to relate them to serphitids. Furthermore, they and Rasnitsyn (1980), concluded that presence of sensilla on the antennae of mymarids indicated contradictory evidence of relationships, because members of other taxa they assigned to Diaprioidea lack antennal sensilla. They hypothesized the similar sensilla of mymarids and chalcidoids could be the result of independent gain, because ichneumonoids and cynipoids also have elongate antennal sensilla.

Barlin and Vinson (1981) showed that antennal sensilla of chalcidoids differ in at least four states from the superficially similar sensilla of ichneumonoids. Chalcidoid sensilla have the distal end free from the antennal surface and they are not surrounded by grooves, as in ichneumonoids. Furthermore, chalcidoid sensilla have pore tubules, unlike the sensilla of other Hymenoptera examined, and in most female chalcidoids studied there were two types of antennal sensilla. Unfortunately, mymarids and cynipoids were not included in the study.

I examined external structure of the antennae of males and females of *Acmopolynema* Ogloblin, *Anaphes* Haliday, *Camptoptera* Förster, *Chaetomymar* Ogloblin, *Gonatocerus* Nees, *Ooctonus* Haliday, and *Polynema* Haliday (Mymaridae), using SEM. Males examined had at least some sensilla on all flagellomeres, except for the ring-like second flagellomere of *Camptoptera*. The sensilla were not surrounded by grooves, were ridge-like raised above the antennal surface, and the apex of each sensillum was extended beyond the apex of the article (Fig. 3.4). Females had few or no sensilla on the flagellomeres, but all had sensilla on the club. The sensilla were projected beyond the apex of flagellomeres, but only rarely so on the club. Debauche (1948) studied distribution of the antennal sensilla in a larger number of mymarid taxa, though he did not examine their structure. He concluded that male mymarids normally have multiporous plate sensilla (= crêtes sensorelles *sensu* Debauche) on all flagellomeres, whereas females have sensilla on the club, but lack these on the first flagellomere and vary in presence or absence of sensilla on other flagellomeres. However, one undescribed species of *Gonatocerus*, does have two sensilla on the first flagellomere (J. Huber, *in litt.*).

I also examined the antennal sensilla of males and females of *Ibalia* Latreille (Ibaliidae), *Pseudeucoila* Ashmead (Eucoilidae), *Anacharis* Dalman (Figitidae) and *Andricus* Hartig (Cynipidae) (Cynipoidea), using SEM. The sensilla were flat, or only slightly raised above the plane of the flagellomere (Figs. 3.5, 3.6); did not project beyond the apex of the flagellomere (Fig. 3.6), or only a few did (Fig. 3.5); and except for the sensilla of *Pseudeucoila* (Fig. 3.6) were surrounded by very fine grooves (Fig. 3.5).

Very few taxa were studied to generalize about the structure of mymarid, and particularly cynipoid antennal multiporous plate sensilla. However, external structure of the sensilla of mymarids appears to be similar to that described for various chalcidoids by Barlin and Vinson (1981), and unlike the antennal sensillar structure of cynipoids and ichneumonoids. Consequently, external structure of the antennal sensilla of mymarids and chalcidoids can be tentatively considered as indicative of monophyly of these two taxa. Supportive evidence for this hypothesis should be acquired through study of internal structure of the sensilla. Barlin and Vinson (1981) showed that internal structure of the multiporous plate sensilla of chalcidoids differed from that of ichneumonoids. It must also be shown that internal structure of the antennal sensilla of mymarids is like that described for chalcidoids, and that this common structure is dissimilar to the internal structure of the sensilla of cynipoids.

Though I presently interpret lack of antennal multiporous plate sensilla as plesiomorphic for Terebrantes, sensilla of various shapes and presumably diverse structure are possessed by many other terebrants. A comprehensive study is required to determine distribution and structure of the sensilla throughout Terebrantes. It is possible that the antennal sensillar structure of mymarids and chalcidoids is not uniquely derived, but is only part of some transformation series and not necessarily indicative of monophyly.

Mymarommatidae is indicated to be at most the sister group of Mymaridae + Chalcidoidea, if absence of antennal sensilla is plesiomorphic, *i. e.*, not due to secondary loss. Furthermore, if absence is plesiomorphic, it is not evidence of a relationship between mymarommatids and serphitids, as suggested by Kozlov and Rasnitsyn (1979).

3.4.5 Exodont mandibles

Exodont mandibles do not overlap at the midline and they have outwardly directed teeth (Figs. 3.7, 3.8). Table 3.1, character 5, lists distribution of exodont mandibles in Terebrantes. Mymarommatids and vanhorniids (*Vanhornia* Crawford) have exodont mandibles, as do individuals of *Exodontomphale* (Chalcidoidea: Eulophidae) (Bouček 1984), and members of four tribes of Ichneumonoidea (Ichneumonidae: Tryphoninae - Idiogrammatini; Braconidae: Alysiinae - Alysiini, Dacusini; Opiinae - Exodontiellini) (Wharton 1977). The reconstructed phylogeny for Braconidae by van Achterberg (1984) indicates exodont mandibles are not a groundplan character of Braconidae, but are secondarily derived in the family. Restricted distribution also indicates exodont mandibles are secondarily and independently derived in Eulophidae and Ichneumonidae. However, common occurrence of such mandibles in vanhorniids and mymarommatids could either be the result of inheritance from a common ancestor, or convergence.

Nothing is known about the life history of mymarommatids, but the very small body size of individuals (0.75 mm or less, excluding antennae) may indicate that they parasitize eggs of other insects, or possibly arachnids. If so, their mandibles may be used to break the chorion of the host egg so that the adult can escape. Exodont mandibles of Alysiinae (Braconidae) are similarly used to break away the cap of the puparium of their host cyclorrhaphous Diptera (Griffiths 1964).

3.4.6 Structure of the head

Mymarommatids differ from other hymenopterans in structure of the head. The head is composed of a convex frontal sclerite (fsc, Figs. 3.8, 3.9), and a separate, flat, occipital sclerite (osc, Fig. 3.9). The two sclerites articulate near each mandibular base, and are connected by pleated membrane along the hyperoccipital region (pmb, Fig. 3.9). The membranous region is extensible because it is pleated, hence the head can expand or contract in an accordion-like manner. Numerous specimens of an undescribed species near *Palaeomymar anomalum* Blood and Kryger showed this. Some of the specimens have the dorsal edge of the occipital sclerite deeply angled in the head, hood-like covered by the vertex, whereas others have the dorsal edge of the occipital sclerite angled away from the frontal sclerite, with the connecting membrane stretched between the two as a convexly expanded region. Apparently sclerotized, arch-like 'ribs' are visible in the membrane, and these presumably function in pleating the membrane.

A pleated, membranous, hyperocciptial region, was not visible in all mymarommatids examined because of the manner in which some specimens were mounted. However, a convex frontal region and a flat occipital region was evident in all individuals, indicating a membranous region was probably also present. Consequently, I interpret a pleated, membranous, hyperoccipital region, as a probable autapomorphy that indicates monophyly of Mymarommatidae.

The head of mymarids is also unusual for hymenopterans. Three sets of sulci, the median (ms), frontal (fs) and supraorbital sulci (ss, Fig. 3.2) subdivide the head into a frontal, dorsal, and two lateral regions. [The sulci are often called carinae or sutures, but I use the terms suture and sulcus as defined by Daly (1964)]. All mymarids have the three sets of sulci (Debauche 1948, Schauff 1984), which Ogloblin (1959) discovered represent lines of inrolled and flexible cuticle (= trabéculas *sensu* Ogloblin).

Other hymenopterans are not known to have this particular head structure, though Trjapitzin (1977) lists four genera of Encyrtidae (Chalcidoidea) with a similar pattern of light colored membranous lines. Numerous Eulophidae (Chalcidoidea) also have a transverse or V-shape sulcus on the frons (see figures in Yoshimoto 1977, 1978 and Schauff 1985), as do some Aphelinidae. Furthermore, some Trichogrammatidae (Chalcidoidea) have both a transverse sulcus on the frons and a vertical sulcus along the inner margin of each eye (see Viggiani 1978, fig. 1). Unfortunately, internal development of the lines or sulci is unknown.

Ogloblin (1959) suggested the lines of inrolled and flexible cuticle on the head of mymarids allow expansion of the head, though function of this was unknown. Bakkendorf (1934) found adults of several different mymarid species he studied used their mandibles to chew through the host egg chorion, as was noted for *Caraphractus cinctus* Walker by Jackson

(1961). Neither author mentioned seeing the head expand during adult emergence from the host egg. Consequently, if the lines of inrolled cuticle are correlated with head expansion, function of this is likely something other than rupturing the egg chorion. Trjapitzin (1977) suggested the lines of weakness on the head of encyrtids give the head a greater elasticity, and the same may be true for the lines of inrolled cuticle of mymarids.

Because only mymarids have the pattern of median, frontal, and supraorbital sulci, this head structure can be tentatively considered as an apomorphic state that indicates monophyly of Mymaridae. However, distribution of similar lines or sulci in Encyrtidae, Eulophidae, Aphelinidae, and Trichogrammatidae, must be studied to determine if they are a groundplan character for each family, or were independently derived in each family. The lines must also be studied to determine if they are internally developed as regions of inrolled cuticle. If so, presence may indicate a relationship with Mymaridae. Functional significance of the sulci and lines should also be determined prior to hypotheses of homology or independent gain.

3.4.7 Position of antennal toruli

Most Mymaridae have a more or less rectangular to triangular head in lateral view, with the toruli and inner eye margins subcontiguous, or separate by only about one diameter of the torulus. Thus, each torulus (to, Fig. 3.3) is much closer to the eye margin than are the toruli to each other. Members of the subfamily Eubroncinae [*Eubroncus* and *Stomarotrum* Yoshimoto, Kozlov and Trjapitzin (1972)] are exceptional in having the head wedge-like projected in lateral view. Vertex and frons are in a continuous plane that is acutely angled to the face, and because the toruli are near the angle of the head they are closer to each other than to the eyes.

Relative distance between the antennal toruli compared with distance between each torulus and eye margin is highly varied in Terebrantes. Most terebrants other than mymarids have the toruli closer to each other than to the eye margin (to, Fig. 3.8), or distance between the toruli is similar to that between each torulus and eye margin. Some Pteromalidae

(Chalcidoidea) have widely spaced toruli similar to most mymarids (Schauff 1984), as do some Eulophidae (Chalcidoidea) (see for example, Miller 1962), and some Ichneumonoidea. Restricted distribution indicates that this is the result of secondary modification in each taxon. Furthermore, toruli position in Eubroncinae (Mymaridae) is correlated with the unusual head structure, which undoubtedly is secondarily derived in the family. Consequently, widely spaced toruli that are positioned very close to the inner eye margins can be considered as an apomorphy that indicates monophyly of Mymaridae.

3.4.8 Pronotal shape

Nikolskaya (1960) considered that chalcidoids were distinguished from other terebrants by their 'saddle-like' pronotum (Figs. 3.18, 3.19). Königsmann (1978a) considered this pronotal shape to indicate probable monophyly of Chalcidoidea, whereas Rasnitsyn (1980) considered the similarly shaped pronota of austroniids and monomachids to indicate a relationship between Chalcidoidea and members of Diaprioidea. Gibson (in press) concluded pronotal shape to be correlated with presence or absence of an independent prepectus.

Individuals of Stephanidae, Monomachidae, and most Chalcidoidea have an independent and relatively large prepectus (*cf.* pre, Figs. 3.15, 3.18, 3.19). They also have the pronotum relatively long in dorsal view, hence more or less 'saddle-like' in lateral view, (Figs. 3.18, 3.19), and loosely connected to the mesopleuron. Consequently, the pronotum is variedly mobile relative to the mesothorax. Terebrants without an independent prepectus have the dorsal surface of the pronotum markedly reduced, hence the pronotum is more or less triangular in lateral view (Fig. 3.16). The pronotum is also rigidly connected to the mesopleuron. Roproniids and austroniids have a relatively small but independent prepectus, and the pronotum is intermediate in both shape, and degree of mobility, between the two extremes described above.

A correlation between an independent prepectus, pronotal shape, and pronotal-mesopleural attachment, is clearly illustrated by different chalcidoids and mymarids. Most chalcidoids have an independent prepectus that is varied in size and shape, and a pronotum that is more or less mobile relative to the mesothorax. Individuals of Eucharitinae (Eucharitidae) and Perilampidae are exceptional in having the prepectus secondarily fused to the pronotum (Bouček 1978), and the latter rigidly attached to the mesopleuron. Eucharitines also have a pronotum that is triangular in lateral view (Fig. 3.21), like the pronota of other terebrants without a prepectus, though the pronotum of perilampids is more or less saddle-like. Most mymarids also have an independent prepectus (pre, Figs. 3.24-3.27, 3.29). Pronotal shape is quite varied, from saddle-like (Figs. 3.24, 3.26) to markedly reduced dorsally (Figs. 3.22, 3.29), but only individuals of *Ptilomymar* Annecke and Doutt have a pronotum that is triangular in profile and rigidly connected to the mesopleuron (Fig. 3.23). Individuals of *Ptilomymar* also lack an evident prepectus, indicating the latter is secondarily fused to the pronotum as in perilampids, eucharitines, and numerous other terebrants.

Pronotal shape is not significant for determining phylogenetic relationships of Chalcidoidea, including Mymaridae, because an independent prepectus is plesiomorphic for Terebrantes (Gibson in press). Hence, a saddle-like and mobile pronotum is undoubtedly also plesiomorphic, and not evidence of monophyly or relationship with other terebrants.

Mymarommatids have a pronotum that is markedly reduced dorsally, hence triangular in lateral view (Fig. 3.10). This is apomorphic, but is correlated with reduction, or loss of the prepectus (see character 9), which is hypothesized to have occurred a probable four times during the evolution of Terebrantes (Gibson in press), in addition to independent loss in Perilampidae, Eucharitinae, and Mymaridae (Chalcidoidea). Because of differences in structure and attachment of the pronotum to the mesopleuron, I suspect that similarity of shape between the pronota of mymarommatids and other terebrants without an independent prepectus is the result of convergence.

3.4.9 Prepectus

Presence of an independent sclerite, the prepectus, between the pronotum and mesopleuron has been used by various authors as a defining state of Chalcidoidea. Chalcidoids were the only terebrants thought to have a prepectus, until Rasnitsyn (1980) discovered the sclerite concealed beneath the posterolateral edge of the pronotum in Stephanidae (pre, Fig. 3.15) and Monomachidae. I studied the various sclerites positioned between the pro- and mesothoracic segments in hymenopterans to determine homologies, and concluded that a prepectus was a groundplan character of the order and plesiomorphic for Terebrantes (Gibson in press).

Table 3.1, character 9, lists distribution of a prepectus in Terebrantes. Because an independent prepectus is plesiomorphic for Terebrantes, presence can not be used as evidence for monophyly of Chalcidoidea, or of relationships with other terebrants with a prepectus. However, the prepectus is exposed in most chalcidoids, at least dorsally adjacent to the lateral edge of the mesoscutum (pre, Figs. 3.18-3.20), and this is apomorphic in Apocrita. Graham (1969) stated that the prepectus was absent from some *Macromesus* Walker (Pteromalidae: Macromesinae), but individuals have a very small prepectus that is visible only near the lateral edge of the mesoscutum (Z. Bouček, pers. comm.). The prepectus is also very small and inconspicuous in numerous Chalcididae, but at least a tiny prepectus is exposed between the mesopleuron, pronotum and mesoscutum (pre, Fig. 3.20). Eucharitines and perilampids lack an evident prepectus, but only because the latter is secondarily fused to the pronotum (Bouček 1978). A carina (Darling 1983, figs. 35-37, 60, 61) or furrow (Fig. 3.21) indicates the probable line of fusion in many eucharitines and perilampids, as does position of the mesothoracic spiracle at the dorsal edge of the carina or furrow (msp, Fig. 3.21) (see character 11 for correlation between position of spiracle and prepectus).

Rasnitsyn (1980) stated that a prepectus is present in some mymarids, but not in others, and in some individuals appears to be a part of the mesopleuron that is incompletely separated by a suture. He suggested the sclerite could be a secondary formation in mymarids, and not homologous with the true prepectus. The prepectus certainly is highly varied in Mymaridae, probably as much so as for other Chalcidoidea, but there is no evidence supporting an hypothesis of secondary formation. The prepectus is closely associated with the mesopleuron in numerous mymarids, and it is variedly fused to the mesopleuron in some, but the same is true for the prepectus of other chalcidoids. The prepectus (**pre**) is moderately sized, and subrectangular (Fig. 3.25) to triangular (Fig. 3.29) in numerous mymarids, but it is very large (Fig. 3.24) or extremely reduced (Figs. 3.22, 3.27) in others, as also in other chalcidoids. Size and shape of the prepectus is even extremely varied in some mymarids presently classified in the same genus. Some individuals of *Gonatocerus* Nees have a large and conspicuous prepectus (Fig. 3.26), whereas others have a linearly reduced prepectus (Fig. 3.27). Furthermore, individuals of one species of *Gonatocerus* seen did not have an evident prepectus, but had a membranous region between the pronotum and mesopleuron (**mb**, Fig. 3.28). This membranous region is probably secondary and is not the prepectus because the mesothoracic spiracle is near the posterodorsal angle of the membranous region rather than near the anterodorsal angle (**msp**, Fig. 3.28) (see character 11 for correlation between position of spiracle and prepectus).

Rasnitsyn (1980) was correct in stating that the prepectus is absent from some mymarids, but absence is apparently uncommon and there appears to be a correlation between very small body size and a reduced prepectus. Most instances in which the prepectus is superficially absent are because of the very small size of individuals, a reduced prepectus, or both. When the prepectus is markedly reduced, it may appear to be absent without high magnification of scanning electron microscopy (**pre**, Figs. 3.22, 3.27). Furthermore, because most mymarids have the pro- and mesothoracic segments flexibly united, a narrow prepectus can be concealed between the two in air-dried, shrivelled specimens. Schauff (1984) incorrectly concluded that the prepectus was fused to the pronotum in *Stephanodes* Enock because the mesothoracic spiracle is advanced anterior of the more typical position. Individuals of

Stephanodes have a prepectus though (pre, Fig. 3.25), and the advanced spiracular position is simply a secondary modification, as discussed under character 11. Individuals of *Ptilomymar* Annecke and Doutt do lack an externally exposed prepectus (Fig. 3.23), but this apparent absence is most likely the result of secondary fusion of the prepectus with the pronotum (as discussed under character 8).

Scelionidae lack an independent prepectus, but many have a sulcus or row of crenulae delineating a region on the pronotum (net, Fig. 3.16) below the mesothoracic spiracle. Rasnitsyn (1980) considered this region to be the prepectus fused to the pronotum, but Masner (1979) considered it to be a secondarily delineated part of the pronotum, which he termed the netrion. I agree with Masner (1979) that the n[illegible]n is a secondarily delineated part of the pronotum, for reasons given in Gibson (in [illegible]

Serphitids lack an externally visible prepectus, but because only amber inclusions are available for study I could not determine whether an independent prepectus exists beneath the posterolateral edge of the pronotum, as in stephanids, monomachids and roproniids. I suspect that the prepectus is absent because the posterolateral edge of the pronotum appears to be rigidly attached to the mesopleuron, and the pronotum is of a similar shape to the pronota of terebrants without an independent prepectus.

Mymarommatids also lack an externally visible prepectus, and the pronotum is similarly shaped to the pronota of most terebrants that lack an independent prepectus (*cf.* Figs. 3.10, 3.16). Though this indicates an independent prepectus is absent, presence or absence remains uncertain even after internal study of the pronotum. A structure was revealed on the inner surface of pronota dissected from specimens of an undescribed species near *Palaeomymar anomalum* Blood and Kryger. The structure (pre?, Fig. 3.12) and posterolateral edge of the pronotum form a wide groove (gr, Fig. 3.12), hence the posterolateral edge of the pronotum is clearly visible from an inner view (Fig. 3.12). The structure is apparently connected to the anterolateral margin of the mesopleuron by membrane from its posterior margin (*cf.* mb, Figs.

3.12, 3.13), but because of the minute size of the pronota I was unable to determine if the structure was sclerotized, or whether it was an independent or fused prepectus.

For most terebrants without an independent prepectus I hypothesized (Gibson in press) that the prepectus was reduced and fused to the inner edge of the pronotum as the 'posterior pronotal inflection' (**ppi**, Fig. 3.17). A relatively deep groove is formed between the inner posterior pronotal inflection and outer posterolateral pronotal edge in such individuals (**gr**, Fig. 3.17), and the pronotum and mesopleuron are rigidly united because the anterior edge of the mesopleuron fits into the groove in a tongue-and-groove interlocking mechanism. The posterior pronotal inflection is at the same level as the posterolateral pronotal edge, hence the outer edge of the pronotum is not visible from an inner view (Fig. 3.17). Internal structure of the pronotum of these individuals is thus similar, but differs in details, from the internal structure of the pronotum of mymarommatids (*cf.* Figs. 3.12, 3.17). Consequently, if the internal structure on the mymarommatid pronotum is the fused prepectus, I suspect that fusion occurred independently to other terebrants.

I previously hypothesized an exposed prepectus as a groundplan character for Hymenoptera, and a concealed prepectus as a synapomorphy for Siricidae + Xiphydriidae + Orussidae + Apocrita (Gibson in press). Mymarids, chalcidoids, and austroniids, are the only terebrants known to have an independent and at least partly ~~exposed prepectus~~ exposed prepectus, although ceraphronoids and megalyrids have what is hypothesized to be an exposed prepectus that is fused to the pronotum. Exposure of the prepectus in the above terebrants is hypothesized as secondary and apomorphic in Terebrantes. Furthermore, differences in position of the mesothoracic spiracle relative to the prepectus (character 11) indicate exposure of the prepectus in mymarids and chalcidoids was independent to that of other taxa (Gibson in press). Consequently, an exposed prepectus can be considered as a synapomorphy that indicates monophyly of Mymaridae + Chalcidoidea.

Though state of the prepectus is uncertain in serphitids and mymarommatids, the prepectus is at least concealed beneath the posterolateral edge of the pronotum, if present. This is the hypothesized plesiomorphic state for Apocrita, hence either taxon is indicated to be at most the sister group of Mymaridae + Chalcidoidea.

3.4.10 Pronotal relationship to tegula

One of the most commonly used characters to define Chalcidoidea is that the posterolateral edge of the pronotum does not extend to the tegula (Figs. 3.18-3.20). This pronotal state was used by Nikolskaya (1952, 1960), Riek (1970), Königsmann (1978a), Gordh (1979), and Rasnitsyn (1980), though Rasnitsyn indicated the state varied in mymarids, and Yoshimoto (1984) indicated it varied in mymarids and other chalcidoids.

Most chalcidoids and mymarids are the only terebrants with the posterodorsal edge of the pronotum distinctly separate from the tegula (Table 3.1, character 10). This is apomorphic, but the state results from another apomorphy shared by mymarids and chalcidoids, an exposed prepectus that is interposed between the pronotum and tegula. The dorsal surface of the pronotum does extend over the mesoscutum and prepectus to the tegula in members of Leucospidae and Signiphoridae, but this is undoubtedly secondarily, and independently derived. The posterodorsal angle of the pronotum also appears to extend to the tegula in Eucharitinae (Fig. 3.21), Perilampidae (Chalcidoidea), and in *Ptilomymar* (Mymaridae) (Fig. 3.23), but because the prepectus is secondarily fused to the pronotum to form a composite structure. In other chalcidoids, how far removed the pronotum is from the tegula depends on size of the prepectus (*cf.* **pre**, Figs. 3.24, 3.25).

Kozlov and Rasnitsyn (1979) considered that there was a tendency toward widening of the upper part of the mesopleuron in mymarommatids and in *Microserphites* Kozlov and Rasnitsyn (Serphitidae), resulting in a more or less conspicuous dorsal mesopleural region between the pronotum and fore wing base. They interpreted this as evidence that mymarommatids and serphitids were related, and further concluded that *Microserphites* was an intermediate taxon between Mymarommatidae and Serphitidae *s. s.* Though the pronotum is separated from the fore wing base by a narrow dorsal region of the mesopleuron in mymarommatids, widening of the mesopleuron is illusory. All terebrants have the pronotum and fore wing base separated by a narrow mesopleural region, but this is not obvious in most individuals because the intervening mesopleural region is covered by the tegula. The pronotum superficially appears to extend to the base of the fore wing, but actually only extends to the base of the tegula (tg, Figs. 3.23-3.25). Some mymarids apparently have the tegula fused to the dorsal edge of the intervening mesopleural region (tg, Fig. 3.26), and the region consequently is more conspicuous. However, comparing these specimens with mymarids having an independent tegula shows that the only difference is whether the tegula is apparent or not; there is no fundamental difference in structure of the mesopleuron (*cf.* Figs. 3.23 and 3.25 with 3.26). Mymarommatids also lack an evident tegula (Figs. 3.10, 3.11), most likely because of fusion with the mesopleuron, correlated with small body size. Consequently, the dorsal mesopleural region between the pronotum and wing base is more or less conspicuous (Fig. 3.10). The only known specimen of *Microserphites parvulus* also lacks an evident tegula, but absence is probably an artifact because the dorsum of the mesosoma is not preserved in the amber inclusion. The mesopleural region illustrated between the pronotum and fore wing base by Kozlov and Rasnitsyn (1979) is typical of the mesosoma of any terebrant without an evident tegula (*cf.* Fig. 3.26 and fig. 7, Kozlov and Rasnitsyn, 1979). I therefore consider Kozlov and Rasnitsyn's (1979) description of a widened dorsal mesopleural region in mymarommatids and *Microserphites* to be inaccurate. I do not accept such a region as evidence of a relationship between mymarommatids and serphitids, nor as evidence that *Microserphites* is an intermediate taxon between Mymarommatidae and Serphitidae *s. s.*

3.4.11 Relative position of mesothoracic spiracle

Riek (1970, p. 913) initially alluded to the unique placement of the mesothoracic spiracle in chalcidoids, stating that "Chalcidoidea are the only Hymenoptera in which the 'prothoracic' [*sic*] spiracle is situated at or above the level of the tegula". A somewhat more accurate description is that chalcidoids have the mesothoracic spiracle situated at the exposed lateral edge of the mesoscutum (**msp**, Figs. 3.18-3.21). The mesothoracic spiracle is situated below, and is separated from the exposed lateral edge of the mesoscutum in other hymenopterans. The spiracle is either concealed by a prominent pronotal lobe (**prl**, Fig. 3.15), is exposed between the pronotum and mesopleuron, as in scelionids (**msp**, Fig. 3.16) and serphitids, or is situated on the pronotum. However, in all instances there is at least a small region of the pronotum between the spiracle and exposed lateral edge of the mesoscutum (Figs. 3.15-3.17).

I previously proposed that Stephanidae have the plesiomorphic structure of the intersegmentalia (sclerites in the membrane between the pro- and mesothoracic segments) for Terebrantes, and hypothesized that there were at least three independent transformation series from this structure during evolution of the infraorder (Gibson in press). Stephanids have the mesothoracic spiracle above the dorsal edge of the prepectus, with both spiracle (**msp**) and dorsal edge of the prepectus (**pre**) below the lateral edge of the mesoscutum (Fig. 3.15). In one proposed transformation series [represented by ichneumonoids], the prepectus was hypothesized to be reduced and fused to the posterolateral edge of the pronotum, without changes in the relative positions of the prepectus, mesothoracic spiracle, or lateral edge of the mesoscutum. In the second proposed transformation series [represented by terebrants that either have an independent prepectus (Table 3.1, character 9, state 3), or a posterior pronotal inflection (state 3a), which I consider to be the fused prepectus (**ppi**, Fig. 3.17)], the prepectus was hypothesized to be dorsally extended to the lateral edge of the mesoscutum behind the mesothoracic spiracle. Consequently, the spiracle is in a plesiomorphic position relative to the lateral edge of the mesoscutum (below and separate from edge), but in an apomorphic position relative to the prepectus (below dorsal edge). Inclusion of gasteruptionids (state 4), and megalyrids and ceraphronoids (state 3b), in this transformation series is uncertain because of structural differences in the pronotum (see Gibson in press). However, the mesothoracic spiracle is below and is separate from the lateral edge of the mesoscutum in members of these three taxa, hence the hypothesis of autapomorphy made below for Chalcidoidea is not affected. Chalcidoids have both the dorsal edge of the prepectus and the mesothoracic spiracle at the exposed lateral edge of the mesoscutum. This structure is hypothesized to represent a third transformation series from the plesiomorphic stephanid-like condition, in which both prepectus and mesothoracic spiracle were dorsally extended to the lateral edge of the mesoscutum. Consequently, the mesothoracic spiracle retains a plesiomorphic position relative to the prepectus (at anterodorsal angle), but is in an apomorphic position at the lateral edge of the mesoscutum (**msp**, Figs. 3.18-3.21). Some chalcidoids have the spiracle advanced anterior to, or above, the anterodorsal angle of prepectus (Fig. 3.19), rather than adjacent to the prepectus (Fig. 3.18), but I consider these to be secondary modifications.

Mymarids have the mesothoracic spiracle (**msp**) positioned between the pronotum, mesoscutum, and prepectus (Figs. 3.22, 3.29), or formed into a tubercle with the pronotal edge (Figs. 3.24, 3.25), or positioned on the pronotum itself (Figs. 3.26-3.28). However, in all instances the spiracle is at, or is somewhat above the lateral edge of the mesoscutum (**msp**, Figs. 3.22-3.29). I consider the former state to be plesiomorphic for mymarids because it is shared with chalcidoids, and I consider the latter two states to be secondarily derived in Mymaridae. As for some chalcidoids, some mymarids have the mesothoracic spiracle advanced anterior to the anterodorsal angle of the prepectus (*cf.* **msp**, Figs. 3.19, 3.25). I interpret this similarity between some members of both taxa to be the result of convergence.

A mesothoracic spiracle is not externally evident in mymarommatids (Fig. 3.10), but what appears to be the spiracle is visible near the posterolateral edge of the pronotum at about midheight in specimens mounted laterally on slides (**msp**, Fig. 3.14). Though visible in slide mounted specimens, the spiracle is not evident if the pronotum is removed and examined internally by SEM (Fig. 3.12), and must therefore lie between the presumed prepectus and wall of the pronotum.

Mymarids and chalcidoids are the only terebrants with the mesothoracic spiracle at or above the lateral edge of the mesoscutum (Table 3.1, character 11, Figs. 3.18-3.29). Consequently, this position can be considered as apomorphic and indicative of monophyly of Mymaridae + Chalcidoidea, whether or not the three previously hypothesized transformation series are accurate. Furthermore, position of the mesothoracic spiracle relative to the mesoscutum is apparently plesiomorphic in mymarommatids, as it is in scelionids and serphitids. Any of these taxa are thus indicated to be at most the sister group of Chalcidoidea.

Concealment of the mesothoracic spiracle beneath the posterolateral edge of the pronotum is also an apomorphic state that indicates monophyly of Mymarommatidae. Almost all terebrants have the mesothoracic spiracle exposed in lateral aspect (msp, Figs. 3.16, 3.18-3.29), or covered by a prominent pronotal lobe (prl, Fig. 3.15). Only mymarommatids and evaniids have the posterolateral edge of the pronotum straight, with the spiracle concealed below (Gibson in press). This state is apparently secondarily derived in Evaniidae because numerous evaniids have a distinct pronotal lobe concealing the spiracle. Similarity of structure between evaniids and mymarommatids is thus indicated to be due to convergence.

3.4.12 Fore wing venation

Fore wing venation of chalcidoids is reduced to a single vein complex near the costal margin of the wing (Fig. 3.31). Most taxonomists term the veins of this complex as the submarginal (smv), marginal (mv), stigmal (stv), and postmarginal veins (pmv, Fig. 3.31). One or more of these veins are punctiform, or are absent from the fore wings of numerous chalcidoids, but in others there are partially pigmented or otherwise indicated remnants of additional veins (Fig. 3.31). Most scelionids have a fore wing venation similar to that of most chalcidoids, *i. e.*, with only a smv, mv, stv, and pmv. However, some scelionids also have one or more of the veins punctiform or absent. Mymarids likewise have a fore wing venation similar to that of most chalcidoids and scelionids, except that the venation is even more reduced in most mymarids. Individuals of mymarid genera from the Holarctic lack a postmarginal vein, and except for *Arescon* Walker, venation is limited to the basal third of the fore wing (fwv, Fig. 3.32) (Schauff 1984). However, individuals of at least two genera from Australia have a postmarginal vein, and individuals of several genera from Australia and New Zealand have the venation extended half the distance of the wing, or beyond (J. Noyes, *in litt.*). Fore wing venation of mymarommatids is reduced to a single, short, thick vein within the pedunculate wing base.

Königsmann (1978a) considered the "characteristic venation" of chalcidoids to indicate probable monophyly of the superfamily, and Rasnitsyn (1980) used reduced fore wing venation as one state to characterize Chalcidoidea, as have most workers before him. Both concluded that reduced fore wing venation was important for recognition of, and phylogenetic analysis of, Chalcidoidea, and each considered the similarily reduced venation of chalcidoids and scelionids as the result of convergence, because of small body size, rather than phyletic relationship. Convergence is certainly possible, if not probable, as is indicated by the highly reduced fore wing venation of Ceraphronoidea, Platygastridae, Diapriidae, and most Proctotrupidae and Cynipoidea. However, an hypothesis of homoplasy rather than synapomorphy for the similar venation of chalcidoids and scelionids is based on ideas of relationships formed from an analysis of other characters, not on an analysis of the venation itself.

Fore wing venation of mymarids and mymarommatids could be derived through reduction from the venation of chalcidoids or scelionids. Consequently, venation can not be used as evidence for relationships between these taxa, but it does indicate that Serphitidae is at most the sister group of Scelionidae, and was not derived from Scelionidae, as proposed by Rasnitsyn (1980). Serphitids are unlike mymarids, mymarommatids, chalcidoids, and scelionids, having a more complete fore-wing venation, including a large pterostigma (Rasnitsyn 1980, fig. 132). The more complete venation would have to be the result of reversal if serphitids were derived from scelionids.

3.4.13 Fore wing hypochaeta

One of two states that Schauff (1984) considered as autapomorphic for Mymaridae was presence of a hypochaeta, *i. e.*, a distally hooked seta on the ventral surface of the fore wing that is inserted near the costal margin and is directed towards the anal margin (**hyc**, Fig. 3.32). All mymarids apparently have a hypochaeta (Debauche 1948), and members of some genera have more than one, though Schauff (1984) found the hypochaeta to be small and often difficult to see in members of five genera he studied. These genera apparently comprise a monophyletic group in Mymaridae, and a single reduction was hypothesized to explain character-state distribution of the reduced hypochaeta. Consequently, a fore wing hypochaeta can be interpreted as an autapomorphy that indicates monophyly of Mymaridae.

3.4.14 Reticulate fore wing

The membrane of mymarommatid fore wings is not smooth as in other hymenopterans; rather, it has a reticulate or alveolate appearance when viewed with a dissecting or compound microscope.

Fore wings of individuals of the extinct mymarommatid genus, *Archaeromma*, were described as reticulate in the original description, but non-reticulate in the discussion (Yoshimoto 1975). Study of type-material of *Archaeromma nearcticum* Yoshimoto shows the fore wings to be reticulate, though the pattern is often obscure in fossil specimens because of the optical properties of amber. Study of the fore wings of one mymarommatid species by scanning electron microscopy also shows that the reticulate pattern is formed by a mesh-like network of raised lineations (Fig. 3.30). I assume the reticulate pattern is likewise formed in other mymarommatid species, and consequently interpret a mesh-like pattern of raised lineations as an autapomorphy that indicates monophyly of Mymarommatidae.

3.4.15 Hind wing structure

The hind wings of most Hymenoptera are broadest beyond the articulation with the metathorax, with the wing membrane narrowed toward and extended to the articulation. Most mymarids are exceptional in having petiolate hind wings, *i. e.*, origin of the wing membrane is distal to the metathorax on a long stalk-like vein (Fig. 3.32). The wing membrane is also more or less parallel-sided (Fig. 3.32), though the membrane is so reduced in individuals of *Mymar* Curtis that the hind wing resembles a bristle. Schauff (1984) noted that a petiolate hind wing is often used as a character to distinguish mymarids from other chalcidoids, and that it could be a synapomorphy for members of the family. However, he also noted that the hind wings of individuals of *Paranaphoidea* Girault are broader and more typically "chalcidoid". Furthermore, the wing membrane extends to the base of the hind wing, albeit very narrowly, in individuals of *Anagroidea* Girault, and in Eubroncinae. Consequently, the hind wings are similar to those of some other chalcidoids, including many trichogrammatids (see Doutt and Viggiani 1968). If the hind wing structure of Eubroncinae and *Anagroidea* is plesiomorphic for Mymaridae, stalked hind wings can not be used as an apomorphy supporting monophyly of Mymaridae.

Mymarommatids differ from other hymenopterans in having each hind wing reduced to a stalk-like structure that is bulbously expanded at the base and terminated in a bifurcation (**hw**, Figs. 3.11, 3.33). The distal bifurcation is presumably formed by a single hamulus and the reflexed end of the reduced wing (Fig. 3.33). The anal margin of the fore wing is clasped by the bifurcation in natural repose so that fore wing and hind wing act as one. This unique hind wing structure can be interpreted as a further autapomorphy that indicates monophyly of Mymarommatidae.

3.4.16 Mesotrochanteral depressor

The mesotrochanteral depressor is a mesothoracic muscle that inserts into the basomedial edge of the mesotrochanter. Mesocoxa and trochanter are so articulated that contraction of the muscle rotates the apex of the trochanter ventrally and medially. I previously described states of the mesotrochanteral depressor from representatives of most families of Hymenoptera, and hypothesized the plesiomorphic state for Apocrita to be a muscle with three sites of origin: a small fan-shaped muscle from the mesofurca (mesofurcal-trochanteral depressor: fu_2-tr_2), and a larger tubular muscle (mesotergal-trochanteral depressor: t_2-tr_2) from the axilla and from the posterior of the mesoscutum (Gibson in press).

Table 3.1, character 16, lists states of the mesotrochanteral depressor in Terebrantes. Megalyridae have the hypothesized plesiomorphic state for Apocrita, except for a slightly different site of origin for fu_2-tr_2 (Gibson in press, fig. 44). Other terebrants for which states of the mesotrochanteral depressor are known lack one or more of the three original parts. Only Stephanidae, Ceraphronoidea, Chalcidoidea, and Diapriidae (other than Ismarinae) retain a tergal (t_2-tr_2) part of the depressor. Stephanids and non-ismarine diapriids have fu_2-tr_2 and the axillar portion of t_2-tr_2 (Gibson in press, figs. 41, 42), whereas ceraphronoids lack fu_2-tr_2, but have both the mesoscutal and axillar portions of t_2-tr_2 (Gibson in press, fig. 43). Fu_2-tr_2 is also absent from chalcidoids and t_2-tr_2 appears to consist of two parts in many taxa. If an anterior part (**t_2-tr_2b**) is distinguished, it seemingly originates from the mesoscutum, whereas the posterior part originates from the axilla (**t_2-tr_2a**) (Fig. 3.34). However, this similarity to the mesotrochanteral depressor of ceraphronoids is superficial. Chalcidoids differ from other hymenopterans with t_2-tr_2 in that the anterior portion of these muscles do not arise from the mesoscutum, but from axillar phragmata that project beneath the mesoscutum from the axilla (**axp**, Fig. 3.35). [The axillar phragmata of chalcidoids have also been termed the "anterior connecting processes of the postmesoscutum" by Grandi (1929), "apodemes of the posterior plate of the mesonotum" by James (1926), and "pseudophragma of the postscutellum" by Bucher (1948).]

I previously hypothesized that chalcidoids evolved from an ancestor having only the axillar portion of the mesotrochanteral depressor, and that this muscle was secondarily increased in size through origin of an axillar phragma in the common ancestor of Chalcidoidea (Gibson in press). All chalcidoids I dissected had at least tiny axillar phragmata, except for some members of Eupelmidae. These exceptions will be described in a subsequent paper, but result from the mesosoma being secondarily modified for increased jumping ability.

The mesotrochantinal depressor of mymarids (Fig. 3.34) is as described for non-eupelmid chalcidoids. Examination of slide-mounted mymarommatid specimens shows a similar state of the muscle, except that origin of t_2-tr_2 is only from the axillar phragma (t_2-tr_2), the axilla itself being without muscle.

State of the mesotrochanteral depressor in scelionids is very different from that described for most chalcidoids. The muscle originates from the mesopleuron adjacent to the mesofurcal lateral arm (Gibson in press, fig. 51). I consider this structure to represent the terminal state in a transformation series composed of three events. The first event was loss of t_2-tr_2 from the hypothesized plesiomorphic state of the mesotrochanteral depressor for Apocrita, leaving only fu_2-tr_2 (Table 3.1, character 16, state 3). The second event was expansion of fu_2-tr_2 from the mesofurcal lateral arm onto the mesopleuron as pl_2-tr_2 (state 3a), and the third event was loss of the furcal portion of the muscle to leave only pl_2-tr_2 (state 3b). Individuals of Proctotrupidae, Pelecinidae, Evaniidae and Vanhorniidae have what I consider as the intermediate state in this transformation series (Table 3.1). Consequently, one or some combination of these four families (excluding Platygastridae and other families for which state of the mesotrochanteral depressor is unknown) is indicated as the sister group of Scelionidae.

Relationships of serphitids with extant terebrants can not be inferred using state of the mesotrochantinal depressor because it is not possible to examine internal structure in fossil inclusions. However, state of this muscle does not support Kozlov and Rasnitsyn's (1979), and

Rasnitsyn's (1980) hypothesis that Mymaridae, and Serphitidae *s. l.* (inclusive of mymarommatids), were derived from Scelionidae. It is not possible to derive the mesotrochanteral depressor of mymarids and mymarommatids directly from the depressor of scelionids. The muscles of mymarids and mymarommatids appear to represent terminal states in one transformation series, and the muscle of scelionids the terminal state in an independent transformation series, from the hypothesized plesiomorphic state of the mesotrochantinal depressor of Apocrita. Thus, not only is a sister-group relationship not supported, but mymarids and mymarommatids are indicated to be only distantly related to scelionids.

Only ceraphronoids, mymarommatids, mymarids and chalcidoids are known to have a mesotrochanteral depressor composed of only t_2-tr_2. I consider similarity of the mesotrochanteral depressor in ceraphronoids and the latter taxa to be the result of convergence because I consider the anterior portion of t_2-tr_2 in mymarommatids, mymarids, and chalcidoids to be secondarily derived and non-homologous with the anterior portion of the muscle in ceraphronoids. Whether this is accurate, or not, only mymarommatids, mymarids and chalcidoids have axillar phragmata for attachment of t_2-tr_2. Consequently, axillar phragmata can be interpreted as a synapomorphy that indicates monophyly of the taxa. I further consider absence of the axillar portion of t_2-tr_2 in mymarommatids to be the result of secondary loss, and hence a further autapomorphy that indicates monophyly.

3.4.17 Two-segmented petiole

A petiole formed from two segments (Mt_1 and Mt_2, Fig. 3.36) was the primary evidence that Kozlov and Rasnitsyn (1979), and Rasnitsyn (1980), used to support their hypothesis that mymarommatids are more closely related to serphitids than to mymarids. Mymarommatids and serphitids are the only terebrants to have a petiole that is definitely two-segmented. Yoshimoto (1975) described the chalcidoid genus *Distylopus* (Tetracampidae: Distylopinae) from Canadian Cretaceous amber, and described a two-segmented petiole for the single male for which the genus was established. However, study of the holotype of *D.*

bisegmentus Yoshimoto indicates the petiole is probably only one-segmented. The basal region that Yoshimoto interpreted as the first petiolar segment appears to be a constricted portion of the petiole for insertion into the propodeal orifice. A false impression of segmentation is enhanced by color differences between the basal, yellowish translucent region, and the apical, brownish opaque region. This color difference apparently is because the basal region does not contain remnants of body material, whereas the apical region does. Whether the petiole of *D. bisegmentus* is two-segmented or not, the two-segmented petiole of mymarommatids and serphitids could either be the result of convergence, or inheritance from a common ancestor.

3.4.18 Metasomal spiracles and cerci

Table 3.1, characters 18a and 18b, lists distribution of metasomal spiracles and cerci, respectively, in Terebrantes. Most chalcidoids can be distinguished from most other terebrants by the combination of these two character states.

Chalcidoids either have digitiform or button-like cerci on the eighth metasomal segment (or ninth segment if this is separate) and spiracles on only the seventh metasomal segment. Domenichini (1953) stated that individuals of *Encyrtus fuliginosus* Compere (Encyrtidae) and *Monopleurothrix kiefferi* Mayr (Eupelmidae: Tanaostigmatinae) also have spiracles on the petiole (first metasomal segment), but this is untrue for the first species (J. Noyes, *in litt.*) and likely is untrue for the latter species. Ichneumonoids are the only terebrants to have functional spiracles on more than the seventh metasomal segment. Mymarommatids and most mymarids are similar to chalcidoids in having cerci on the eighth metasomal segment (cer, Figs. 3.37, 3.39), and metasomal spiracles on only the seventh segment (sp_7, Figs. 3.37, 3.39). Individuals of four mymarid genera studied by Schauff (1984) lack metasomal spiracles, and three independent losses were hypothesized for absence in these taxa.

Most other terebrants differ from typical chalcidoids in state of the metasomal spiracles, cerci, or both. Most ichneumonoids have spiracles on the first five to seven metasomal segments; scelionids, platygastrids, proctotrupids, vanhorniids, trigonalids and ceraphronoids lack metasomal spiracles; and though female pelecinids have spiracles on the seventh metasomal segment, the spiracles are not externally visible (Mason 1984). Furthermore, evaniids, platygastrids, pelecinids, roproniids, proctotrupids, vanhorniids, scelionids and most cynipoids either have the cerci concealed, reduced to setiferous sensory plates, or absent. Presence or absence of metasomal spiracles and cerci was not determined for most fossil serphitids because of their poor state of preservation. However, one well preserved female (MCZ #5330) had digitiform cerci on the eighth metasomal segment and metasomal spiracles on the seventh segment only. I assume these states are the same for other serphitids.

W. R. M. Mason (pers. comm.) considers functional spiracles on metasomal segments one through seven as the groundplan state for Apocrita because aculeates and most ichneumonoids have this pattern. He further proposes that reduction of metasomal spiracles to only the seventh segment may be a synapomorphy for Apocrita exclusive of aculeates and ichneumonoids. If so, functional spiracles on the seventh metasomal segment in chalcidoids is plesiomorphic. Retention of distinct cerci is undoubtedly a plesiomorphic state, so that chalcidoids differ from most other terebrants only in retention of both plesiomorphic states. This is useful to identify chalcidoids, but not as evidence of monophyly of Chalcidoidea, nor as evidence of relationships with other terebrants.

Presence of spiracles on the seventh metasomal segment in Mymaridae, Mymarommatidae, and Serphitidae does not support Kozlov and Rasnitsyn's (1979), and Rasnitsyn's (1980) hypothesis that these taxa were derived from within Scelionidae. Scelionids lack these spiracles and presence in members of the former taxa indicates that their ancestor(s) had metasomal spiracles.

3.4.19 Metasomal structure of females

Female chalcidoids and mymarids have all metasomal sterna displaced anterior to the base of the ovipositor, or have some of the sterna extended beneath the ovipositor sheaths toward the apex of the metasoma. The ovipositor sheaths are visible along the ventral midline of the metasoma in the former instance, but in the latter instance the sheaths are partly or entirely concealed by one or more of the sterna. During oviposition the ovipositor rotates about its base so that the apex is lowered from the metasoma anterior to the apex of the metasoma. Rotation of the ovipositor is possible because the sterna are only loosely connected to the terga, and the apex of any sternum that extends over the sheaths is widely displaced downward away from the metasomal apex.

Similarity in metasomal structure and mode of ovipositor extension led Schauff (1984) to mention this as one possible synapomorphy for Mymaridae + Chalcidoidea, though he cautioned the similarity could be symplesiomorphic. Rasnitsyn (1980) stated that the similarity indicated contradictory conclusions regarding relationships of Mymaridae. Females of most other taxa he included in Diapriodea, including those of Scelionidae, have the sterna and terga relatively rigidly united so that they can not be widely displaced from each other. The ovipositor is concealed within the metasoma in normal repose, and is protruded posteriorly from the metasomal apex during oviposition, rather than rotated ventrally away from the metasoma.

Serphitids and mymarommatids have the ovipositor concealed by the apical sternum, or hypopygium (**hyp**, Figs. 3.37, 3.39). However, the hypopygium can be widely displaced in mymarommatids, and apparently could be displaced to a lesser extent in serphitids (Rasnitsyn 1980). Metasomal structure and mode of ovipositor extension is thus similar to that of chalcidoids and mymarids. Because Rasnitsyn (1980) considered mymarids, mymarommatids, and serphitids to be derived from scelionids, he suggested the metasomal structure and mode of ovipositor protrusion characteristic of scelionids was secondarily lost in the former three taxa.

Table 3.1, character 19, lists type of metasomal structure and mode of ovipositor extension in Terebrantes. Numerous other terebrants have a similar metasomal structure and mode of ovipositor extension to that of chalcidoids, mymarid[illegible]ommatids, and serphitids. The structure is undoubtedly plesiomorphic for Apocrita and Terebrantes because a similar structure is also characteristic of Symphyta. Unlike Rasnitsyn (1980), I consider the similar metasomal structures of mymarids, mymarommatids, and serphitids to be due to symplesiomorphy, and not the result of secondary loss of the apomorphic scelionid structure.

Metasomal structure different from the plesiomorphic condition is simply listed as "apomorphic" in Table 3.1, character 19. This is because recent studies of Proctotrupidae (= Serphidae *sensu* Townes and Townes 1981), Scelionidae (Austin 1983), Vanhorniidae (Mason 1983) and Pelecinidae (Mason 1984) have shown structure of the metasomal-ovipositor complex to be conspicuously varied. Austin (1983) suggested differences in structure indicate that the ovipositor was concealed in the metasoma several independent times during the evolution of Terebrantes, most likely for greater protection of the fragile ovipositor.

3.4.20 Basal ring in male genitalia

Rasnitsyn (1980) stated that mymarids are like chalcidoids, but unlike scelionids, in absence of a basal ring from the male genitalia. Snodgrass (1941) first discovered that a basal ring was absent from the phallobase [*sensu* Snodgrass, = genital sheath *sensu* Vasey (1974)] of the male genitalia of most chalcidoids. However, there was a groove across the ventral surface near the base of the phallobase in males of two species he studied, *Torymus fagopyrum* (Provancher) [= *Callimome sackeni* (Ashmead)] (Torymidae), and *Leucospis affinis* (Say) (Leucospidae). Snodgrass interpreted the basally delineated region of the phallobase (**br**, Fig. 3.38b) as remnants of a basal ring that was fused to the parameres. This structure of the phallobase was found for other leucospids by Bouček (1974), for males of *Trichogramma* Westwood (Trichogrammatidae) by Nagarkatti and Nagaraja (1968), and for males of some Pteromalidae by Vasey (1974). However, these studies, and the comprehensive survey of chalcidoid male genitalia by Domenichini (1953), indicate that a complete annular or independent basal ring is lacking.

Male genitalia of mymarids remain inadequately studied, but the comparative study of Viggiani (1973) indicates a basal ring is lacking from the phallobase. A basal ring was also lacking from the genitalia of males of two extant mymarommatid species that I examined, *Palaeomymar anomalum*, and a closely related, undescribed species from Japan. Whether or not male serphitids had a basal ring could not be determined from the fossils available for study.

Snodgrass (1941, figs. R, S, plate 10) illustrated male genitalia for only two species of Scelionidae, representing the genera *Scelio* Latreille and *Sparasion* Latreille (Scelioninae). The genitalia were similar and had a distinctively elongate, tubular, or at least ventrally sclerotized basal ring at the base of the aedeago-volsellar shaft (*sensu* Snodgrass). Such an elongate basal ring was previously illustrated by Nixon (1936) for males of two species of *Telenomus* Haliday and one species of *Trissolcus* Ashmead (= *Microphanurus* Kieffer) (Telenominae). Nixon did not illustrate a basal ring in the male genitalia of different species of *Telenomus*, *Trissolcus*, and *Eumicrosoma* Gahan (= *Nardo* Nixon) in other papers, but he stated in one (Nixon 1937) that the drawings were incomplete and did not show details that seemed to be of no specific value or that were difficult to see. Basic structure of the basal ring does not appear to vary in Telenominae except for relative size (N. Johnson, *in litt.*). Consequently, it is likely that a basal ring was present, but that the latter was left out of the illustrations because Nixon did not consider it to be of taxonomic value. Ritchie and Masner (1983) likewise did not illustrate the basal ring in the genitalia of *Baryconus* Förster (Scelioninae) males, because they considered the basal ring of no value in distinguishing species (A. Ritchie, *in litt.*). An elongate basal ring in the male genitalia is thus indicated as a groundplan character of Scelionidae.

Table 3.1, character 20, lists known distribution of a basal ring in Terebrantes. Vasey (1974) described male genitalia for representatives of most families of Terebrantes, but did not include Austroniidae, Megalyridae, Vanhorniidae, Roproniidae, Monomachidae, and Trigonalidae. Presence or absence of a basal ring is unknown for Austroniidae and Megalyridae because male genitalia have not been described for these taxa, but Mason (1983) recently found a basal ring present in the male genitalia of *Vanhornia eucnemidarum* Crawford (Vanhorniidae). I dissected one male each of *Ropronia garmani* Ashmead (Roproniidae), *Monomachus* sp. (Monomachidae) and *Poecilogonalos costalis* (Cresson) (Trigonalidae), and all had a basal ring. Presence of a basal ring listed in Table 3.1 for the latter three families is based only on my dissections.

Presence of an independent basal ring in the genitalia of male Symphyta and most male Apocrita indicates this as a groundplan character of Hymenoptera and as symplesiomorphic for Terebrantes. Absence of an independent basal ring from the male genitalia of Mymarommatidae, Mymaridae, and Chalcidoidea may thus be a synapomorphy that indicates monophyly of these taxa. However, the basal ring is lacking from the male genitalia of *Atanycolus* Förster (Ichneumonoidea: Braconidae) and *Aphanogmus* Thomson (Ceraphronoidea: Ceraphronidae) (Vasey 1974), and is indicated to be absent from the male genitalia of *Psilus* Panzer (= *Galesus* Haliday) (Diapriidae) (Snodgrass 1941). Furthermore, the basal ring is reduced to a linear strip at the base of the phallobase in many terebrants, and may be present as an incomplete ring (Vasey 1974). Absence of the basal ring from the male genitalia of the above-listed taxa is undoubtedly the result of secondary loss because other ichneumonoids, ceraphronoids, and at least some diapriids have a basal ring (Snodgrass 1941, Vasey 1974). However, the above examples illustrate that independent reduction or loss of the basal ring is possible. Consequently, I do not consider absence of a basal ring from the male genitalia of mymarommatids, mymarids, and chalcidoids as reliable evidence of monophyly.

3.4.21 Cuspis in male genitalia

Königsmann (1978a) proposed absence of cuspides from the male genitalia as a synapomorphy for Cynipoidea + Chalcidoidea. Males of both taxa have the volsella composed of only a digitus, if volsellae are present. A "chelate structure" in the genitalia of male *Trichogramma* Westwood (Chalcidoidea: Trichogrammatidae) was tentatively proposed as the fused cuspis and digitus by Nagarkatti and Nagaraja (1968). However, other known chalcidoid males lack cuspides, and it is likely that the chelate structures are only secondarily modified digiti. Cuspis-like processes are also known from the genitalia of male *Synergus* Hartig (Cynipoidea: Cynipidae) (Vasey 1974), but again these processes are likely the result of secondary modification because they are lacking from other cynipoids.

Table 3.1, character 21, lists known distribution of cuspides in the genitalia of male terebrants. The list was compiled primarily from Snodgrass (1941), Vasey (1974), and my own dissections (discussed under character 20). Listed distribution is based on very few taxa, but indicates absence of cuspides from the male genitalia of cynipoids and chalcidoids is not likely synapomorphic, but more likely reflects loss at a more inclusive phylogenetic level, or is the result of independent loss.

3.4.22 Metallic luster of adults

Königsmann (1978a) considered metallic luster, characteristic of numerous chalcidoids, as a groundplan character of Chalcidoidea that indicated probable monophyly of the superfamily. He considered a single derivation of metallic luster in the common ancestor of Chalcidoidea, and subsequent loss of the luster several independent times, as more probable than multiple origins of the luster in the superfamily. However, known Signiphoridae, Aphelinidae, and Trichogrammatidae, and almost all known Leucospidae, Chalcidoidea, and Eurytomidae lack metallic luster. Because phyletic relationships are unresolved in Chalcidoidea, it is not possible to postulate whether the common ancestor of chalcidoids had metallic luster, or whether metallic luster evolved once or more in one or more clades.

Mymarommatids lack metallic luster, as do almost all mymarids. Some species of *Erythmelus* Enock have a slight, but distinct metallic luster (J. Huber, *in litt.*), though this is most likely secondarily derived. Consequently, absence of metallic luster from mymarommatids and mymarids is indicated as symplesiomorphic, and not valuable for determining phyletic relationships of these taxa.

3.4.23 Structure of larvae

Rasnitsyn (1980) concluded that the most reliable indicator of mymarid relationships was the structure of their larvae. He considered their larvae to share a rather distinctive structure with scelionid larvae.

Two general types of first-instar mymarid larvae ("saciform" and "mymariform") were described by Clausen (1940). It is the typical mymariform larvae that are most similar to the "teleaform" first-instar larvae of Scelionidae. Mymariform and teleaform larvae have a long caudal appendage and most representatives have long body setae. Both types of larvae also have prominent cephalic processes and are unsegmented, or only have indistinct segmentation.

Though mymariform and teleaform larvae are superficially similar, character states either differ in detail or are shared with larvae of some other terebrants. Clausen (1940), for example, also termed one type of first-instar larva of Trichogrammatidae (Chalcidoidea) as mymariform, most likely because it too has a caudal appendage and long body setae. Jackson (1961) also discovered that larvae of some mymarid species, which are otherwise typically "mymariform", lack body setae. Furthermore, mymarid first-instar larvae have several transverse rows or rings of setae, if present, whereas scelionid first-instar larvae have only a single row or ring of setae near the anterior edge of the abdomen. Because both caudal appendage and setae function in movement of the larvae in the host egg (Clausen 1940), independent gain of these states is probable. Differences in details also occur in the cephalic processes and segmentation of mymariform and teleaform larvae. Mymariform larvae have the head extended as a median curved process above the minute mandibles, whereas teleaform larvae have large mandibles, often a fleshy lateral process above each ma[illegible] median process below the mandibles, or both. Most scelionid first-instar larvae also have the body subdivided into more or less equal parts by a distinct constriction, but otherwise are without segmentation. Segmentation is apparent or inapparent in mymarid first-instar larvae, but the body is not differentiated by a distinct constriction.

Königsmann (1978a) hypothesized similarity of mymarid and scelionid first-instar larvae to be the result of convergence because individuals of both taxa are parasitoids of eggs of other insects (scelionids also of spider eggs), and consequently the larvae have a similar habitat. Though the larvae are superficially similar, differences in details of structure tend to support Königsmann's hypothesis. Trichogrammatidae are also egg parasitoids, and since some of their larvae are similar to mymariform larvae this further supports Königsmann's hypothesis. As Schauff (1984) stated, our knowledge of scelionid and mymarid larvae remains limited. Until more comprehensive surveys are made, and homology and function of similar larval structures are determined in an effort to distinguish homoplasy from synapomorphy, hypotheses of relationship based on larval structure must be considered tenuous at best.

Table 3.1. Matrix of character states analyzed in the text (excluding 12, 22 and 23), with an explanation of the symbols used for the matrix and hypotheses of transformation of the states in Terebrantes (* = exception discussed in text).

Taxon	1	2	3	4	5	6	7	8	9	10	11	13	14	15	16	17	18a	18b	19	20	21
Chalcidoidea	4-26	+/-	+*	1	-*	0	0*	0*	2*	1*	1	-	0	0	4a	1	Mt7	0,1	0	-[12]	-
Mymaridae	7-13[1]	-	+	1	-	2	1	0*	2*	1*	1	+	0	0,1	4a	1	Mt7	0,1	0	-	-
Mymarommatidae	9-[illegible][2]	-	+	2	+	1	0	2	?[8]	0	0	-	1	2	4b	2	Mt7	1	0	-	-
Serphitidae	10:9	-	+	2	-	0	0	2	?[8]	0	0	-	0	0	?	2	Mt7	0	0	?	?
Scelionidae	6-14[3]	-	+	2	-	0	0	2	3a	0	0	-	0	0	3b	1	0	0,1	1	+	-
Platygastridae	7-10	-	+	2	-	0	0	2	3a	0	0	-	0	0	?	1	0	1,2	1	+	-
Ceraphronoidea	10:11	-	+	2	-	0	0	2	3b	0	0	-	0	0	2	1	0	0,1[10]	0	+*	-
Proctotrupidae	13:13	-	-	2	-	0	0	2	3a	0	0	-	0	0	3a	1	0	1	1	+	-
Vanhorniidae	13:13	-	-	2	+	0	0	2	3a	0	0	-	0	0	3a	1	0	1	1	+	-
Evaniidae	13:13[4]	-	-	2	-	0	0	2	3a	0	0	-	0	0	3a	1	Mt7	2	0	+	+
Cynipoidea	10-20[5]	-	-	2	-	0	0	2	3a	0	0	-	0	0	3	1	Mt7	0,1,2	0	+	-
Gasteruptionidae	14:13	-	-	2	-	0	0	2	4	0	0	-	0	0	3	1	Mt7	0	0	+	+
Pelecinidae	14:14	-	-	2	-	0	0	2	3a	0	0	-	0	0	3a	1	Mt7*	2	1	+	-
Roproniidae	14:14	-	-	2	-	0	0	1	3	0	0	-	0	0	3	1	Mt7	2	0	+	+
Megalyridae	14:14	-	-	2	-	0	0	2	3b?	0	0	-	0	0	0	1	Mt7	0	0	?	?
Diapriidae	12-15[6]	-	+	2	-	0	0	2	3a	0	0	-	0	0	1*	1	Mt7	0,1[11]	1	+*	-
Monomachidae	15:14	-	-	2	-	0	0	0	3	0	0	-	0	0	3	1	Mt7	0	1	+	-
Austroniidae	15:14	-	-	2	-	0	0	1	3	0	0	-	0	0	?	1	Mt7	0	0	?	?
Heloridae	16:16	+	-	2	-	0	0	2	3a	0	0	-	0	0	3	1	Mt7	1	1	+	-
Trigonalidae	14-32	-	-	2	-	0	0	2	3a	0	0	-	0	0	3	1	0	0	1	+	+
Stephanidae	30-40	-	-	2*	-	0	0	0	0	0	0	-	0	0	1	1	Mt7[9]	0	1	+	+
Ichneumonoidea	10-70	-	-	2	+/-[7]	0	0*	2	1	0	0	-	0	0	3	1	1-7*	0,1,2	0	+*	+/-[13]

Footnotes for Table 3.1

[1] 7-11 ♀♀; 10-13 ♂♂.

[2] 9-11 ♀♀, 13 ♂♂, and 13:13 in Cretaceous representatives.

[3] 14:14 hypothesized as groundplan number by Masner (1970).

[4] 10:10 in one undescribed genus (L. Masner, pers. comm.).

[5] 13:14 most common, and characteristic of most families and subfamilies (see Weld 1952 and Quinlan 1979).

[6] 15:14 in Ismarinae, Ambositrinae and most Belytinae; 12:14 most common in Diapriinae (L. Masner, pers. comm.).

[7] Exodont in Ichneumonidae: Tryphoninae (Idiogrammatini); Braconidae: Alysiinae (Alysiini, Dacusini), Opiinae (Exodontiellini).

[8] At least concealed, but unknown if free, fused or absent.

[9] In females; males with metasomal spiracles absent (W. R. M. Mason, pers. comm.).

[10] Digitiform in Megaspilidae, sensory plates in Ceraphronidae.

[11] Digitiform in Belytinae, Ambositrinae and Ismarinae; sensory plates in Diapriinae (L. Masner, pers. comm.).

[12] Only demarked by subbasal groove on ventral surface of phallobase if present.

[13] Absent or reduced to small lateral extensions of vosellar plates in Braconidae; state unknown for Paxylommatidae (Vasey 1974).

Definition of symbols used in matrix of Table 3.1 and hypotheses of transformations series

(ts = hypothesized transformation series)

1. **Number of antennal articles.** Number of antennal articles possessed by females given first and separated by ":" from number possessed by males; known range of articles given if number not constant for each sex. A larger number of articles is considered as plesiomorphic and a smaller number is considered apomorphic, but exact transformation series are unknown.

2. **Anellus.** — = absent; + = present. (ts: — → +)

3. **Geniculate antenna.** — = absent; + = present. (ts: — → +)

4. **Multiporous plate sensilla of antennae.** 1 = elongate, ridge-like convex with distal end free from article, not surrounded by groove; 2 = absent, or otherwise structured. Transformation series uncertain because internal and external structure is insufficiently known for antennal sensilla of other terebrants.

5. **Exodont mandibles.** — = absent; + = present. (ts: — → +)

6. **Head structure.** 0 = single sclerotized capsule; 1 = frontal and occipital sclerites connected by pleated, membranous, hyperoccipital region; 2 = single sclerite with median, frontal, and supraorbital sulci. (ts: 0 → 1; 0 → 2)

7. **Position of antennal toruli.** 0 = distance between toruli of similar distance or less than distance between torulus and inner eye margin; 1 = distance between toruli much greater than distance between torulus and inner eye margin. (ts: 0 → 1)

8. **Pronotal structure.** 0 = long dorsally, hence saddle-like in lateral view, loosely attached to mesopleuron and highly mobile relative to mesothorax; 1 = intermediate in shape and degree of mobility between 0 and 2; 2 = reduced dorsally, hence triangular in lateral view, and rigidly united with mesopleuron. (ts: 0 → 1 → 2)

9. **Prepectus.** 0 = dorsal edge below spiracle and lateral edge of mesoscutum, concealed, independent; 1 = dorsal edge below spiracle and lateral edge of mesoscutum, concealed, fused to posterolateral edge of pronotum; 2 = dorsal edge extended with spiracle to lateral edge of mesoscutum, exposed, independent; 3 = dorsal edge extended above spiracle to lateral edge of

mesoscutum, concealed, independent; **3a** = as for state 3, except fused to posterolateral edge of pronotum in form of groove with outer edge of pronotum; **3b** = as for state 3, except exposed and fused to pronotum, with spiracle on pronotum; **4** = lost. (**ts:** 0 → 1; 0 → 2; 0 → 3 → 3a, 3b; 0 or 3 → 4)

10. Relationship of pronotum to tegula. 0 = extended posterodorsally to tegula; 1 = separated from tegula by interposed prepectus. (**ts:** 0 → 1)

11. Placement of mesothoracic spiracle. 0 = below and separate from exposed lateral edge of mesoscutum; 1 = at exposed lateral edge of mesoscutum. (**ts:** 0 → 1)

13. Forewing hypochaeta. — = absent; + = present. (**ts:** — → +)

14. Forewing membrane. 0 = smooth; 1 = reticulate. (**ts:** 0 → 1)

15. Hindwing structure. 0 = wing membrane extended to base of wing; 1 = wing membrane origin distally from stalk-like vein; 2 = with only stalk-like vein, no membrane. (**ts:** 0 → 1; 0 → 2)

16. Mesotrochanteral depressor. 0 = with fu_2-tr_2, and origin of t_2-tr_2 from mesoscutum and axilla; 1 = with fu_2-tr_2, and origin of t_2-tr_2 from axilla only; 2 = with t_2-tr_2 only, origin from mesoscutum and axilla; 3 = with fu_2-tr_2 only; **3a** = with fu_2-tr_2 and pl_2-tr_2; **3b** = with pl_2-tr_2 only; **4** = with t_2-tr_2 only, origin from axilla (this state not known for any extant terebrant); **4a** = with t_2-tr_2 only, origin from axilla and axillar phragma; **4b** = with t_2-tr_2 only, origin from axillar phragma. (**ts:** 0 → 2; 0 → 1 → 3 → 3a → 3b, or 0 → 1 and 0 → 3 → 3a → 3b; 0, 1 or 2 → 4 → 4a → 4b)

17. Petiole. 1 = 1 segment; 2 = 2 segments. (**ts:** 1 → 2)

18a. Metasomal spiracles. 1-7 = segments 1-7; Mt7 = segment 7 only; 0 = none. (**ts:** 1-7 → Mt7 → 0)

18b. Cerci. 0 = digitiform; 1 = reduced (flattened button-like structures or as setiferous, sensory plates); 2 = absent. (**ts:** 0 → 1 → 2)

19. Relative structure of metasoma and ovipositor. 0 = ovipositor rotates about basal line of axis, protruded ventrally from metasoma anterior to metasomal apex during ovipostion, and if covered by sterna then latter widely displaced from terga during oviposition. 1 = modified from above, "apomorphic". (ts: 0 → 1)

20. **Basal ring of male genitalia.** + = present; — = absent. (ts: + → —)

21. **Cuspis of male genitalia.** + = present; — = absent. (ts: + → —)

3.5 Discussion

Figure 3.1 illustrates proposed phyletic relationships of Chalcidoidea, Mymaridae, and Mymarommatidae based on hypotheses of character-state evolution proposed in the text and summarized in Table 3.1. Numbers in parenthesis correspond to numbering of the characters in the text.

3.5.1 Relationships of Mymaridae and Chalcidoidea

A relationship of Mymaridae with Chalcidoidea is much more strongly supported by this anlysis than is the relationship of Mymaridae and Scelionidae proposed by Rasnitsyn (1980). Monophyly of Chalcidoidea, including Mymaridae, is supported by three hypothesized synapomorphies for members: an unique external structure of the antennal multiporous plate sensilla, position of the mesothoracic spiracle at the lateral edge of the mesoscutum, and an exposed prepectus. Adult mymarids are additionally like other chalcidoids, and dissimilar to scelionids, in having a mesotrochanteral depressor consisting of only the axillar part of t_2-tr_2 (lacking mesoscutal part); in having an axillar phragma as a partial site of origin for t_2-tr_2, and in lacking an independent basal ring from the male genitalia. These latter three character states are hypothesized as synapomorphies for Mymarommatidae + Chalcidoidea. Whereas adult mymarids are hypothesized to share six apomorphic states with other chalcidoids, I found no states shared by mymarid and scelionid adults that I interpret as apomorphic. Furthermore, state of the mesotrochanteral depressor in scelionids indicates members of this taxon are only distantly related to mymarids and chalcidoids. I therefore consider the similar first-instar larval structure of mymarids and scelionids to be the result of convergence, most likely because of a similar larval habitat.

It is tempting to hypothesize a sister-group relationship of Mymaridae with other Chalcidoidea because of the distinctive structure of adult mymarids. However, presence of an anellus is the only known apomorphic state that indicates possible monophyly of Chalcidoidea exclusive of Mymaridae. Because at least some members of most chalcidoid families lack an anellus, and because the first flagellomere of some mymarids is quite small, I do not consider an anellus as reliable evidence of monophyly of Chalcidoidea excluding Mymaridae. Consequently, relationship of mymarids to other chalcidoids remains unresolved.

3.5.2 Relationships and classification of Mymarommatidae

I include Mymaridae in Chalcidoidea because I consider that there are no reliable apomorphies supporting monophyly of Chalcidoidea excluding Mymaridae. Whether Mymarommatidae should also be classified in Chalcidoidea depends on what character states are used to delimit the superfamily. Mymarommatidae would be included in Chalcidoidea if the superfamily is defined on presence of axillar phragmata; presence of only an axillar portion of the mesotrochanteral-depressor muscle, and absence of a basal ring from the male genitalia (Fig. 3.1). Alternatively, if Chalcidoidea is diagnosed on structure of the multiporous plate sensilla, presence of an exposed prepectus, and postion of the mesothoracic spiracle (Fig. 3.1), Mymarommatidae would be excluded. I prefer to delimit Chalcidoidea on the latter three external character states, rather than on internal characters, and I thus exclude Mymarommatidae from Chalcidoidea.

As the hypothesized sister group of Chalcidoidea (Fig. 3.1), mymarommatids should be accorded the same superfamily status. However, there is considerable disagreement concerning membership and validity of established terebrant superfamilies. I see little present advantage in recognizing one more, monotypic superfamily, particularly when relationships of mymarommatids and serphitids remain uncertain. Monophyly of Mymarommatidae + Chalcidoidea is only supported by internal character states that can not be examined in fossil serphitids. It is therefore possible that Mymarommatidae + Serphitidae are a monophyletic clade, based on a two-segmented petiole, and that they together are the sister group of Chalcidoidea. Though I presently consider this to be unlikely, for reasons given below, I propose that mymarommatids be treated as a family and not be assigned to any superfamily until relationships proposed in this paper are more fully investigated and tested with additional characters.

Though mymarommatids and serphitids share a two-segmented petiole, external structure of individuals is otherwise very different. Kozlov and Rasnitsyn (1979) considered serphitids to be more similar to scelionids in structure, particularly in structure of the head and mesosoma. Furthermore, most female serphitids have a secondary bend in the flagellum of the antenna, similar to the antennae of many female scelionids and platygastrids. The lateral regions of the metasomal terga also appear to be slightly flexed in some individuals with a fully expanded metasoma, and there is a distinct submarginal groove (*sensu* Masner 1980) in some specimens with a compressed metasoma. This metasomal structure is not evident in all specimens and could be an artifact of preservation, but it might also represent an incipient stage in the evolution of laterotergites, characteristic of most Scelionidae. Scelionids have several apomorphic states (highly reduced fore wing venation, modified metasomal structure, absence of metaso[illegible] spiracles) that indicate serphitids were not actually derived from Scelionidae as suggested by Kozlov and Rasnitsyn (1979), but they could be closely related to scelionids based on similarities of external structure. Though synapomorphies are not yet documented for Serphitidae + Scelionidae, this relationship requires much less secondary modification in external structure of individuals than does a sister-group relationship between Serphitidae and Mymarommatidae. Consequently, I consider the only apomorphic state shared by serphitids and mymarommatids, a two-segmented petiole, to be the result of convergence.

3.5.3 Relationships of the clade Mymarommatidae + Chalcidoidea

If Mymarommatidae is the sister group of Chalcidoidea, it remains to be answered what is the sister group of Mymarommatidae + Chalcidoidea. Königsmann (1978a) proposed Cynipoidea as the sister group of Chalcidoidea, and Evanioidea (Evaniidae, Aulacidae and Gasteruptionidae *sensu* Königsmann) as the sister group of Cynipoidea + Chalcidoidea.

Evanioids were proposed as the sister group of cynipoids and chalcidoids based on restriction of metasomal spiracles to only the seventh metasomal segment, and on common possession of 13 antennal articles by males and females (13:14 in most cynipoids was hypothesized to be a modified groundplan character). Distribution of metasomal spiracles (character 18a) and number of antennal articles (character 1) given in Table 3.1 shows that the character states are not tenable synapomorphies for Evanioidea + Cynipoidea + Chalcidoidea.

Königsmann (1978a) proposed Cynipoidea as the sister group of Chalcidoidea based on absence of cuspides from the volsellae of male genitalia, and because in females the third valvulae (sheaths) extend into the second valvifers in a continuous transition. I was unable to determine if Königsmann originally proposed this latter state as a synapomorphy for Cynipoidea + Chalcidoidea, but Domenichini (1953) stated that many chalcidoid females have the third valvulae differentiated from the second valvifers as articulated appendages. Distribution of cuspides in the male genitalia of terebrants also indicates that their absence is not a tenable synapomorphy for Cynipoidea + Chalcidoidea (Table 3.1, character 21).

Though actual distribution of the character states do not appear to support any of Königsmann's purported synapomorphies for Evanioidea + Cynipoidea + Chalcidoidea, a relationship between Cynipoidea and Chalcidoidea has long been suggested. Ashmead (1896) considered chalcidoids to be derived from cynipoids, uniting the taxa on the basis of one symplesiomorphy (structure of the female metasoma and ovipositor) and one apomorphy (fore wing without stigma). Bradley (1958) also hypothesized a close relationship between cynipoids and chalcidoids, stating that fore wing venation of chalcidoids could only be derived and interpreted from the fore wing venation of cynipoids. He interpreted fore wing venation of chalcidoids based on similarities between the venation of *Leucospis* Fabricius (Chalcidoidea: Leucospidae) and *Ibalia* Latreille (Cynipoidea: Ibaliidae) (Bradley 1955). However, this does not establish phylogenetic affinity. Furthermore, Rasnitsyn (1980) considered fore wing venation and some variants of hind wing venation of chalcidoids to resemble venation of

Proctotrupoidea (*sensu* Rasnitsyn), though the predominance of hind wing venation was said to be more typical of Diaprioidea (*sensu* Rasnitsyn) or Mesoserphidae (an extinct family assigned by Rasnitsyn to Proctotrupoidea). The similarities were attributed to a "common tendency" by Rasnitsyn, rather than to inheritance. Finally, Farish (1972) noted a similarity in cleaning behavior between cynipoids and chalcidoids. They were the only apocritans studied not to have one type of wing-cleaning movement, in which the wings are held at the side and the hind legs clean only the dorsal surface of the wings. Cynipoids, chalcidoids, and some ichneumonoids studied used both hind legs to clean the dorsal and ventral surface of a wing simultaneously. However, generalizations were based on study of only one cynipoid, 11 chalcidoids, several ichneumonoids, two diapriids, one helorid, and one evaniid.

Convincing evidence for a sister-group relationship between Cynipoidea and Chalcidoidea thus appears to be lacking. If cynipoids are the sister group of chalcidoids this necessitates the common ancestor had both t_2-tr_2 and fu_2-tr_2, and that chalcidoids lost fu_2-tr_2 whereas cynipoids lost t_2-tr_2, convergent towards most other terebrants (Table 3.1, character 16). It also requires the common ancestor had the plesiomorphic position and structure of the mesothoracic spiracle and prepectus, and that this was modified in cynipoids so the prepectus was projected above [illegible] spiracle and fused to the pronotum to form a tongue-and-groove interlocking mechanism with the mesopleuron, also as in most other terebrants (Table 3.1, character 9, state 3a).

Rasnitsyn (1980) suggested chalcidoids probably were most closely related to either Diaprioidea *sensu* Rasnitsyn or to the extinct family Mesoserphidae, which he included in Proctotrupoidea. These relationships were proposed on the basis of similarities in fore wing and hind wing venation, an independent prepectus in chalcidoids and some diaprioids (which Rasnitsyn thought might have been inherited from mesoserphids), and on similarities in pronotal shape and structure of the antennae in chalcidoids, austroniids, and monomachids. However, at least the independent prepectus and correlated pronotal shape are symplesiomorphic.

No apomorphic states were found in the present study to indicate the probable sister group of Mymarommatidae + Chalcidoidea, but I suspect that it is some combination of several higher taxa of Terebrantes and not just one family, or one superfamily such as Cynipoidea. I consider this likely because I believe Mymarommatidae + Chalcidoidea represent a very early clade in the evolution of Terebrantes, based on the number of plesiomorphic features members retain (an independent prepectus, mesothoracic spiracle at the anterodorsal angle of the prepectus, mesotrochanteral depressor with a tergal portion, cerci and metasomal spiracles present, and structure of the female metasoma). If an early divergence of mymarommatids and chalcidoids in the evolution of terebrants is correct, then such apomorphic states as geniculate antennae, reduced number of antennal articles, and reduced fore wing venation are most probably convergent with most or all other terebrants with these same states. Of unknown significance is the interesting pattern exhibited by chalcidoids of retained plesiomorphic features that are conspicuously modified. These include, for example, an independent prepectus that is exposed; a mesothoracic spiracle that is at the anterodorsal angle of the prepectus, but also at the lateral edge of the mesoscutum; and a tergal portion of the mesotrochanteral depressor that arises all or in part from an axillar phragma.

Although I have not resolved relationships of Mymarommatidae + Chalcidoidea with other Terebrantes, I have indicated the problems involved for doing so. My primary interest in discussing these problems, to paraphrase Gordh (1979, p. 744), is to stimulate research on Chalcidoidea and other Terebrantes because they are a fertile area for investigations in biology, behavior, ecology, and systematics. A more accurate understanding of the true phyletic relationships of Chalcidoidea will not only require more detailed investigations of this superfamily, but also of other Terebrantes, both extant and extinct.

Figure 3.1. Cladogram illustrating hypothesized evolution of character states and relationships of taxa. Numbers correspond to numbers used for character-state analysis in text.

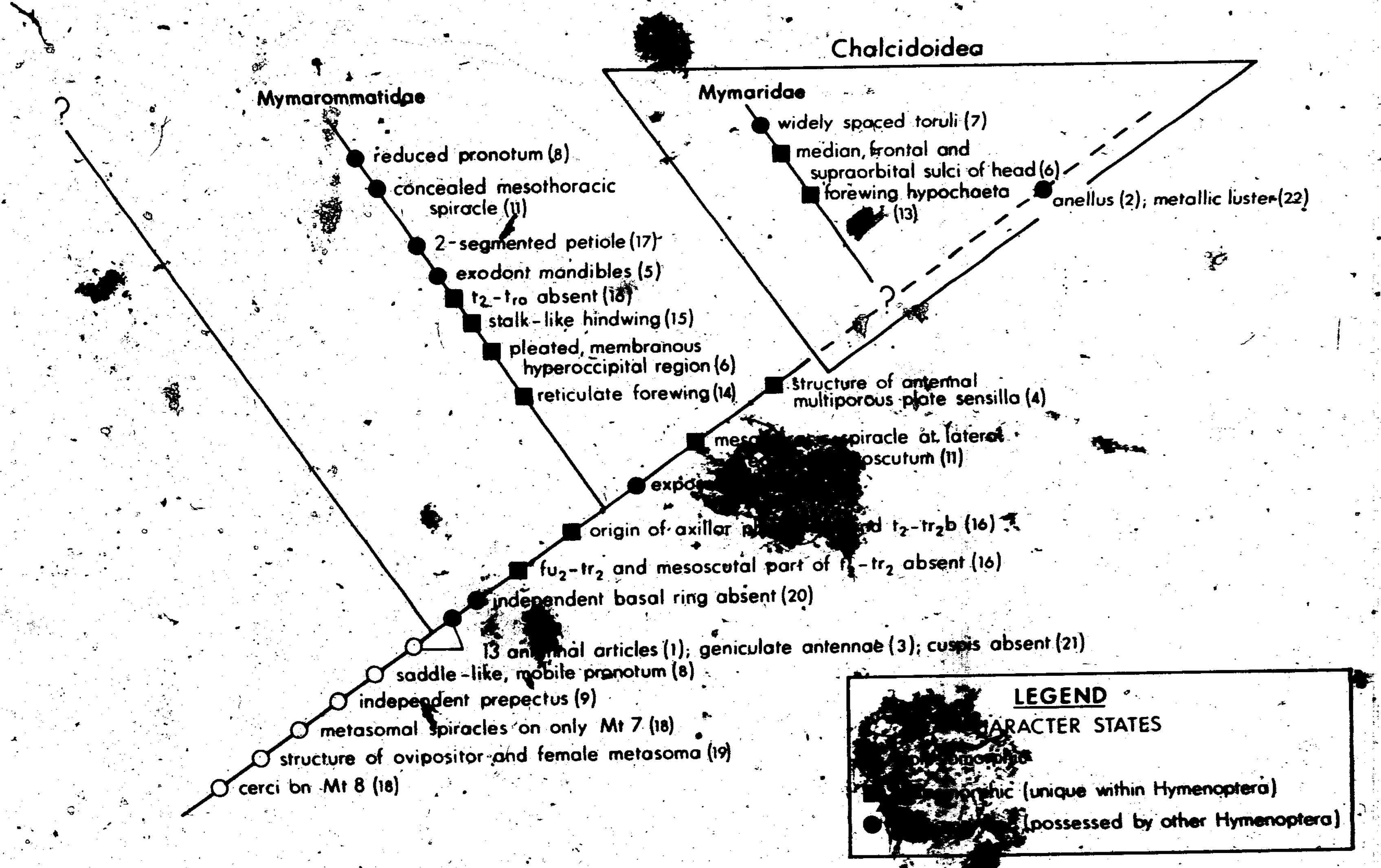
Chalcidoidea
Mymarommatidae
Mymaridae
?
?
reduced pronotum (8)
concealed mesothoracic spiracle (11)
2-segmented petiole (17)
exodont mandibles (5)
t_2-t_{ro} absent (16)
stalk-like hindwing (15)
pleated, membranous hyperoccipital region (6)
reticulate forewing (14)
widely spaced toruli (7)
median, frontal and supraorbital sulci of head (6)
forewing hypochaeta (13)
anellus (2); metallic luster (22)
structure of antennal multiporous plate sensilla (4)
mes[illegible] spiracle at lateral [illegible]oscutum (11)
expo[illegible]
origin of axillar [illegible]d t_2-tr_2b (16)
fu_2-tr_2 and mesoscutal part of [illegible]-tr_2 absent (16)
independent basal ring absent (20)
13 an[illegible]nal articles (1); geniculate antennae (3); cuspis absent (21)
saddle-like, mobile pronotum (8)
independent prepectus (9)
metasomal spiracles on only Mt 7 (18)
structure of ovipositor and female metasoma (19)
cerci on Mt 8 (18)
LEGEND
[illegible]ARACTER STATES
[illegible]
[illegible]hic (unique within Hymenoptera)
● [illegible] (possessed by other Hymenoptera)

Figure 3.2. *Gonatocerus* sp., head and basal antennal articles, male.

Figure 3.3. *Gonatocerus* sp., head and basal antennal articles, female.

Figure 3.4. *Gonatocerus* sp., antennal articles, male.

Figure 3.5. *Anacharis* sp., antennal articles, female.

Figure 3.6. *Pseudeucolla* sp., antennal articles, male.

Figure 3.7. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), anterior view of head.

Figure 3.8. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), frontal view of head.

Figure 3.9. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), posterolateral view of head.

Scale bar = μm.

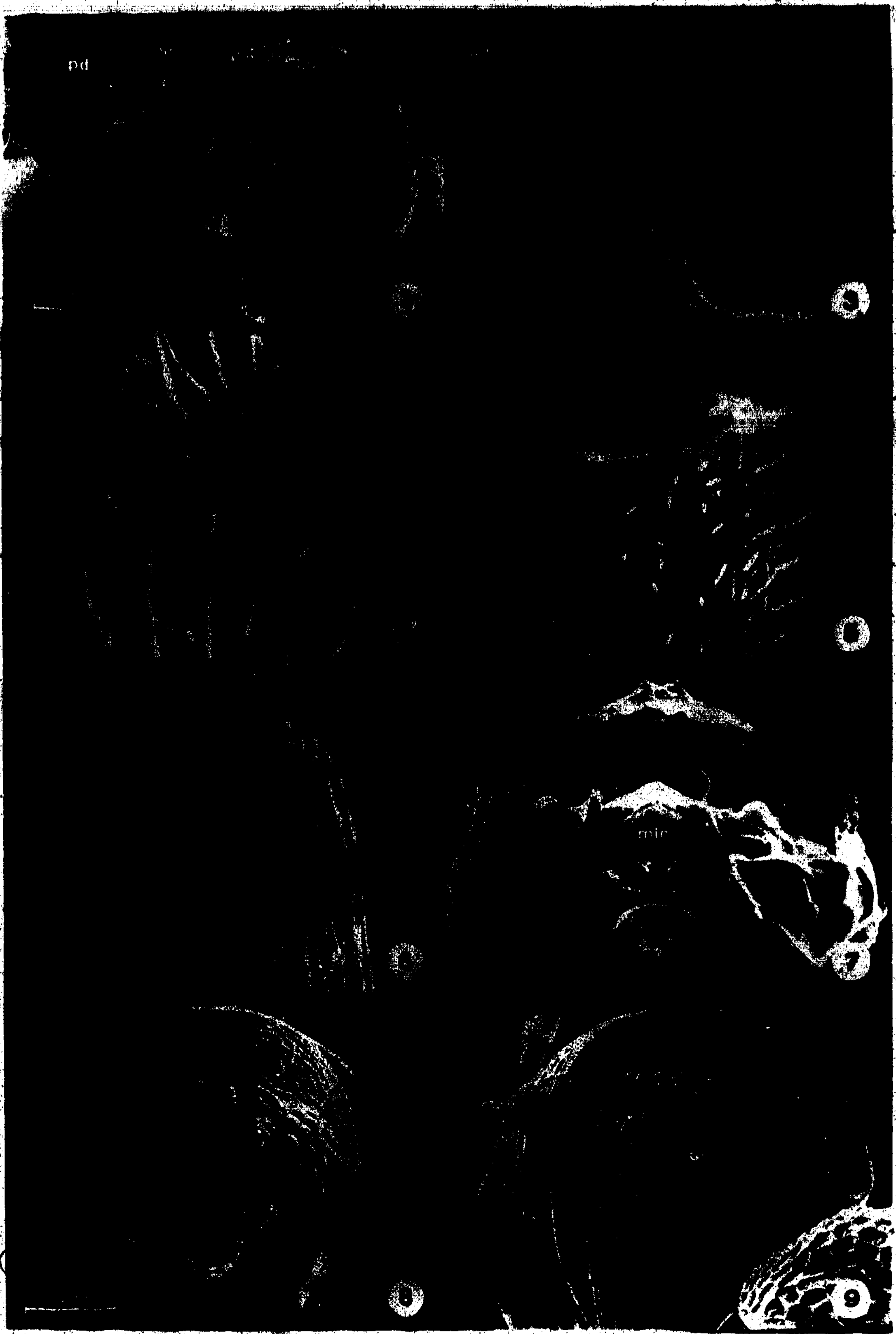
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Figure 3.10. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), lateral mesosoma.

Figure 3.11. *Palaeomymar insulare* (Valentine), dorsolateral mesosoma.

Figure 3.12. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), internal pronotum.

Figure 3.13. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), frontolateral mesosoma, pronotum removed.

Figure 3.14. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), lateral pronotum-mesothorax. Slide mounted (arrow denotes dorsum).

Figure 3.15. *Megischus texanus* Cr., prepectus and posterolateral region of pronotum.

a. outer view.

b. inner view.

Figure 3.16. *Calliscelio* sp., lateral pronotum-mesothorax.

Figure 3.17. *Paridris* sp., posterolateral view of isolated pronotum.

Scale bar = μm.

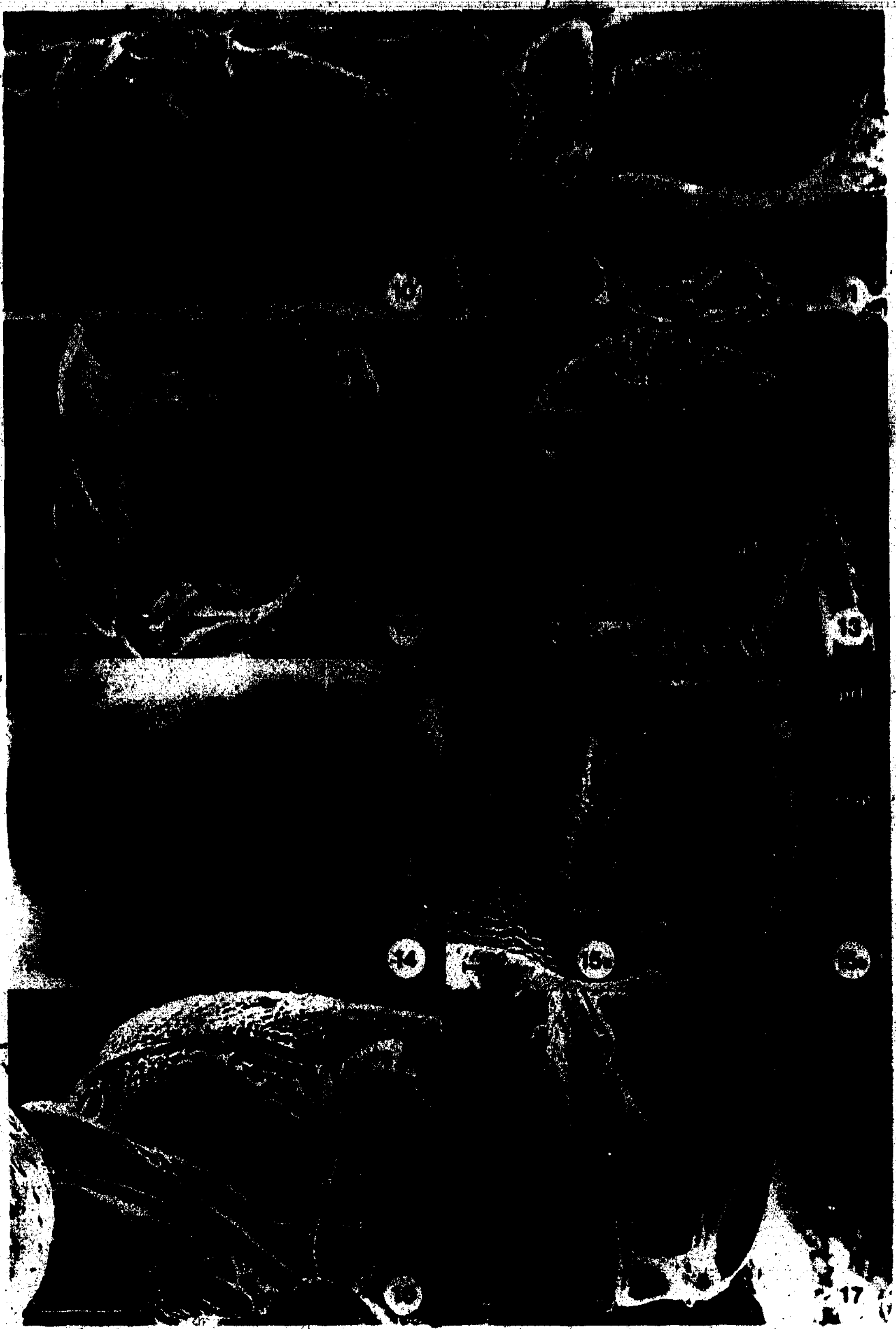
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Figure 3.18. *Torymus* sp., lateral pronotum-mesothorax.

Figure 3.19. *Pnigalio pallipes* (Provancher), lateral pronotum-mesothorax.

Figure 3.20. *Brachymeria obscurata* (Walker), lateral pronotum-mesoth[illegible]

Figure 3.21. *Pseudometagea* sp, lateral pronotum-mesothorax.

Figure 3.22. *Camptoptera (Macrocamptoptera)* sp., lateral pronotum-mesothorax.

Figure 3.23. *Ptilomymar* sp., lateral pronotum-mesothorax.

Figure 3.24. *Bruchomymar* sp., lateral pronotum-mesothorax.

Figure 3.25. *Stephanodes* sp., lateral pronotum-mesothorax.

Scale bar = µm.

Figure 3.26. *Gonatocerus* sp., lateral pronotum-mesothorax.

Figure 3.27. *Gonatocerus* sp., lateral pronotum-mesothorax.

Figure 3.28. *Gonatocerus* sp., lateral pronotum-mesothorax.

Figure 3.29. *Polynema* sp., lateral pronotum-mesothorax.

Figure 3.30. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), fore wing.

Figure 3.31. *Leucospis a. affinis* Say, fore wing.

Figure 3.32. *Gonatocerus* sp., fore and hind wing.

Figure 3.33. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), hind wing.

Scale bar = μm.


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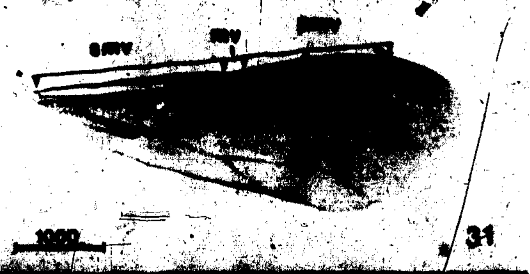

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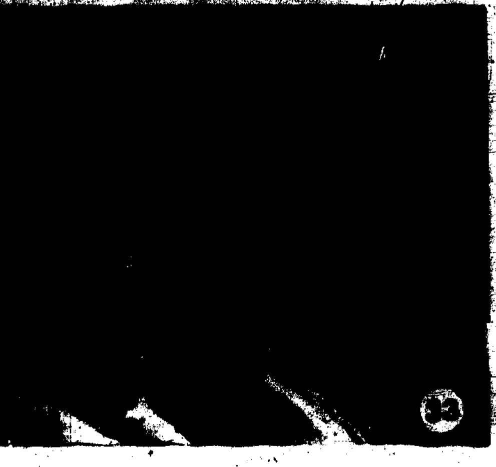


Figure 3.34. *Gonatocerus* sp., sagittal section of mesosoma, mesofurca and various muscles removed.

Figure 3.35. *Gonatocerus* sp., isolated scutellar-axillar complex.

Figure 3.36. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), petiolar segments.

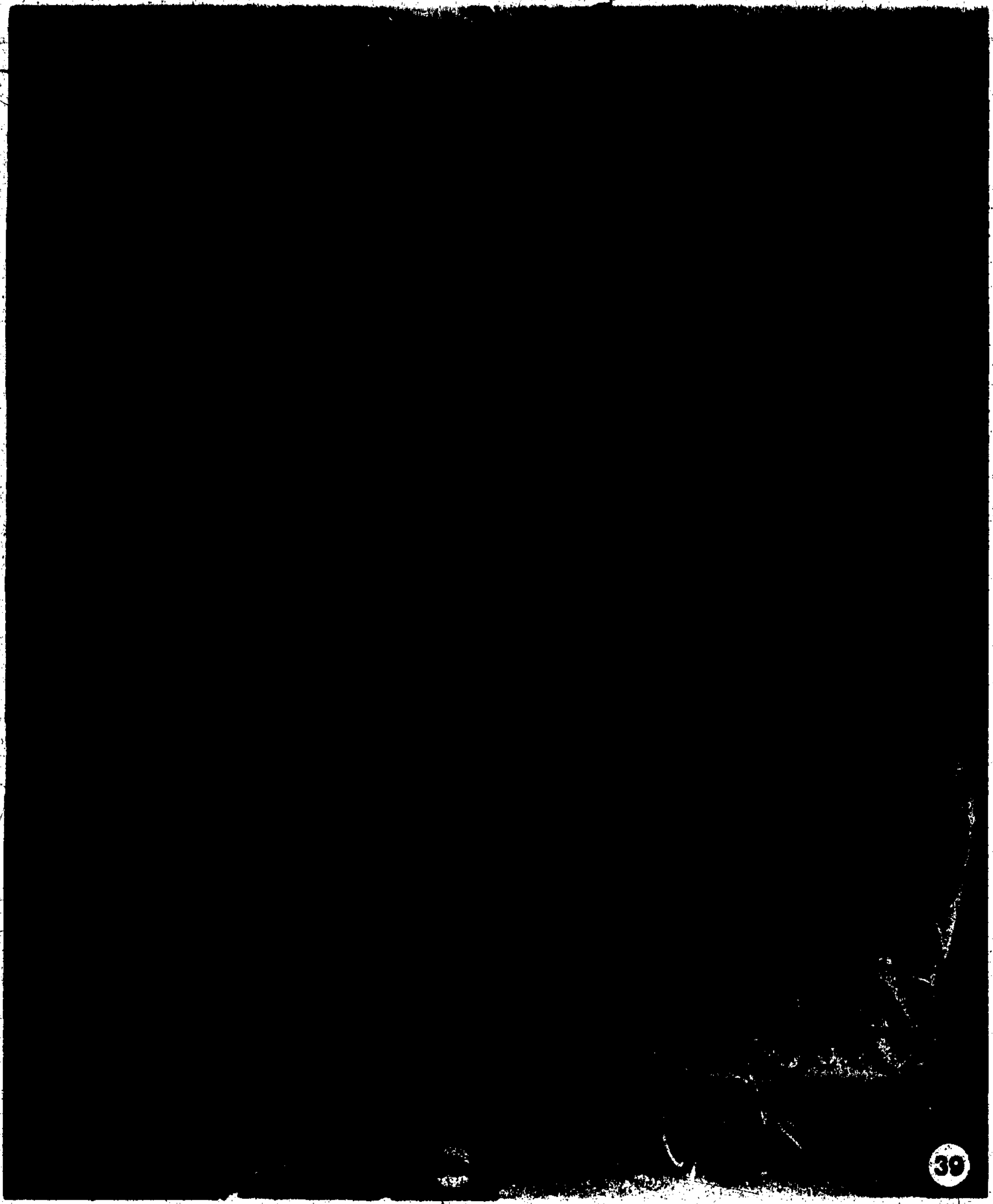
Figure 3.37. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), metasoma exclusive of petiolar segments.

Figure 3.38. *Leucospis a. affinis* Say, male genitalia.

a. dorsal view.

b. ventral view.

Figure 3.39. *Palaeomymar* sp., nr. *anomalum* (Bl. & Kr.), apex of metasoma. Scale bar = μm.



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3.7 Appendix: List of abbreviations used for figures

aed: aedeagus

ax: axilla

axp: axillar phragma

br: basal ring

cer: cercus

cx: coxa

fs: frontal sulcus

fsc: frontal sclerite

fwv: fore wing venation

gr: posterolateral pronotal groove

hw: hind wing

hyc: hypochaeta

hyp: hypopygium

man: mandible

mb: membrane

mlc: maxillo-labial complex

mpl: mesopleuron

ms: median sulcus

msp: mesothoracic spiracle

mt: metasomal tergum

mv: marginal vein

net: netrion

oof: occipital foramen

osc: occipital sclerite

pd: pedicel

phl: phallobase

pmb: pleated membrane

pmv: postmarginal vein

ppi: posterolateral pronotal inflection

ppl: propleuron

pre: prepectus

prl: pronotal lobe

sc: scape

scl: scutellum

sct: mesoscutum

smv: submarginal vein

sp: spiracle

ss: supraorbital sulcus

stv: stigmal vein

t_2-tr_2: mesotergal-trochanteral muscle

tg: tegula

to: torulus

tsa: transscutal articulation

4. MESOTHORACIC SKELETOMUSCULATURE AND MECHANICS OF FLIGHT AND JUMPING IN EUPELMINAE (HYMENOPTERA: CHALCIDOIDEA: EUPELMIDAE)[4]

4.1 Synopsis

Mesothoracic skeletomusculature of male and female Eupelminae is described and compared with that of other Eupelmidae, Chalcidoidea, and Hymenoptera. Various external mesopleural features and structural dimorphism between the sexes are explained by differences in muscle form and placement. A set of terms for mesothoracic structure is proposed that is equally applicable to male and female eupelmines and to other chalcidoids. Mechanics of flight and jumping in male eupelmines, and of jumping in females is also described. The flight mechanism of males is similar to that previously described in other hymenopterans and is structurally independent of the jumping mechanism. Contraction of large mesotergal-mesotrochanteral muscles, originating from the axillae and axillar phragmata, act directly to retract the mesotrochanters into the mesocoxae for jumping. Females have coadapted the flight and jumping mechanisms into a single mechanism to greatly improve jumping. The mesotergal-mesotrochanteral muscles are reduced to slender, tendon-like muscles originating from the anteroventral angle of each lateral axillar surface. Jumping in females results from contraction of large mesopleural-mesotergal muscles that insert into anterolateral processes of the mesoscutum by pads of resilin. The pads are stretched during contraction of the mesopleural-mesotergal muscles and the potential energy thus stored is subsequently released to flex the mesonotum along the transscutal articulation. The first and second axillary sclerites are modified to function as a hinge to control mesonotal flexing for jumping. Flexing the mesonotum rotates the lateral axillar surfaces anteriorly and dorsally, thereby pulling up on the mesotergal-mesotrochanteral muscles and changing a horizontally directed force into a vertical force that is used to retract the mesotrochanters for jumping. A mesothoracic lock mechanism to prevent initial mesonotal flexing is proposed, but is not documented.

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[4] A version of this chapter has been accepted for publication in The Canadian Entomologist.

'Contortion' of female eupelmines is described, and is a consequence of the increased degree of mesonotal flexing required for their jumping mechanism. The modified mesocoxal articulation of females is hypothesized to function in rotating the middle legs cephalad to protect the head and antennae during landing. It is questioned whether female eupelmines can fly, and the adaptive significance of enhancement of jumping at the expense of flight in females, and of sexual dimorphism in the subfamily, is discussed.

4.2 Introduction

Chalcidoidea is undoubtedly the most diverse superfamily of parasitic Hymenoptera (Terebrantes), biologically and structurally. It may also ultimately prove to be the most speciose terebrant superfamily, though Ichneumonoidea presently has more described species (Noyes 1978, Gordh 1979). Structural diversity in Chalcidoidea, and resulting problems for higher classification in the superfamily, is well illustrated by the family Eupelmidae. Eupelmids are treated as a family level taxon in many classifications, but in some are included in Encyrtidae (*e. g.*, Riek 1970). Graham (1969, p. 7) also suggested that they might be included in Pteromalidae for a "more mature classification" of the superfamily.

The subfamily Eupelminae[5] partly accounts for the various concepts of eupelmid relationships and classification. Female eupelmines have a number of apomorphic character states, including an undifferentiated, convexly expanded lateral mesopleuron (ac, Fig. 4.30); a ventral membranous region anterior to each mesocoxa (mh, Figs. 4.15, 4.17); mesocoxae that rotate anteroventrally about a transverse line of axis out of their combined fossa (*cf.* Figs. 4.29, 4.30); an elongate and thickened mesotibial spur (Fig. 4.19); and either a dense pad of setae, lateral row(s) of pegs, or both, on the ventral surface of each mesotarsus (Fig. 4.19). These states are shared with males and females of most Calosotinae and Tanaostigmatinae, the

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[5] Excluding *Metapelma* Westwood and *Neanastatus* Girault as interpreted here. A new subfamily will be established for these two genera and an undescribed genus in a subsequent paper.

other two presently recognized eupelmid subfamilies, and are generally regarded as 'family' characters. However, various combinations of the states are also shared with males and females of Encyrtidae and a few Aphelinidae, whereas male eupelmines possess none of the apomorphic character states of the 'family', except for an elongate (not thickened) mesotibial spur (Fig. 4.20). Males most closely resemble many members of Pteromalidae in structure, particularly those of the subfamilies Chalcedectinae and Cleonyminae (*cf.* Figs. 4.1, 4.2), which also have variedly long mesotibial spurs. Chalcedectines have dentate hind femora and are readily identified, but many male eupelmines and cleonymines are difficult to distinguish from one another.

Male and female eupelmines are each more similar to individuals of other higher taxa than they are to each other. This sexual dimorphism might be interpreted as evidence that the subfamily was derived from some pteromalid ancestor, and that Eupelminae is the plesiomorphic sister group of Calosotinae + Tanaostigmatinae + Encyrtidae. However, Calosotinae is generally regarded as the most plesiomorphic eupelmid subfamily (Bouček 1958, 1967). Males and females, primarily of undescribed taxa, exhibit intermediate structures and apparent transformation series in structure between the most plesiomorphic (pteromalid-like), and most apomorphic eupelmid structures. Individuals of the genus *Oodera* Westwood, for example, have the apomorphic middle leg structure of most eupelmids, but not other apomorphies of the family. Consequently, *Oodera* has been assigned tentatively to both Cleonyminae (Pteromalidae) and Calosotinae (Eupelmidae) in different classifications (Graham 1969).

Analysis of sexual dimorphism in Eupelminae is important for determining the phylogenetic relationships of the taxon. Determining homologous mesothoracic regions between the sexes is also important in order to stabilize use of structural terms within the family and superfamily. Additionally, eupelmid and encyrtid structure is inherently interesting on the basis of functional morphology. It has long been known that female eupelmines are apt to die in a 'contorted' position (*cf.* Figs. 4.21, 4.22). Calosotines do also, but less conspicuously, and tanaostigmatines and encyrtids only slightly (Bouček 1967). Contortion of female eupelmines was first described for the "back-rolling wonder" (Clausen 1927, p. 466), *Anastatus mirabilis* (Walsh and Riley), by Walsh and Riley (1869a, b). They most aptly described contortion as: "And in this genus—most wonderful to relate—the insect rolls itself up in an upward instead of downward direction, like a clown turning a back summerset, so that the breast becomes the convex side of the curve, and the back the concave side" (Walsh and Riley 1869a, p. 157). Less poetically, the head, mesosoma, and metasoma are aligned in a relatively straight plane in uncontorted specimens (Fig. 4.21). In contorted individuals the mesonotum is highly arched, and the head and metasoma reflexed dorsally so that the body is more or less U-shaped (Fig. 4.22), or, in the most extreme condition, head and metasoma touch above the mesosoma so the body is dorsally curled into a circle.

Walsh and Riley (1869a) proposed that individuals curled the body in an effort to hide from predators. Peck, Bouček and Hoffer (1964, p. 60) suggested that contraction of the dorsolongitudinal indirect flight muscles flexed the mesoscutum and "serve obviously for jumping"~~, but did not~~ indicate how. Riek (1970) considered jumping ability of encyrtids and eupelmids to be correlated with an increased size of mesothoracic muscles and the convexly expanded mesopleura, but again no explanation of jumping was offered. Though encyrtids, and eupelmids with expanded mesopleura are acknowledged to be excellent jumpers, quantitative studies have yet to be made showing how far or how high they can jump.

I address four topics in this paper. First, I describe the mesothoracic skeletomusculature of male and female eupelmines and attempt to homologize their components. I then propose a single set of terms for mesothoracic structure that is equally applicable to male and female eupelmines, and to other eupelmids and chalcidoids. Third, I correlate the different skeletomusculature of male and female eupelmines with differences in function, and fourth, describe the principal differences in mesothoracic musculature between eupelmines and other eupelmids.

4.3 Materials and methods

4.3.1 Materials

Descriptions of external structure in males and females, and study of external aspects of contortion in female eupelmines are based on study of specimens from all biogeographic regions. Study, descriptions, and illustrations of mesothoracic musculature, and of the flight and jumping mechanisms of male and female eupelmines are based primarily on dissections of representatives of *Eupelmus* Dalman and *Brasema* Cameron. Females of *Anastatus reduvii* (Howard) and *Macroneura vesicularis* (Retzius) were also dissected for analysis of musculature involved in jumping. Comparisons of the musculature of male and female eupelmines with that of other chalcidoids are based on dissections of individuals of *Metapelma spectabile* Westwood, *Neanastatus* spp., and *Zaischnopsis schwarzii* Ashmead (representing an undescribed genus related to the previous two genera (Eupelmidae); *Eusandalum* spp., *Calosota metallica* (Gahan) and *Calosota* sp. (Eupelmidae: Calosotinae); *Tanaostigmoides howardii* Ashmead, *Tanaostigma* n. sp., and *Cynipencyrtus flavus* (Ishii)[6] (Eupelmidae: Tanaostigmatinae); *Encyrtus fuscus* (Howard), *Leptomastix* sp., and *Charitopus* sp. (Encyrtidae); *Chalcedectus* sp. (Pteromalidae: Chalcedectinae); and *Cleonymus* sp., *Epistenia* sp., *Lycisca* sp., and *Oodera* sp. (Pteromalidae: Cleonyminae).

4.3.2 Specimen preparation

The single specimens of *C. flavus*, *Z. schwarzii*, and *Oodera* sp. that were available for dissection were air-dried. These were rehydrated before dissection as described in Gibson (in

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[6] Originally described within Encyrtidae, but transferred to Tanaostigmatidae (*sensu* LaSalle and Noyes) by LaSalle and Noyes (in press).

press, a). The specimens of the latter two taxa had the muscles sufficiently preserved so that states of the pleural and tergal muscles were determined, but only state of the t_2-tr_2 (see table 4.1) muscle was determined for *C. flavus*. Other dissections for internal structure and musculature were of ethanol-preserved specimens. The head, metasoma, and legs excluding coxae were dissected from individuals in 70% ethanol. The mesosoma was then dehydrated through 98% ethanol, or cut sagittally into halves before dehydration, and critical-point dried to avoid shrinkage of muscles. Double-sided sticky tape was used to position the dried specimens on scanning electron microscope stubs and silver paint was used to ground and rigidly affix the specimens for further dissection and cleaning. The latter was performed under a binocular microscope using fine scalpels, minutien pins, and double-sided sticky tape. Scalpels were used to remove cuticle, and minutien pins and double-sided sticky tape to remove unwanted internal tissue, such as muscle layers, connective tissue, tracheae, and dried haemolymph. Lightweight probes were made by inserting a minutien pin into the end of thin dowels. Double-sided sticky tape was affixed next to the mounted specimen and the tip of the minutien pin scratched across the surface of the tape to pick up a small amount of the adhesive. This was then used to pick out extraneous tissue without disturbing the structures to be viewed. Cleaned specimens were gold coated with a sputter-coater (except for the individual in figure 4.27), and photographed with a Cambridge Stereoscan 250 scanning electron microscope.

The pl_2-t_2c muscle, including the anterior pad of material into which it inserts, and the t_2-tr_2 muscle were tested for resilin by staining with a solution of toluidine blue. Stained pieces were rinsed in water, dehydrated through 98% ethanol, transferred to xylene, and mounted in Canada balsam on microscope slides. Unstained test pieces were also placed in welled microscope slides in a 1:1 solution of glycerine and water, and tested for fluorescence under ultraviolet light. A Zeiss Photomicroscope 1 with an epi-fluorescence condenser III RS was used to do so, and results were photographed with a 35mm camera. Color, 2x2 transparencies are in the author's collection.

Descriptions of flight mechanics of male eupelmines are based on an analysis of structure and on comparison of this with previously described flight mechanisms of other hymenopterans. The jumping mechanics of males is based only on analysis of structure. High speed photography of jumping by females was attempted with a Super 8mm camera at 300 frames per second. The front tibiae and tarsi of females of *Eupelmus* sp. were removed with a pair of fine scissors to inhibit walking, and jumping induced by touching the ovipositor with a hot probe.

4.3.3 Terms

Designation of muscles follows Daly (1963, 1964). Muscles that are figured or discussed in the text are designated by numbers corresponding to description of the muscles in Table 4.1. Designation of parts of the mesofurca follows Duncan (1939). Use of the terms suture, articulation, line, sulcus, phragma and apodeme are explained in Gibson (in press, a). Most terms used for parts of the mesonotum and for the intersegmentalia are defined in the same paper. For other structural terms that are not in common use, either first use or a major reference for each is given in brackets following the term. Terms accepted for external structure of the mesothorax are printed in bold face when first described. Abbreviations designating structure are given in bold face with the number of the figure(s) illustrating the structure, and listed in the appendix. Terms proposed for regions of the mesopleuron, based on site of origin of muscles, are defined below:

Acropleuron (**ac**, Figs. 4.1, 4.2, 4.26, 4.27, 4.30, 4.51): region of the mesopleuron that is the site of origin of pl_2-t_2c (5) and pl_2-3ax_2a (7).

Acropleural sulcus (**acs**, Figs. 4.1, 4.25, 4.27, 4.28, 4.29): sulcus that delineates the acropleuron from the mesepimeron and mesepisternum.

Transepimeral line, sulcus or pit (**tps**, Figs. 4.2, 4.25): line, sulcus or pit that marks the ventral edge of pl_2-fu_2 (12) and divides the mesepimeron into an upper and lower mesepimeron.

Upper mesepimeron ($uepm_2$, Figs. 4.2, 4.26, 4.51): dorsal region of the mesepimeron that is the site of origin of pl_2-fu_2, if marked ventrally by a change of sculpture, or a transepimeral line, sulcus or pit.

Lower mesepimeron ($lepm_2$, Figs. 4.2, 4.26, 4.27, 4.28, 4.51): ventral region of the mesepimeron that is the site of origin of pl_2-sa_2 **(16)** and pl_2-$3ax_3a$ **(19)**, if marked dorsally by a change of sculpture, or a transepimeral line, sulcus or pit.

Transepisternal line or sulcus (tss, Figs. 4.24, 4.26): line or sulcus on the mesepisternum that marks the line of separation between pl_2-t_2a (3), and the combined ventral edges of pl_2-ba_2b (10), pl_2-$3ax_2b$, c (8, 9), and pl_2-cx_2 (13).

Upper mesepisternum ($ueps_2$, Figs. 4.24, 4.26): region of the mesepisternum that is the site of origin of pl_2-ba_2b, pl_2-$3ax_2b$, c, and pl_2-cx_2, and if a transepisternal line or sulcus is delineated, region of the mesepisternum between the transepisternal line or sulcus, acropleural sulcus, and pleural suture.

Lower mesepisternum ($leps_2$, Figs. 4.24, 4.26): region of the mesepisternum that is the site of origin of pl_2-t_2a, and if a transepisternal line or sulcus is delineated, region of the mesepisternum between the transepisternal line or sulcus and discrimen.

4.4 Skeletomusculature of adults

4.4.1 Musculature

Nineteen pairs of mesothoracic muscles were found for male and female eupelmines. The muscles are described in Table 4.1, listed in the order given in table I of Daly (1964). Only two of the muscles, pl_2-t_2c (5), and t_2-tr_2 (17) are significantly different in size between the sexes. The latter muscle also differs in site of origin, as do pl_2-t_2b (4), pl_2-fu_2 (12), and pl_2-$3ax_3a$ (19). Sexual dimorphism in sites of origin of the latter three muscles is because of the dimorphism in size of pl_2-t_2c (5) (see "Correlation of musculature with external structure").

4.4.2 Comparison with other Hymenoptera

Though the nineteen pairs of mesothoracic muscles described in Table 4.1 are documented only for representatives of Eupelminae, it is probable that most are characteristic of all Chalcidoidea. Individuals of Encyrtidae and the other eupelmid subfamilies dissected have the same musculature, but members of each higher taxon differ characteristically in form of one or more of the muscles, particularly in form of t_2-tr_2 (17). These differences are described elsewhere in this paper. Only Eupelminae are sexually dimorphic in form of the muscles. The musculature of the pteromalids studied was very similar to that of male eupelmines, except pl_2-$3ax_2a$ (7) was conspicuously larger, and pl_2-t_2b (4) originated from both the mesepimeron and upper mesepisternum only in *Oodera* (Cleonyminae). The latter muscle originated entirely from the mesepimeron (*cf.* Figs. 4.5, 4.6 and 4.7, 4.8) in the other pteromalids dissected.

The only other study of chalcidoid musculature is by Daly (1963). He examined adults of numerous Hymenoptera, including representatives of five chalcidoid families to determine the histological types of selected muscles. Six of the above-described nineteen pairs of mesothoracic muscles were documented for the chalcidoids examined: 1ph-2ph (2), pl_2-t_2a (3), pl_2-ba_2b (10), pl_2-sa_2 (16), t_2-tr_2 (17), and 2ph-3ph (18). The muscles appear to be similar to those described for male Eupelminae, except pl_2-ba_2b is two-parted in at least *Chalcis divisa* (Walker) (Chalcididae) (Daly 1963, fig. 7). Daly (1963) discovered that chalcidoids lack pl_2-ba_2a, a second basalare muscle which many other hymenopterans possess. Only chalcidoids had t_2-tr_2 in the Apocrita studied by Daly, but this muscle is also present in individuals of Stephanidae, Megalyridae, Ceraphronoidea, non-ismarine Diapriidae, and some Formicidae

Table 4.1. Mesothoracic muscles of males and females of Eupelminae.

No.	Muscle	Origin	Insertion	Form	Function/Designation	Figures
1	fu_2-fu_1	Anterior submedian edge of mesofurcal bridge	Horizontal plate of profurca	Tubular, slender	Intersegmental retractor of prosternum	Not figured
2	1ph-2ph	First phragma (1ph) and median mesoscutal lobe (mml)	Second phragma (2ph)	Tubular, large	Indirect depressor of fore wing (Flexor of mesoscutum, ♂)	♂: 9, 10 (2) ♀: 35, 36, 39, 40 (2)
3	pl_2-t_2a	Lower mesepisternum ($leps_2$)	mesoscutal lateral lobes (mll)	Tubular, large	Indirect elevator of fore wing (Depressor of mesoscutum)	♂: 4 (3) ♀: 36 (3)
4	pl_2-t_2b	♂: Mesepimeron (epm_2) between pl_2-fu_2 (12) and pl_2-$3ax_2a$ (19), and upper mesepisternum ($ueps_2$) ♀: Inner wall forming pocket for pl_2-t_2c (5), and along inner wall from upper mesepisternum ($ueps_2$)	Ventral edge of lateral axillar surface (las)	Fan-like	Retractor of scutellar-axillar complex	♂: 5, 7 (4) ♀: 33 (4)
5	pl_2-t_2c	Acropleuron (ac) [small dorsal region of mesopleuron in ♂; entire lateral mesopleuron in ♀]	Process of anterolateral edge of mesoscutum [by slender, tendon-like ligament in ♂; pad of resilin (res) in ♀]	♂: Fan-like, small ♀: Pad-like, large	Retractor of mesoscutum (Flexor of mesoscutum, ♀)	♂: 5, 7 (5) ♀: 31, 32 (5)
6	pl_2-sp_2	Apodeme on anterolateral margin of prepectus (pre)	Peritreme of mesothoracic spiracle	Tubular, slender	Occlusor of mesothoracic spiracle	Not figured
7	pl_2-$3ax_2a$	Dorsal edge of acropleuron (ac) between mesopleural wing process (wp_2) and pl_2-t_2c (5)	Mesothoracic third axillary sclerite (iam of 3ax)	Tubular, slender	First flexor of fore wing	♂: 7 (7) ♀: 32 (7)

table 4.1, cont.

8	**pl$_2$-3ax$_2$b**	Upper mesepisternum (ueps$_2$) between pl$_2$-ba$_2$b (10) and pl$_2$-3ax$_2$c (9)	Mesothoracic third axillary sclerite (iam of 3ax)	Fan-like	Second flexor of fore wing	♂: 7 (8) ♀: 33 (8)
9	**pl$_2$-3ax$_2$c**	Upper mesepisternum (ueps$_2$) posterior to pl$_2$-3ax$_2$b (8)	Mesothoracic third axillary sclerite (iam of 3ax)	Fan-like	Third flexor of fore wing	♂: 7 (9) ♀: 33 (9)
10	**pl$_2$-ba$_2$b**	Upper mesepisternum (ueps$_2$), near anterior margin	Mesothoracic basalare (ba)	Fan-like	Basalare muscle	♂: 7 (10)
11	**fu$_2$-2ph**	Median and dorsal surfaces of mesofurcal arm, and dorsal posterior edge of mesofurcal bridge	Lateral process of second phragma (2ph)	Fan-like	Furcal retractor of second phragma	♂: 9 (11) ♀: 35 (11)
12	**pl$_2$-fu$_2$**	♂: Upper mesepimeron (uepm$_2$) ♀: Inner wall forming pocket for pl$_2$-t$_2$c (5) above pl$_2$-3ax$_2$a (19)	Lateral end of mesofurcal arm	Conical	Mesothoracic furco-pleural muscle	♂: 7 (12) ♀: 32 (12)
13	**pl$_2$-cx$_2$**	Upper mesepisternum (ueps$_2$) along line between combined ventral edges of pl$_2$-3ax$_2$a, b (7, 8), and pl$_2$-t$_2$b (4)	Ventrolateral rim of mesocoxal orifice adjacent to fu$_2$-cx$_2$a (14)	Fan-like	Mesopleural promotor of mesocoxa	♂: 7 (13) ♀: 17, 33 (13)
14	**fu$_2$-cx$_2$a**	Vertical plate of mesofurca	Ventrolateral rim of mesocoxal orifice adjacent to pl$_2$-cx$_2$ (13)	Fan-like	Mesofurcal promotor of mesocoxa	♂: 9 (14) ♀: 17, 35 (14)

table 4.1, cont.

15	fu$_2$-cx$_2$b	♂: Vertical plate of mesofurca ♀: Vertical plate of mesofurca and ventral surface of mesofurcal lateral arm	Dorsal rim of mesocoxal orifice mesad of coxal lobe (cxl)	Fan-like	Mesofurcal remotor of mesocoxa	♂: 9 (15) ♀: 18, 35 (15)
16	pl$_2$-sa$_2$	♂: Lower mesepimeron (lepm$_2$) between pl$_2$-fu$_2$ (12) and pl$_2$-3ax$_3$a (19) ♀: Inner wall forming pocket for pl$_2$-t$_2$c (5) between pl$_2$-fu$_2$ (12) and pl$_2$-3ax$_3$a (19)	Mesothoracic subalar (su)	Conical	Subalar muscle	♂: 7 (16) ♀: 32 (16)
17	t$_2$-tr$_2$	♂: Dorsal axillar surface (das) and axillar phragma (axp)	♂: Large golf tee-like pedicel (pdl) ventrally in body cavity, the pedicel tendon-like extended through mesocoxa to basomedial edge of mesotrochanter	♂: Tubular, large	Tergal depressor of mesotrochanter	♂: *cf.* 4, 53 (17a, b)
		♀: Anteroventral angle of lateral axillar surface (las)	♀: Basomedial edge of mesotrochanter	♀: Slender, tendon-like		♀: 33, 35 (17)
18	2ph-3ph	Posterior surface of second phragma (2ph)	Propodeum	Tubular, large	Intersegmental retractor of second phragma	♂: 9 (18) ♀: 39, 40 (18)
19	pl$_2$-3ax$_3$a	♂: Lower mesepimeron (lepm$_2$) below pl$_2$-fu$_2$ (12) ♀: Inner wall forming pocket for pl$_2$-t$_2$c (5) below pl$_2$-fu$_2$ (12)	Metathoracic third axillary sclerite	Conical	Intersegmental first flexor of hind wing	♂: 7 (19) ♀: 32 (19)

(Gibson in press, a). Chalcidoids, and individuals of the family Mymarommatidae (presently unplaced to superfamily) are the only hymenopterans with each t$_2$-tr$_2$ originating partly from an axillar phragma (**axp**, Figs. 4.4, 4.5, 4.53, 4.54) (Gibson in press, b).

Daly (1964), Maki (1938) and Matsuda (1970) tabulated the musculature of different hymenopterans, and Matsuda (1970) listed taxa studied and publications about musculature of Hymenoptera. Of the nineteen pairs of muscles found for Eupelminae, pl$_2$-t$_2$c (5) is otherwise recorded from adults only in representatives of Symphyta, and pl$_2$-3ax$_3$a (19) is unknown for other Hymenoptera. This latter muscle is the functional analog, if not the homolog of pl$_3$-3ax$_3$a in other hymenopterans. The unusual intersegmental nature of pl$_2$-3ax$_3$a in Chalcidoidea may be because the metapleuron is markedly reduced (**pl$_3$**, Figs. 4.1, 4.27-4.29), with the muscle transferred to the mesopleuron for functional requirements.

Presence of pl$_2$-t$_2$c (5) is probably symplesiomorphic for Chalcidoidea. Maki (1838) recorded pl$_2$-t$_2$c (muscle #28) for *Eutomostethus formosanus* Enslin (Tenthredinoidea: Tenthredinidae), and Tait (1962) for *Perga affinis* Kirby (Tenthredinoidea: Pergidae) (muscle #15). I have also seen pl$_2$-t$_2$c in my dissections of *Orussus sayii* (Westwood) (Orussoidea: Orussidae) and various Pamphiliidae (Megalodontoidea) and Siricidae (Siricoidea). The muscle extends from the lateral edge of the mesoscutum to the mesopleural ridge (internal apodeme of the mesopleural suture), in the narrowed dorsal region known as the mesopleural wing process. Pl$_2$-t$_2$c inserts into the mesopleural ridge by a slender tendon-like ligament in *Orussus*. In other symphytes it is as an undifferentiated, slender, tubular muscle. Pl$_2$-t$_2$c is recorded only for adults of Chalcidoidea within Apocrita, though Daly (1964) found this muscle developed in the early pharate pupa of *Apis mellifera* L. (Apoidea: Apidae). He states that it arises "From mesepisternum, below region of incipient pleural wing process ..." (Daly 1964, p. 32), and that it degenerates in the early pharate adult.

Retention of pl_2-t_2c (5) in chalcidoids is probably correlated with a relatively loosely connected pronotum, mesonotum and mesopleuron. This character state is characteristic of Symphyta and is the hypothesized plesiomorphic state for Hymenoptera (Gibson in press, a). The loose pro- and mesothoracic condition is partly the result of various intersegmentalia between the pronotum and mesopleuron. Most Apocrita lack intersegmentalia and the pronotum, mesonotum, and mesopleuron are more or less rigidly connected. However, chalcidoids retain the prepectus (one of the intersegmentalia), and the pronotum is more or less loosely connected to the mesothorax as in Symphyta (Gibson in press, a). Pl_2-t_2c probably functions in both taxa to adjust how tightly the mesonotum is appressed against the pronotum, intersegmentalia, and mesopleuron. Further studies may show this muscle to be present in adults of other Apocrita that do not have the pronotum and mesopleuron connected in a rigid tongue-and-groove interlocking mechanism (see Gibson in press, a).

4.4.3 External structure

MALES. The **mesonotum** (**no_2**, Fig. 4.2) is divided into an anterior **mesoscutum** (**msc**, Fig. 4.1) and a posterior **scutellar-axillar complex** (**sac**, Fig. 4.1) by the **transscutal articulation** (**tsa**, Figs. 4.1, 4.3). The dorsal surface of the mesoscutum is evenly, variedly convex. It is subdivided into a **median mesoscutal lobe** (**mml**, Figs. 4.2, 4.3) and two separate **mesoscutal lateral lobes** (**mll**, Figs. 4.2, 4.3) by percurrent, linear, usually fine **notauli** (**not**, Fig. 4.3) that are widely separate posteriorly. The posterolateral edge of the mesoscutal lateral lobe is reflexed towards the transscutal articulation as the **parascutal carina** (**psc**, Figs. 4.1, 4.41). The vertical **preaxilla** (*sensu* Michener 1944) (**pax**, Figs. 4.41-4.43) is distinguished below the parascutal carina and terminates posteroventrally in two lobes that together constitute the **anterior notal wing process** (**anwp**, Fig. 4.43). The scutellar-axillar complex is composed of a variedly convex median **scutellum** (**scl**, Fig. 4.3) and two lateral **axillae**, separated by the **scutoscutellar suture** (**sss**, Fig. 4.3). In some taxa the scutellum has a horizontal **axillular sulcus** (**axas**, Fig. 4.3) near the lateral edge, and this sulcus defines the **axillula** (**axa**, Fig. 4.3) between itself and the scutoscutellar suture. Each axilla has a subtriangular, more or less horizontal and posteriorly declined **dorsal axillar surface** (**das**, Figs. 4.1, 4.3, 4.42, 4.43) distinguished from a vertical **lateral axillar surface** (**las**, Figs. 4.1, 4.42, 4.43) by the **axillar carina** (**axc**, Figs. 4.2, 4.41). The lateral axillar surface terminates ventrally in an outwardly directed lobe, the **posterior notal wing process** (**pnwp**, Fig. 4.43). The **tegula** (**tg**, Fig. 4.2) and fore wing conceals the **preaxilla** and lateral axillar surface in normal repose.

The lateral and ventral surfaces of the mesothorax are composed of an anterior **prepectus** (**pre**, Fig. 4.1) and a posterior **mesopleuron**. The prepectus superficially appears as independent triangular sclerites on either side of the mesothorax (Fig. 4.1), but it is narrowly continuous along the anteroventral edge of the mesopleuron (Fig. 4.10). A shallowly concave **femoral groove** (**fg**, Fig. 4.2) extends diagonally from the anterolateral corner of the mesocoxa towards the prepectus. A distinct **mesopleural suture** is lacking, but I interpret the posterodorsal margin of the femoral groove as the mesopleural suture. The mesopleural suture does not extend to the anterior corner of the **mesopleural wing process** (*cf.* **wp$_2$**, Figs. 4.28, 4.50), but bifurcates dorsally (Fig. 4.1). One arm of the sulcus extends to the anterior margin of the mesopleuron below the mesopleural wing process, and the other extends to the dorsal margin of the mesopleuron behind the mesopleural wing process (Fig. 4.1). This latter sulcus is not externally obvious in all males, but extends from the apex of the **subalar pit** (*sensu* Michener 1944) (**sap**, Fig. 4.1) to the angle formed by the change in direction of the dorsal edge of the femoral groove, or mesopleural suture (*cf.* Figs. 4.1, 4.2). The region of the mesopleuron delineated below the mesopleural wing process by the bifurcated sulcus is the **acropleuron** (**ac**, Fig. 4.1), and the sulcus that defines the region ventrally and posteriorly is the **acropleural sulcus** (**acs**, Fig. 4.1). The convex region of the mesopleuron dorsal to the mesopleural suture and posterior to the acropleuron is the **mesepimeron** (**epm$_2$**, Fig. 4.1), and the region anteroventral of the acropleuron and mesepimeron is the **mesepisternum** (**eps$_2$**, Fig. 4.1). The mesepimeron is undifferentiated in some males, but in many it is subdivided into an **upper mesepimeron** (**uepm$_2$**, Fig. 4.2) and a **lower mesepimeron** (**lepm$_2$**, Fig. 4.2) by a difference in sculpture between the two regions, or by a **transepimeral line, sulcus**, or pit (**tps**, Fig 2). The mesepisternum is undifferentiated except for the concave femoral groove in most males, but in representatives of some taxa a light-colored line, the **transepisternal line** (*cf.* **tss**, Figs. 4.24, 4.26), extends from near the anterolateral corner of the mesocoxa towards the procoxa. The transepisternal line, when present, divides the mesepisternum into an **upper mesepisternum** (*cf.* **ueps**$_2$, Figs. 4.24, 4.26) above it, and a **lower mesepisternum** (*cf.* **leps**$_2$, Figs. 4.24, 4.26) below it. The mesepisternum of each pleuron extends ventrally to meet at the **discrimen** (**dis**, Fig. 4.12).

FEMALES. Mesonotal structure of females differs from that of males primarily in that the mesoscutum (**msc**) is relatively much larger than the scutellar-axillar complex (**sac**), the notauli (**not**) are furrow-like rather than linear in most taxa, and the median mesoscutal lobe (**mml**) is not extended to the transscutal articulation (**tsa**) so the region posterior to it is concave relative to the convex mesoscutal lateral lobes. (*cf.* Figs. 4.3, 4.23).

The prepectus of females superficially appears as independent lateral sclerites (**lps**, Fig. 4.29), but as for males it is narrowly continuous along the anteroventral edge of the mesopleuron (Fig. 4.38). Females are conspicuously different from males in structure of the mesopleuron (*cf.* Figs. 4.1, 4.29). Almost the entire lateral mesopleural surface is composed of an undifferentiated, convexly expanded acropleuron (**ac**, Fig. 4.30). The acropleural sulcus (**acs**, Fig. 4.29) extends posteriorly from the mesopleural wing process to the metapleuron (**pl**$_3$), and here curves ventrally as a deep sulcus to separate the acropleuron from the metapleuron and metacoxa. It curves anteriorly above the mesocoxa as a straight, broadly curved, or sinuate sulcus, with the apical portion more abruptly reflexed anterodorsally in many taxa. The largely ventral mesopleural region below the acropleural sulcus is the mesepisternum (**eps**$_2$, Fig. 4.30). This is undifferentiated in some females, but many have a light-colored line, or an obscure line of finer sculpture extended from near the anterolateral corner of the mesocoxa towards the procoxa (*cf.* tss, Figs. 4.24, 4.26). This transepisternal line segregates the mesepisternum into an upper (ueps$_2$) and lower (leps$_2$) mesepisternum as in some males (*cf.* Figs. 4.24, 4.26).

4.4.4 Correlation of musculature with external structure

External structure of the mesonotum of males and females is not substantially different. Notauli (not) delimit the line of separation between muscles 1ph-2ph (2) and pl$_2$-t$_2$a (3) in both sexes, but the linear notauli of males are internally developed as phragmata (*cf.* Figs. 4.3, 4.5) whereas the furrow-like notauli of females are not (*cf.* Figs. 4.23, 4.34). Three large muscles arise from the mesonotum in males, 1ph-2ph (2), pl$_2$-t$_2$a (3), and t$_2$-tr$_2$ (17). Only the last muscle is conspicuously different in size and site of origin in females (*cf.* 17, Figs. 4.4, 4.33) and this sexual dimorphism is not reflected in obvious differences in external mesonotal structure. However, mesonotal structure of females is much more varied than in males. This is because males are fully winged, whereas females of numerous taxa are brachypterous to different extents and the mesonotum may be secondarily modified as a result. Reid (1941) described some of the characteristic modifications correlated with wing reduction in female eupelmines.

Unlike the dorsal mesothoracic surface, external structure of the lateral and ventral mesothoracic surfaces is highly correlated with form and position of different mesopleural muscles. The Cleonyminae and Chalcedectinae (Pteromalidae) described previously as having very similar mesopleural musculature to male eupelmines also have a very similar external structure (*cf.* Figs. 4.1, 4.2). The acropleural sulcus (acs) externally indicates a robust $\supset$-shape apodeme that forms a shallow pocket from which pl$_2$-t$_2$c (5) originates (*cf.* Figs. 4.1, 4.7 and 4.2, 4.8); the transepimeral line, sulcus, or pit (tps), if present, externally indicates the ventral edge of pl$_2$-fu$_2$ (12) (*cf.* Figs. 4.2, 4.8); and the transepisternal line (tss), if present, externally marks the line of separation between the outer edge of pl$_2$-t$_2$a (3) and the combined ventral edges of pl$_2$-ba$_2$b (10), pl$_2$-3ax$_2$b, c (8, 9), and pl$_2$-cx$_2$ (13) (*cf.* Figs. 4.26, 4.33). Only pl$_2$-t$_2$a originates from the lower mesepisternum, whereas the last three muscles originate from the upper mesepisternum. Pl_2-fu_2 (**12**), pl_2-sa_2 (**16**), and pl_2-$3ax_3a$ (**19**) originate entirely from the mesepimeron, whereas pl_2-t_2b (**4**) originates both from the mesepimeron and upper mesepisternum [male eupelmines and *Oodera* (Cleonyminae) (Figs. 4.5, 4.7)], or entirely from the mesepimeron [chalcedectines and most cleonymines (Figs. 4.6, 4.8)].

In female eupelmines most of the lateral surface of the mesopleuron is convexly expanded as a single undifferentiated region because of the massively enlarged pl_2-t_2c muscle (**5**) (*cf.* Figs. 4.29, 4.31). The acropleural sulcus is deeply invaginated posteriorly to form a thin inner cuticular wall, which together with the the outer acropleural surface forms a large pocket for pl_2-t_2c (**5**, Fig. 4.32). Pl_2-fu_2 (**12**), pl_2-sa_2 (**16**), and pl_2-$3ax_3a$ (**19**) originate from the surface of the inner cuticular wall in the same relative positions as do the muscles from the mesepimeron in males (*cf.* Figs. 4.7, 4.32). This indicates that the mesepimeron is not exposed in female eupelmines, and that the mesopleuron anterior and ventral to the acropleural sulcus is composed of only the mesepisternum. When evident, the transepisternal line (**tss**) externally indicates the line of separation between the outer edge of pl_2-t_2a (**3**), and the combined ventral edge of pl_2-ba_2b (**10**), pl_2-$3ax_2b$, c (**8**, **9**), and pl_2-cx_2 (**13**) (*cf.* Figs. 4.26, 4.33), as for males.

I do not know of any mesopleural structure in Eupelminae that is intermediate between the structures described for the two sexes. However, there are eupelmids in other subfamilies that do have what appears to be intermediate mesopleural structures. These taxa primarily belong to undescribed genera of Calosotinae. A mesopleural structure most closely resembling that of male eupelmines is possessed by individuals of undescribed genus "A", as illustrated in Fig. 4.25. The acropleuron is enlarged, but is not extended to the metapleuron or mesocoxa and is relatively flat and undifferentiated from the rest of the mesopleuron. A distinct acropleural sulcus (**acs**) delineates the acropleuron posteriorly, but ventrally the sulcus is abruptly reflexed anterodorsally as an obscure line of altered sculpture. The mesopleural suture ($\mathbf{pls_2}$) is distinct and dorsally recurved as the transepimeral sulcus (**tps**) near the acropleural sulcus. The three define among them a small subtriangular upper mesepimeron, and a larger rectangular lower mesepimeron. The acropleuron is more convexly expanded in individuals of undescribed genus "B" (**ac**, Fig. 4.26), but the mesepimeron is still conspicuous. The latter is incompletely divided into an upper (**uepm**$_2$) and lower (**lepm**$_2$) mesepimeron by the dorsally recurved mesopleural suture (**pls**$_2$). Individuals of undescribed genus "C" (Fig. 4.27) have a large convex acropleuron (**ac**) that is dorsally extended to the metapleuron (**pl**$_3$) so that the upper mesepimeron is not exposed, or is only linear between the acropleuron and metapleuron. A rectangular lower mesepimeron (**lepm**$_2$) is evident below the acropleuron, distinguished anteriorly by a distinct mesopleural suture (**pls**$_2$). The acropleural sulcus (**acs**) is abruptly reflexed anterodorsally as a more obscure line, similarly to individuals of genus "A".

Ethanol-preserved specimens of the above three taxa were unavailable for dissection so that a direct correlation can not be confirmed between the musculature and external mesopleural structure. Specimens of some species of other calosotine genera that have the acropleuron completely expanded, except for a small differentiated region between the metapleuron and mesocoxa (Fig. 4.28), were available for dissection. These dissections show that pl_2-fu_2 (**12**) originates from the cuticular wall forming the inner wall of the pocket for pl_2-t_2c (**5**), and that pl_2-sa_2 (**16**) and pl_2-$3ax_2a$ (**19**) arise from the small region of the mesopleuron exposed between the metapleuron and mesocoxa. The latter region is thus the lower mesepimeron (**lepm**$_2$, Fig. 4.28).

I interpret the mesopleural skeletomusculature of male eupelmines to be plesiomorphic for Eupelmidae. This is based on the similarity in form and placement of mesopleural muscles between male eupelmines, cleonymines, and chalcedectines, and on similarity in external mesopleural structure between male eupelmines and many other chalcidoids, particularly Pteromalidae. External mesopleural structure of various Calosotinae indicates the apomorphic skeletomusculature of female eupelmines was derived from a system similar to that of male eupelmines through gradual enlargement of pl_2-t_2c (**5**). Enlargement of this muscle resulted in expansion of the acropleuron, and in the robust ɔ-shape acropleural apodeme (Figs. 4.7, 4.8) being expanded as an extensive inner cuticular wall to form a deep pocket for pl$_2$-t$_2$c (**5**, Fig. 4.32). Expansion of the acropleuron (**ac**, Fig. 4.1) reduced the mesepisternum (**eps**$_2$) and mesepimeron (**epm**$_2$), with the acropleuron probably first extended posteriorly to the metapleuron (**pl**$_3$) and then ventrally to the mesocoxa. This expansion successively eliminated the upper (**uepm**$_2$) and lower (**lepm**$_2$, Fig. 4.2) mesepimeron, and in so doing, the respective muscles of these two regions [pl$_2$-fu$_2$ (**12**), and pl$_2$-sa$_2$ (**16**) and pl$_2$-3ax$_2$a (**19**)] were transferred to the inner wall of the cuticular pocket for pl$_2$-t$_2$c (*cf.* Figs. 4.7, 4.32). This gradual change in form and placement of the muscles, and in correlated external structure between male and female eupelmines, can be summarized in the following transformation series in grade of structure: male Eupelminae (Fig. 4.1) → genus "A" (Fig. 4.25) → genus "B" (Fig. 4.26) → genus "C" (Fig. 4.27) → some *Calosota* (Fig. 4.28) → female Eupelminae (Fig. 4.29).

Individuals of the genus *Metapelma* Westwood are the only other eupelmids I know of with an upper and lower mesepimeron exposed (Fig. 4.51). The acropleuron (**ac**) is greatly enlarged, but there is a slender upper mesepimeron (**uepm**$_2$) and a small lower mesepimeron (**lepm**$_2$) between the acropleuron and metapleuron (**pl**$_3$). This interpretation of external structure was confirmed by placement of muscles (*cf.* Figs. 4.51, 4.52). Individuals of *Metapelma* differ from other eupelmids and encyrtids for which musculature is known by having pl$_2$-t$_2$b more or less tubular and originating entirely from the lower mesepimeron (**4**, Fig. 4.52). Pl$_2$-t$_2$b is fan-like in other known taxa, and originates partly from the inner cuticular wall forming the pocket for pl$_2$-t$_2$c, and partly from the upper mesepisternum adjacent to the inner wall, or entirely from the latter position (**4**, Fig. 4.34).

4.4.5 Terms for mesopleural structure

Most interpretations of the lateral and ventral mesothoracic structures of Hymenoptera are based on acceptance of one, or both, of two theories: Heymons' (1899) hypothesis that the thoracic pleuron of insects was derived from a subcoxal segment, and Weber's (1928) theory

Table 4.2. **Terms proposed for hypothesized plesiomorphic mesopleural structure of Eupelmidae compared with terms used in previous studies for homologous structures.** (Unnamed = illustrated, but not named; n/a = not illustrated, not comparable).

Proposed term	**Ulenberg** (1983)	**Gordh** (1975)	**Bouček** (1974)	**Domenichini** (1969)	**Bucher** (1948)
acropleuron	unnamed	anapleurite	subalar area	unnamed	mesepimeron, in part
acropleural sulcus	unnamed	anapleural suture	unnamed	unnamed	pleural suture, in part
mesepimeron	epimeron	mesepimeron	mesepimeron	epimeron	mesepimeron, in part
upper mesepimeron	anepimeron	n/a	upper mesepimeron	epimeron	unnamed
lower mesepimeron	catepimeron	n/a	lower mesepimeron	catepimeron	unnamed
transepimeral line, sulcus, pit	precoxal suture	n/a	unnamed	precoxal suture	dimple of the mesepimeron
mesepisternum	mesosternum	mesepisternum	mesepisternum	anepisternum + precoxal	mesepisternum
upper mesepisternum	n/a	n/a	upper mesepisternum, + lower mesepisternum	anepisternum + precoxal	n/a
lower mesepisternum	n/a	n/a	unnamed	precoxal, in part	n/a
transepisternal line	n/a	n/a	unnamed	secondary suture	n/a
pleural suture	pleural suture	pleural suture	unnamed	pleural suture	pleural suture
discrimen	mesolcus	discrimen	n/a	discrimen	sternal groove

Ulenberg (1983): *Apocrypta perplexa* Coquerel (Torymidae: Sycophaginae).
Gordh (1975): *Idarnes spp.* (Torymidae: Idarninae).
Bouček (1974): Leucospidae.
Domenichini (1969): terms based on figures of *Cleonymus* sp. (Pteromalidae: Cleonyminae) and *Tetrastichus pubescens* Nees (Eulophidae: Tetrastichinae).
Bucher (1948): *Monodontomerus dentipes* (Dalman) (Torymidae: Monodontomerinae).

Table 4.3. Terms proposed for hypothesized apomorphic mesopleural structure of Eupelmidae compared with terms used in previous studies for the same structures.

Proposed term	**Domenichini** (1969)	**Matsuda** (1960a, b)	**Richards** (1956a)	**Snodgrass** (1910)
acropleuron	anepisternum + epimeron	anepisternum	mesepisternum	mesopleuron, in part
acropleural sulcus	anapleural suture	anapleural suture + basal margin of trochantin + pleural suture	precoxal + pleural suture	median episternal groove
mesepisternum	precoxal	prespisternum + basisternum	subpleural area, or precoxale	mesopleuron + mesosternum, in part
upper mesepisternum	unnamed	preepisternum	unnamed	mesopleuron, in part
lower mesepisternum	unnamed	basisternum	mesosternum	mesosternum
transepisternal line	secondary suture	unnamed	unnamed	sternopleural suture
discrimen	discrimen	median longitudinal groove	mid-ventral mesosternal line	unnamed

Domenichini (1969): ***Calosota*** sp. (Calosotinae), ***Eupelmus urozonus*** Dalman (Eupelminae).
Matsuda (1960a, b): ***Eupelmus allynii*** (French) (Eupelminae).
Richards (1956a): ***Eupelmus urozonus*** Degeer (Eupelminae).
Snodgrass (1910): ***Eupelmus cushmani*** (Crawford) (Eupelminae).

that, in holometabolous insects, the sternum is invaginated as the "cryptosternite". The more important comparative studies of the mesothorax of Hymenoptera include those of Snodgrass (1910), Richards (1956a, b), Matsuda (1960a, b; 1970), Compere (1962), and Saini and Dhillon (1980). All but the last work includes either an encyrtid, a female eupelmine, or both, in the analysis. Female eupelmine structure was usually included because most authors interpreted the ventral region of the mesothorax between the transepisternal lines (tss, Fig. 4.24) as the mesosternum, or some part of it. Otherwise, only a few Symphyta (Snodgrass 1910; Richards 1956a, b) or Encyrtidae (Compere 1962, Matsuda 1970) are considered to have an exposed mesosternum in Hymenoptera.

There are as many different interpretations of the homology of parts of the female eupelmine mesothorax as there are authors who have studied them. These different interpretations are reflected in different terms used by the authors for the same structures. Table 4.3 compares the terms proposed in this paper for the apomorphic eupelmid mesopleural structure, represented by female eupelmines, with terms used in previous works of comparative morphology for the same structures. The terms I use for the apomorphic structure of female eupelmines are based on hypothesized homologies, based on site of origin of muscles, with what I interpret as the plesiomorphic structure exhibited by male eupelmines. Table 4.2 compares the terms I use for the plesiomorphic structure with terms proposed in previous works for homologous structures in other chalcidoids.

Bouček (1972) originated the terms "upper" and "lower" mesepimeron, and (1974) "upper" and "lower" mesepisternum for external regions of the mesopleuron of various chalcidoids with the plesiomorphic structure. His use of upper and lower mesepimeron are as in this paper, but upper mesepisternum was used for only that part of the mesepisternum above the femoral groove and lower mesepisternum was used for the concave part of the mesepisternum within the femoral groove. The latter region is part of the upper mesepisternum as defined in this paper. I have redefined Bouček's terms "upper" and "lower" mesepisternum, and "upper" and "lower" mesepimeron relative to site of muscle origin so that they are less arbitrary terms that can be used to denote homologous mesopleural regions throughout Chalcidoidea.

Bouček (1974) also designated the mesopleural region that I call the acropleuron as the "subalar area" in individuals of Leucospidae. This term was originated in Hymenoptera by Michener (1944) for a mesopleural region in bees (Apoidea) below the fore wing base and above the subalar pit. The subalar area in bees is the site of origin of pl_2-$3ax_2a$ (Daly 1964). Most other studies of chalcidoid mesopleural structure did not distinguish what I term the acropleuron from other regions of the mesopleuron. Graham (1969, fig. 20) considered it and the upper mesepimeron as part of the mesepisternum in Pteromalidae. He also considered the expanded lateral region of the mesothorax in encyrtids (fig. 9) and eupelmids (fig. 10) as the mesepisternum. Others have generally regarded the region as part of the mesepimeron in chalcidoids that exhibit the plesiomorphic structure (Table 4.2), though Gordh (1975) called it the "anapleurite", and the sulcus that separates it from the mesepisternum as the "anapleural suture". He concluded that "The anapleural suture must be a secondary development and consequently the sclerite formed must be part of the mesepisternum" (Gordh 1975, p. 403), though later stating that the anapleurite could be partly epimeral and partly episternal.

The acropleuron is part of the mesepisternum if pl_2-t_2c (5) of chalcidoids and various symphytes are homologous. I conclude this on basis of the shape of pl_2-t_2c, and on its mesopleural site of attachment. Because pl_2-t_2c of symphytes either attaches as a simple tubular muscle or as a ligament to the pleural ridge, the expanded fan-like muscle of chalcidoids (5, Figs. 4.7, 4.8) must be secondary, and at least the posterior part of the mesopleural apodeme from which it arises a part of the mesopleural ridge. If so, the acropleuron is mesepisternal in origin. The apodeme defining the acropleuron ventrally (*cf.* Figs. 4.1, 4.7 and 4.2, 4.8) may be secondary, or also part of a modified mesopleural ridge.

Though site of origin of pl_2-t_2c indicates the acropleuron to be episternal in origin, in many chalcidoids the region is externally more similar to the mesepimeron than it is to the mesepisternum (Figs. 4.1, 4.2). Furthermore, individuals of undescribed calosotine genera "A" and "B", which have a relatively plesiomorphic mesopleural structure, have the anterior portion of the acropleural sulcus abruptly reflexed dorsally (acs, Fig. 4.27). To a lesser extent this is also evident in individuals of many other eupelmid taxa (Fig. 4.29). The reflexed portion superficially looks like a part of the mesopleural suture that has been displaced from the posteroventral part of the suture (pls_2) because of expansion of the acropleuron (ac) (Fig. 4.27). This may indicate that the acropleuron is part of the epimeron rather than the episternum.

A comprehensive study of the skeletomusculature of Chalcidoidea and other Hymenoptera is required before any hypothesis of homology of the acropleuron is more than conjectural. However, I do not use Gordh's (1975) terms, "anapleurite" and "anapleural suture", because the latter is the suture that separates the anepisternum from the preepisternum in the subcoxal theory of the origin of the pleuron (Matsuda 1960a). Gordh's terms imply homology with the primitive regions, whereas I believe the acropleuron is a secondary development in Chalcidoidea, whether mesepisternal or mesepimeral. Similarly, I do not consider the mark that differentiates an upper and lower mesepimeron (transepimeral line, sulcus, or pit), or the mark that differentiates an upper and lower mesepisternum (transepisternal line or sulcus), as evidence of fusion of primitively separate sclerites. Rather, I believe the marks are secondary features of Chalcidoidea due to internal muscle origins. I therefore interpret the ventral surface of the mesothorax as part of the mesopleuron rather than the mesosternum, and do not use terms that imply regions of the sternum in the subcoxal theory of the origin of the pleuron.

Bouček's (1974) term "subalar area" is certainly descriptive of the dorsally differentiated mesopleural region in those chalcidoids that exhibit the plesiomorphic structure.

It is less descriptive of the expanded region that forms almost the entire lateral mesosoma in encyrtids and most eupelmids. Bouček calls the homologous mesopleural region in individuals of the latter two taxa as the "mesopleural shield" (*e. g.* Bouček 1967), but for recognition of homology a single term should be used to denote both regions. I propose replacing "subalar area" and "mesopleural shield" with the term "acropleuron", from the greek words "akron" (meaning "top") and "pleuron". This term is noncommittal with respect to being of episternal or epimeral origin and it denotes relative position in chalcidoids that exhibit the plesiomorphic structure, but can be used equally as well for the apomorphic mesopleural region of encyrtids and most eupelmids. I prefer not to use subalar area (*sensu* Bouček 1974), because the region in chalcidoids is a consequence of pl_2-t_2c (5). Presence of this muscle is probably symplesiomorphic for Chalcidoidea, but the somewhat expanded, fan-like mesopleural site of origin is probably autapomorphic for Chalcidoidea in Apocrita, based on structure of the muscle in symphytes. The region should therefore be distinguished from the subalar area (*sensu* Michener 1944) of Apoidea.

4.4.6 Mesopleural-mesocoxal articulation

Male and female eupelmines also differ conspicuously in how the mesocoxa articulates with the mesopleuron. In males, the posterior edge of the ventral mesopleural surface is differentiated as a transverse-linear flange that abuts against the exposed basal edges of the coxae (Figs. 4.11, 4.12). The flange is reflexed internally at an acute angle to the ventral mesopleural surface to form a rectangular median plate, the **mesotrochantinal plate (mtp**, Fig. 4.13), between the coxal orifices. Membrane, **intercoxal membrane** *sensu* Domenichini 1952 (**icm**, Fig. 4.13), stretches between the mesotrochantinal plate, acropleuron, and metathorax. Consequently, the internal ventrobasal surface of each coxa abuts against the mesotrochantinal plate, and the dorsobasal surface of the latter abuts against the intercoxal membrane.

Each mesocoxa has a dicondylic articulation with the mesopleuron. The lateral edge of the coxal orifice is protruded into a lobe (**cxl**, Fig. 4.14) that projects anterodorsally into the body because of the posteroventral alignment of the coxa (Fig. 4.9). The coxal lobe lies within an oblique groove on the inner surface of the mesopleuron at the ventral edge of the mesopleural suture (**mgr**, Figs. 4.8, 4.13) and forms the lateral mesopleural-mesocoxal articulation. The second articulation is formed by a posteriorly projected lobe from the lateral edge of the mesotrochantinal plate, the **mesotrochantinal lobe** (*sensu* Graham 1969) (**mtl**, Fig. 4.13). The apex of the mesotrochantinal lobe projects into a deep groove on the ventral, basal surface of the coxa mesad of the coxal orifice (**cxg**, Fig. 4.14). This is externally visible unless the coxa is slightly pronated as in Fig. 4.12.

In females, the ventral mesopleuron is deeply incurved as membranous regions (**mb**, Figs. 4.15, 4.17) anterior to each coxa. The mesotrochantinal plate is not inflected into the body as in males, but is external and projects posteriorly as a small median plate that terminates in two subcontiguous lobes (**mtp**, Fig. 4.17). The apex of each lobe fits into a groove on the anteromedial ventral surface of the respective coxa to form the median mesopleural-coxal articulation (**mca**, Fig. 4.17). The lateral mesopleural-coxal articulation (**lca**, Figs. 4.17, 4.18) is formed by the blunt ventrolateral angle of the coxa that fits into a depression on the adjoining mesopleuron. Internally, the lateral edge of the coxal orifice is protruded as a lobe similarly to males, but this is able to rotate posteriorly when the coxa rotates anteriorly out of the fossa (**cxl**, Fig. 4.18). Because there is no internal mesotrochantinal plate, the entire region basal to the coxae, the **mesocoxal fossa**, is membranous (**icm**, Fig. 4.18).

In males, both mesopleural-coxal articulations are within the mesocoxal fossa dorsad of the ventral level of the mesopleuron (Fig. 4.13). The internal ventrobasal surface of each coxa also abuts against the mesotrochantinal plate so that only a very limited promotion and remotion of the coxa is possible. In females, both mesopleural-coxal articulations are external at the ventral level of the mesocoxal fossa (Fig. 4.17), and the coxa is able to rotate ventrally out of the fossa along a longitudinal axis of rotation (Figs. 4.18, 4.30). Pl_2-cx_2 (**13**) and fu$_2$-cx$_2$a (14) insert into the anteroventral edge of the coxa posterior to (beyond) the coxal axis of rotation (Fig. 4.17). Furthermore, the rim of the coxa is slightly reflexed where pl$_2$-cx$_2$ and fu$_2$-cx$_2$a insert, so the points of insertion are slightly ventral to (below) the axis of rotation. Because the mesopleuron is membranous anterior to each coxa, because the coxa has a ventral longitudinal axis of rotation, and because the points of insertion of pl$_2$-cx$_2$ and fu$_2$-cx$_2$a are beyond and slightly below the coxal axis of rotation, contraction of these two muscles rotates the coxa ventrally and anteriorly out of the fossa (Fig. 4.18) to protract the leg (Fig. 4.22). The coxa is retracted into the mesocoxal fossa by contraction of fu$_2$-cx$_2$b (15, Figs. 4.9, 4.18).

It is beyond the scope of this paper to suggest whether the mesotrochantinal lobes are homologous with the mesotrochantins of primitive insects, or if the mesotrochantinal plate is homologous with part of the mesosternum, and if so what part. The mesotrochantinal plate in chalcidoids has previously been termed the reduplication of the mesosternum (Bucher 1948), spinasternum (James 1926), furcasternum (Matsuda 1960a, b), catepisternum (Domenichini 1969), and epimeral sclerite (Ulenberg 1983). I use the more noncommittal term, mesotrochantinal plate, because of uncertain homology.

4.5 Correlation of skeletomusculture and function

Flying, walking, and jumping are the three main methods of movement for chalcidoids. The mesothorax of most chalcidoids is modified for, and is primarily responsible for two of these methods— flight and jumping. The fore wings are the main organs of flight and the middle legs the primary organs for jumping in most chalcidoids. Chalcidoids with enlarged metafemora (Leucospidae, Chalcididae, and some Pteromalidae and Torymidae), or those with flatly enlarged metacoxae (Elasmidae), probably also use the hind legs to jump. These, however, are secondary modifications.

The mesothoracic mechanisms of jumping and flight are structurally independent of each other in almost all chalcidoids that use the middle legs for jumping, including male eupelmines. Female eupelmines are exceptional in having the flight and jumping mechanisms coadapted for the single purpose of jumping. The mesothoracic jumping and flight mechanisms of male eupelmines are described below to illustrate the plesiomorphic structure from which the female jumping mechanism evolved. The latter mechanism is then described and aspects of contortion in females correlated with their apomorphic jumping mechanism.

4.5.1 Males: jumping mechanism

Jumping in male eupelmines results from a sudden retraction of the base of the mesotrochanter into the apex of the mesocoxa. Each trochanter has a lateral dicondylic articulation with its respective coxa so as to have a single transverse axis of rotation. The base of the trochanter is removed from the apex of the coxa in a pre-jump condition, and in the most extreme position projects dorsally at an acute angle to the coxa (Figs. 4.11, 4.12). The femur is then appressed against the mesopleuron within the femoral groove and the tibia and tarsus extended ventrally at an acute angle to the femur and trochanter (Fig. 4.11). Because the coxa is oriented posteroventrally (Fig. 4.9), the lateral articulation of the trochanter with the coxa results in the arched leg being held at an oblique angle to the long axis of the body (Fig. 4.11). Retraction of the base of the trochanter into the apex of the coxa (*cf.* Figs. 4.15, 4.16) rotates the trochanter and femur ventrally toward the midline of the body, straightens the femoral-tibial joint, and extends the leg. Because the leg is held at an oblique angle to the long axis of the body, sudden straightening of the leg imparts both a vertical and horizontal propulsive force, *i. e.*, the individual jumps upwards and forwards.

Energy for jumping is generated by the two large t_2-tr_2 (17) muscles. Each originates from the dorsal axillar surface and axillar phragma (**axp**), and inserts into an expanded golf tee-like pedicel (**pdl**) ventrally within the body cavity (*cf.* **17a**, **17b**, Figs. 4.4, 4.53). A tendon-like ligament extends through the coxa from the center of the pedicel and inserts into the basomedial edge the trochanter. Contraction of t_2-tr_2 produces a vertical, dorsally directed force that acts directly on the mesotrochanter to retract it into the mesocoxa.

4.5.2 Males: flight mechanism

Matsuda (1970) reviewed the literature on the structural and mechanical basis for flight in Hymenoptera. Almost all studies have been on Aculeata. Structure and mechanics of the flight mechanism are described for *Vespa crabro* L. (Vespoidea: Vespidae) (Weber 1925), and *Apis mellifera* L. (Snodgrass 1942, 1956) and *Bombus* Latreille (Apoidea: Apidae) (Pringle 1961). There are only brief descriptions of the axillary sclerites for Chalcidoidea (Grandi 1929, Hanna 1935, Ulenberg 1983). The following description of structure and mechanics of flight in male eupelmines is more detailed, but primarily describes only those aspects important for understanding modification of the flight mechanism for jumping in female eupelmines.

Structure of the flight mechanism of male eupelmines appears to be similar to that described for aculeates, except there is no fourth axillary sclerite or an independent axillary lever. The wings are articulated to the mesothorax in a complicated manner by three axillary sclerites. Structure is complicated because of the number of interconnections between the wing base, three axillary sclerites, and mesothorax, and because of the three-dimensional relationship between the parts. Figure 4.44 shows the base of the fore wing in an unnatural flattened position, with the three axillary sclerites slightly separated from each other.

The third axillary sclerite (hereafter referred to as "3ax") is an elongate, twisted sclerite (**3ax**, Fig. 4.44). It articulates distally with remnants of the anal vein, ventrally with the dorsal margin of the second axillary sclerite, and proximally is connected to the subalar by a short ligament. Pl_2-$3ax_2$a, b, and c (7-9), insert into a small lobe of 3ax (**iam**, Fig. 4.44), and these muscles function to fold the wing over the body at the end of flight (Pringle 1961).

The fore wing connects to the mesopleuron by the second axillary sclerite (hereafter referred to as "2ax") (**2ax**, Fig. 4.44). The ventral edge of this subtriangular sclerite (Fig.

4.44) lies within a groove along the dorsal edge of the mesopleuron (*cf.* wp_1, Figs. 4.28, 4.50) so as to have a transverse axis of articulation. It also articulates with the base of the submarginal vein by its dorsal angle (Fig. 4.44) and is connected to the subalar by a short ligament from its posteroventral angle (lg, Fig. 4.50).

The fore wing connects to the mesonotum through the first axillary sclerite (hereafter referred to as "1ax") (1ax, Figs. 4.44, 4.45). This sclerite has a long "head" (*sensu* Snodgrass 1942) that articulates with a small sclerotized "costal scale" (*sensu* James 1926) on the anterior proximal edge of the fore wing (Fig. 4.44). The head is separated from the "body" of 1ax by a transverse line of weakness (Figs. 4.44, 4.45), and in natural repose head and body form an abrupt angle. The ventral surface of the body has a basal, longitudinally oblique edge (a, Fig. 4.45) that is hinge-like articulated to a correspondingly oblique edge of the "anterior lobe" (*sensu* Snodgrass 1942) of the anterior notal wing process (a' of anwp, Fig. 4.43). The latter articulating edge is declined, as well as oblique, so that the anterior notal wing process supports 1ax at an angle (1ax, Fig. 4.41). The apex of a small lobe on the mesal edge of the body of 1ax (b, Fig. 4.45) abuts against the curved, digitiform "posterior lobe" (*sensu* Snodgrass 1942) of the anterior notal wing process (b' of anwp, Fig. 4.43). The tapered posterior end of 1ax rests on the posterior notal wing process and is connected to the posteroventral angle of the scutellar-axillar complex (sac) by a slender ligament (lg_1, Figs. 4.41, 4.42, 4.49). Finally, the apex of a lobe on the lateral edge of the body of 1ax (c, Fig. 4.45) fits into a concavity on the ventral surface of 2ax (c', Fig. 4.44). The lobe and concavity are connected by ligaments so that 1ax and 2ax have a ball-and-socket type of articulation.

The main power for moving the wings is produced by alternate contraction of the dorsolongitudinal [1ph-2ph (2)] and dorsoventral [pl_2-t_2a (3)] indirect flight muscles. Contraction of 1ph-2ph (2, Figs. 4.9, 4.10) raises the mesonotum by flexing the mesoscutum (msc) and the scutellar-axillar complex (sac) along the transscutal articulation (tsa) (Fig. 4.1). Raising the mesonotum lowers the fore wings. Contraction of pl_2-t_2a (3, Fig. 4.4) opposes the action of 1ph-2ph, depressing the mesonotum and raising the fore wings. However, flexing the mesonotum not only results in vertical movement of the mesoscutum and scutellar-axillar complex, it also results in horizontal movements of the lateral parts of the sclerites (Fig. 4.41). Flexing the mesonotum along the transscutal articulation pivots the vertical preaxilla (**pax**) and lateral axillar surface (**las**) towards each other, whereas flattening the mesonotum pivots the two sclerites apart (Fig. 4.41). These actions alternately pivot the anterior (**anwp**) and posterior (**pnwp**) notal wing processes (Fig. 4.43) towards and away from each other, respectively increasing and decreasing the angle of inclination of lax (**lax**, Fig. 4.41) on the anterior notal wing process. The rocking movements of lax are transmitted to the wing base through the head of lax and through the other two axillary sclerites to produce the correct wing movements necessary for flight (Pringle 1961).

4.5.3 Females: jumping mechanism and contortion

High speed photography at 300 frames per second was insufficient to record jumping movements of females of *Eupelmus* sp. One frame, at most, during any jumping event showed a blurred image of the individual in the act of jumping. However, it was verified that the body arches into a U-shape during jumping, as reported by Clausen (1927), and that the mesonotum is markedly flexed. Leg movements could not be confirmed so that the following description of jumping is based largely on an anlysis of 'contortion' (Table 4.4) in females.

Jumping in females apparently results from the same middle leg structure and movements as described for males. The mesocoxae lie within their combined mesocoxal fossa in a pre-jump condition and the legs are held in an arched configuration beside the body as in males (*cf.* Figs. 4.11, 4.15). Jumping results from a sudden retraction of the trochanters into the coxae (*cf.* Figs. 4.15, 4.16), which rotates the femora ventrally, straightens the femoral-tibial joints, extends the legs, and provides propulsion. Most females killed in the jump configuration have the middle legs crossed over beneath the body, or only the tibiae and tarsi crossed over (Fig. 4.16). This probably occurs naturally during a jump from continued ventral rotation of the legs when these leave the ground.

Though the act of jumping is the same for both sexes, males and females differ significantly in how the jump is powered. In females, each t_2-tr_2 (17) is reduced to a slender muscle that arises from the anteroventral angle of the lateral axillar surface (**las**) (Figs. 4.33-4.36). Within the body cavity, approximately the dorsal half of the muscle is fibrous and may be functional, but the ventral half is non-fibrous and somewhat sclerotized (*i. e.*, tendon-like). The region of t_2-tr_2 traversing the mesocoxa appears to be comp[illegible] of resilin (see below for properties of resilin). Whether the t_2-tr_2 muscles are functional or not, they are certainly incapable of generating enough energy for jumping (*cf.* Figs. 4.4, 4.33). Rather, jumping in female eupelmines is powered by contraction of the massive pl_2-t_2c (5) muscles that originate from the acropleuron and insert into the anterolateral corners of the mesoscutum (5, Fig. 4.31). Contraction produces a horizontal, posteriorly directed force that pulls back on the mesoscutum (**msc**, Fig. 4.29). This flexes the mesonotum along the transscutal articulation (**tsa**, Fig. 4.29) similarly to contraction of the dorsolongitudinal indirect flight muscles [(1ph-2ph) (2)] in males. These latter muscles apparently do not assist pl_2-t_2c in flexing the mesonotum for jumping in females because they are compressed in the flexed configuration (*cf.* 2, Figs. 4.35, 4.36 and 4.39, 4.40). Flexing the mesonotum along the transscutal articulation raises the anterodorsal edge of the scutellar-axillar complex, thereby rotating the anteroventral angle of the lateral axillar surface (**las**) anteriorly and dorsally, pulling up on t_2-tr_2 (17) to retract the trochanter (*cf.* Figs. 4.33, 4.34).

Mesonotal flexing in male eupelmines is very subtle because flexing functions to move the fore wing bases in a manner suitable for flight, and only slight movements of the mesoscutum relative to the scutellar-axillar complex are neede[illegible]o do so. In females, mesonotal flexing fun[illegible]ons to change a horizontal force, produced by contraction of pl_2-t_2c (5), into a vertical force that is used for jumping. The lateral axillar surface has to be rotated through a much greater arc than in males to sufficiently retract t_2-tr_2 (17) and the trochanters for jumping. Mesonotal flexing is thus much more pronounced in females (*cf.* Figs. 4.29, 4.30) than it is in males.

Table 4.4 describes the different orientations of body parts that constitute 'contortion' in female eupelmines, based on whether the mesonotum is flexed or unflexed. All aspects of contortion in females are a direct result of the jumping mechanism and increased mesonotal flexing, except for orientation of the mesocoxae and resultant differences in direction the middle legs project. The various aspects of contortion in female eupelmines are explained below as modifications of the plesiomorphic male structure to enable extreme mesonotal flexing for jumping.

4.5.3.1 Mesonotal flexing and the axillary sclerites

The change in function and amplification of mesonotal flexing in female eupelmines has resulted in various changes in structure and function of the second axillary, and particularly of the first axillary sclerites. The third axillary sclerite functions to fold the wing over the body in both sexes and its structure is very similar in each (*cf.* 3ax, Figs. 4.44, 4.50). Function of 2ax is also similar in both sexes (partly to connect the fore wing base to the mesopleuron), and structure of the sclerite is likewise similar (*cf.* 2ax, Figs. 4.44, 4.50). However, the anteroventral angle of 2ax is connected to the anterior angle of the mesopleural wing process (**wp$_2$**) by a stout ligament (**lg**) (Fig. 4.50) in females. Furthermore, the ventral cavity (**c'**, Fig. 4.50) for lobe "c" of 1ax is larger, and lobe "c" and the cavity are connected by much stronger ligaments in females. These two modifications resist the greater forces acting on 2ax during mesonotal flexing for jumping.

The most conspicuous differences in structure and function of the axillary sclerites between males and females are in 1ax (*cf.* **1ax**, Figs. 4.44, 4.45 with 4.47). In males, 1ax connects the fore wing base to the mesoscutum. It also transmits the vertical and horizontal movements of mesonotal flexing to the wing base, through the "head" of the sclerite and through its connection with 2ax. The primary function of 1ax in females is to act as a hinge,

Table 4.4. Positional differences of body parts comprising contortion in female Eupelminae, relative to a flexed or unflexed mesonotum.

Structures	Orientation when mesonotum unflexed	Orientation when mesonotum flexed
Mesoscutum and scutellar-axillar complex	flat (Figs. 4.21, 4.29)	arched (Figs. 4.22, 4.30)
Wings	raised (Fig. 4.21), or flat on dorsum	lowered, or on dorsum but bent with metasoma (Fig. 4.22)
Head and pronotum	extended anteriorly (Fig. 4.21)	extended dorsally to various extents in most individuals (Fig. 4.22)
Metasoma	extended posteriorly (Fig. 4.21)	extended dorsally to various extents in most individuals (Fig. 4.22)
Middle femur, tibia and tarsus	femur extended laterally from body and tibia and tarsus at abrupt angle to femur so legs are held on either side of body (Fig. 4.15)	Legs straight and together beneath ventral midline of body, or only femora together along ventral midline of body and tibia and tarsus at abrupt angle to femur so as to be crossed over beneath body (Fig. 4.16)
Mesocoxa	base of coxa within fossa (Fig. 4.29) so t[illegible]xtends posteroventrally (Fig. 4.16), or base of co[illegible]ved from fossa (Fig. 4.30) so that coxa and leg extend anteriorly beneath body (Fig. 4.22)	base of coxa within fossa (Fig. 4.29) so that leg extends posteroventrally (Fig. 4.16), or base of coxa removed from fossa (Fig. 4.30) so that coxa and leg extend anteriorly beneath body (Fig. 4.22)
First and second axillary sclerites	second axillary sclerite in horizontal plane and first axillary sclerite concealed (Figs. 4.23, 4.29)	second axillary sclerite in vertical plane and first axillary sclerite partly exposed (Fig. 4.30)
Prepectus (difference only in some genera)	extended from pronotum to tegula between mesoscutum and mesopleuron (Fig. 4.29)	extended from pronotum over anterior of mesopleuron and away from mesoscutum and tegula (Fig. 4.30)

regulating movements of the mesoscutum and scutellar-axillar complex relative to each other and to the mesopleuron during mesonotal flexing. This change in function for 1ax in females is reflected in conspicuous changes in its shape. The first axillary sclerite of females (Fig. 4.47) consists only of the "body", without a "head" (*cf.* Figs. 4.44, 4.47), so that the fore wing base is disconnected from 1ax and the mesoscutum. Disconnecting the fore wing from the mesoscutum allows extreme flexing of the mesonotum, which would not be possible if the fore wings were attached to both the mesonotum and the mesopleuron. It also enables the fore wings to be folded over the body when the mesonotum is flexed (Fig. 4.22), rather than extended ventrally beside the body as in males. Folding the wings over the body reduces drag during a jump and thereby contributes to length of the jump.

The main function of 1ax as a hinge results from changes in its articulation with the anterior notal wing process and with 2ax. In males, 1ax is supported along a longitudinally oblique ventral edge (**a**, Fig. 4.45) by the anterior lobe of the anterior notal wing process (**a'**, Fig. 4.43). It is also connected to 2ax in a ball-and-socket type of articulation, with this articulation (**c**, Fig. 4.45) at the same level as its articulation with the anterior notal wing process (**a**, Fig. 4.45). 1ax is able to move in both a longitudinal and transverse direction because of its respective articulations, but only relatively slight movements are possible. In females, 1ax has an almost transverse articulatory edge with the anterior lobe of the anterior notal wing process (*cf.* **a** and **a'**, Figs. 4.46-4.49). Furthermore, lobe "b" of 1ax projects anteriorly in females instead of mesally as in males (*cf.* **b**, Figs. 4.45, 4.47). The recurved apex of the posterior lobe of the anterior notal wing process (**b'**, Fig. 4.46) fits into the notch formed between "a" and "b" (Fig. 4.48). Because this is at the same level as the articulatory edge of the anterior lobe, "a", 1ax has a single longitudinal axis of rotation with the anterior notal wing process (*cf.* **1ax**, Figs. 4.35, 4.36). Critical for the function of 1ax as a hinge is that unlike males it is not connected to 2ax at the same level as its articulation with the anterior notal wing process. Rather, the ball-and-socket articulation with 2ax is near the posterolateral angle of lax (c, Figs. 4.47-4.49).

When the mesonotum is unflexed, lax has an horizontal alignment (Figs. 4.35, 4.49). This is not visible because 2ax is folded down horizontally over the posterior end and the anterior end is concealed by the tegula (tg) (*cf.* Figs. 4.31 with 4.23, 4.29). Contraction of pl_2-t_2c (5) pulls back on the mesoscutum, producing a posteriorly directed force through the anterior notal wing process. lax is prevented from moving posteriorly because of its articulation with 2ax, but because of its longitudinal axis of rotation with the anterior notal wing process the anterior end of lax rotates dorsally and posteriorly around the pivot formed by its ball-and-socket joint with 2ax (Fig. 4.35). lax thus rotates to a vertical position (Fig. 4.36) and deflects the posterior edge of the mesoscutum dorsally (Fig. 4.30) as the mesoscutum is pulled posteriorly by contraction of pl_2-t_2c (Fig. 4.31). This in turn lifts the anterior edge of the scutellar-axillar complex (sac), rotating the lateral axillar surface (las) anteriorly and dorsally inside of the preaxilla (pax) (*cf.* Figs. 4.39, 4.40) to pull up on t_2-tr_2 (17) (*cf.* Figs. 4.33, 4.34) for jumping. As lax rotates to a vertical position, so does 2ax beside it, thereby exposing the anterior end of lax as a brownish lobe between the preaxilla, lateral axillar surface, and 2ax and the mesopleuron (Figs. 4.26, 4.28, 4.30). The height to which the mesonotum is flexed is determined by the length of lax between its respective articulations with the anterior notal wing process and 2ax (*cf.* Figs. 4.35, 4.36).

As for males, lax is not directly articulated with the lateral axillar surface. However, the posteroventral surface of lax is broad and slightly concave so that it fits over the lateral axillar surface (*cf.* Figs. 4.48, 4.49). It is also connected to the apex of the lateral axillar surface (posterior notal wing process) by ligament (lg_1, Fig. 4.48). The posterodorsal edge of lax is connected to the posteroventral angle of the scutellar-axillar complex by a thin, band-like ligament (lg_2, Figs. 4.48, 4.49).

4.5.3.2 Mesonotal flexing and alignment of the head and pronotum

Contraction of pl_1-t_2c (5) flexes the mesonotum because it pulls back on, or retracts, the anterior edge of the mesoscutum (Fig. 4.29). However, the mesoscutum is connected to the pronotum so that this also has to be retracted for mesonotal flexing to occur (Fig. 4.30). Retraction of the pronotum is possible because position of the prepectus can be altered to reduce the distance between the prothorax and mesopleuron. This allows the prothorax to be retracted against the anterior margin of the mesopleuron.

In males, the prepectus consists of subtriangular lateral sclerites that are narrowly continuous along the anteroventral edge of the mesopleuron (**pre**, Fig. 4.10). The anterior angles of the prepectus are extended into short lobes (**prel**, Fig. 4.10) that abut against the ventrolateral edge of the mesoscutum. The prepectal lobes act as fulcra and when the mesonotum flexes the mesoscutum rotates dorsally to a slight degree about the anterior pivots formed by the lobes. A slight gap appears between the dorsal edge of the prepectus and the mesoscutum when this happens.

The prepectus also consists of subtriangular lateral sclerites in females (**lps**, Figs. 4.29, 4.30, 4.38). However, these incurve abruptly to form small, anteroventrally faced prepectal surfaces posterior to the procoxae (hereafter referred to as the frontal prepectal surfaces: **fps**, Fig. 4.38). The frontal prepectal surfaces are narrowly continuous along the the anteroventral edge of the mesopleuron (Fig. 4.38) and are flexibly united to the mesopleuron in a hinge-like articulation. The entire line of attachment with the mesopleuron forms a longitudinal axis of rotation for the frontal prepectal surfaces ("dashed line", Fig. 4.38). The mesal edge of each frontal prepectal surface is also internally thickened as a strong ridge (**mpe**, Figs. 4.36, 4.37). This ridge is dorsally expanded into a spatulate apex, the concave inner surface of which fits over the apex of the anterolateral mesoscutal process for attachment of pl_1-t_2c (**rsp**, Fig. 4.37), pinched between the mesoscutal process and the mesoscutum (Figs. 4.35-4.38). Thus, the prepectus has a ball-and-socket articulation with the mesoscutum in addition to the longitudinal hinge-like articulation with the mesopleuron. Retraction of the mesoscutum rotates the frontal prepectal surfaces posteriorly about the ventral axis of rotation formed between the prepectus and mesopleuron (*cf.* Figs. 4.37, 4.38). This changes the frontal prepectal surface from an anteroventrally faced direction (Fig. 4.37) to an anteriorly or anterodorsally faced direction (**fps**, Fig. 4.38). In longitudinal view, the angle of inclination of the frontal prepectal surface is changed from a relatively even continuation of the ventral surface of the mesopleuron (when the mesonotum is unflexed), to a more or less abrupt angle with the ventral surface of the mesopleuron (when the mesonotum is flexed) (*cf.* "dashed arrows", Figs. 4.29, 4.30 and 4.33, 4.34).

Figures 4.29 and 4.31 show how the prothorax is attached to the mesothorax along an oblique dorsoventral angle. Retraction of the mesoscutum rotates the frontal prepectal surfaces posteriorly about the ventral articulation with the mesopleuron, decreasing their angle of inclination and decreasing the distance between the prothorax and mesopleuron. If the frontal surfaces are rotated to a more or less vertical position so that the anterior margin of the mesoscutum and frontal prepectal surfaces are approximately in line (Fig. 4.38), the prothorax is merely compressed against the anterior margin of the mesothorax. The pronotum and head extend more or less anteriorly in such individuals so as to have the same approximate alignment as when the mesonotum is unflexed (*cf.* Figs. 4.29, 4.30). However, if the mesoscutum is retracted to a greater extent the frontal prepectal surfaces are rotated further over the anterior edge of the mesopleuron to face anterodorsally. Because the prothorax is rotated with the frontal prepectal surfaces, the pronotum and head are also projected dorsally at an abrupt angle to the long axis of the body over the anterior edge of the mesopleuron (*cf.* Figs. 4.21, 4.22).

The dorsal and ventral edges of the lateral prepectal surface (**lps**) are free from the mesoscutum and acropleuron, respectively. When the mesonotum is unflexed the lateral prepectal surface extends from the prothorax (**no$_1$**) to the tegula (**tg**) between the mesoscutum and acropleuron (Fig. 4.29). In individuals of many genera, posterior rotation of the frontal prepectal surface during mesonotal flexing results in the lateral prepectal surface being rotated ventrally away from the tegula and over the acropleuron (*cf.* **lps**, Figs. 4.29, 4.30).

4.5.3.3 Mesonotal flexing and alignment of the metasoma

The head and pronotum of female eupelmines are often reflexed dorsally when the mesonotum is flexed because they are retracted with the mesoscutum. The metasoma is often similarly reflexed dorsally when the mesonotum is flexed (*cf.* Figs. 4.21, 4.22), but this is due to rotation of the scutellar-axillar complex and metanotum. The scutellar-axillar complex (**sac**) and metanotum (**no$_3$**) rotate as a unit about a longitudinal axis of rotation between the metanotum and propodeum (**pro**) (Fig. 4.39). Lifting the anterior edge of the scutellar-axillar complex depresses the posterior edge of the complex and the metanotum. This depresses the anterior edge of the propodeum, thereby rotating the posterior surface of the propodeum, and hence the metasoma (**Mt**), dorsally (*cf.* "solid arrows", Figs. 4.39, 4.40). Individuals of species that have the propodeum linear or very narrow medially tend to have the metasoma abruptly reflexed when the mesonotum is flexed, whereas those with a propodeum that is longer medially tend to have the metasoma less conspicuously reflexed.

The scutellum and internal second phragma (**2ph**, Figs. 4.39, 4.40) form a rigid structure. Consequently, the second phragma is rotated anteriorly when the anterior edge of the scutellar-axillar complex is raised during flexing. This results in the 2ph-3ph (**18**) muscles being stretched (*cf.* **18**, Figs. 4.39, 4.40). Presumably, contraction of these muscles opposes that of the pl$_2$-t$_2$c (**5**) muscles and helps to flatten the mesonotum once flexed. Other muscles that may also help to flatten the mesonotum are pl$_2$-t$_2$a (**3**, Fig. 4.4), to depress the mesoscutum; pl$_2$-t$_2$b (**4**, Figs. 4.33, 4.34), to retract the scutellar-axillar complex; and possibly fu$_2$-2ph (**11**, Figs. 4.35, 4.36), to help retract the second phragma.

4.5.4 Females: modifications for increased jumping ability

Jumping in most chalcidoids depends on how forcefully contraction of the t_2-tr_2 (17) muscles retract the mesotrochanters into the mesocoxae. Because the force exerted by a muscle is proportional to its cross-sectional area (Chapman 1982), the larger the area of mesonotal attachment for t_2-tr_2, the higher or longer a jump should be possible. I previously proposed that axillar phragmata were secondarily derived in the common ancestor of Chalcidoidea + Mymarommatidae (Gibson in press, b) to increase the mesonotal area of attachment of t_2-tr_2, and hence jumping ability (Gibson in press, a). However, mesonotal expansion of t_2-tr_2 is limited by position of the indirect flight muscles, by 1ph-2ph (2) medially and by pl_2-t_2a (3) anteriorly. Female eupelmines have circumvented this limitation by coadapting their flight and jumping mechanisms, changing the role of t_2-tr_2 from generating the force used for jumping to transmitting the force produced by a secondarily enlarged pleural muscle, pl_2-t_2c (5). The outer cross-sectional area of pl_2-t_2c in female eupelmines (5, Fig. 4.31) is much greater than the mesonotal area of attachment of t_2-tr_2 in other chalcidoids, and the total cross-sectional area of the muscle is even greater because of the posterior inner wall for attachment of pl_2-t_2c (5, Fig. 4.32). Consequently, much greater forces should be produced for jumping than is possible in chalcidoids that use t_2-tr_2 to provide power for jumping.

Increased jumping ability of female eupelmines is probably only partly due to the large size of pl_2-t_2c. These muscles do not insert directly into the anterolateral corners of the mesoscutum. Rather, each muscle inserts into a mass of material that is formed into an eliptical pad (rsp, Fig. 4.32), with the narrowed anterior end of the pad attached to an anterolateral process of the mesoscutum (Figs. 4.31-4.33, 4.37). Pl_2-t_2c appears to cover the pad only externally (*cf.* 5, Figs. 4.31, 4.32), but the inner posterior rim of the pad declines abruptly to the insertion of the muscle fibers and continues as a thin sheet down the center of the muscle. Consequently, pl_2-t_2c inserts into the lobe and sheet in a pinnate manner, the outer muscle fibers into both the pad and outer surface of the sheet, and the inner fibers into the inner surface of the sheet.

The pad of amorphous material into which pl_2-t_2c inserts stains with toluidine blue and fluoresces a brilliant bluish color in ultraviolet light. It is hard, brittle, and opaque when dried or in ethanol, but swells and becomes transluscent and rubbery in water. The latter states can be reversibly altered by changing the solution from water to ethanol and back. All of these are properties of the structural protein resilin (Andersen and Weis-Fogh 1964). Resilin contains 50-60% water in the natural state so as to be rubbery (Alexander 1983) and has been measured to have an elastic efficiency of about 96% (Jensen and Weis-Fogh 1962), *i. e.*, energy released is 96% of energy input.

One of the functions of resilin in insects is to store energy produced over the duration of muscular contraction for release over a much shorter period of time, thereby greatly increasing the power of an impulse. I suspect that contraction of the pl_2-t_2c muscles in female eupelmines does not directly flex the mesonotum. Rather, it stretches the pads of resilin attached to the mesoscutum. The potential energy thus stored is then suddenly released to retract the mesoscutum and violently flex the mesonotum for jumping. This proposed mechanism requires the operation of some type of mesothoracic lock, which can be selectively released, to prevent initial flexing of the mesonotum during contraction of pl_2-t_2c. I did not find an obvious lock mechanism, but I believe there is one because of the function I assume for the resilin pads. Also, females can be induced to flap their wings if they are lifted from the substrate. Wing flapping occurs without at least extreme mesonotal flexing, presumably by alternate contraction of the indirect flight muscles, and therefore supports an hypothesis of a selective mesothoracic lock mechanism. Articulation of the mesoscutum, scutellar-axillar complex, mesopleuron, fore wing axillary sclerites, and subalar is very complex. I suspect that if there is a mesothoracic lock mechanism it is composed of some of the above sclerites that interact to prevent flexing of the mesoscutum relative to the scutellar-axillar complex. Alternatives include mechanisms that prevent retraction of the prepectus and prothorax, or that prevent posterior rotation of the metanotum plus scutellar-axillar complex.

A mesothoracic lock mechanism is not yet demonstrated, but modification of the middle legs of females presumably reflects the much greater forces produced by their jumping mechanism. Females have the medial surface of each mesocoxa extended into a flange beyond the apex of the coxa (cxf, Fig. 4.17). This medial extension likely acts as a stop for the trochanter, preventing possible damage from over-rotation of the trochanter when t_2-tr_2 is retracted. Also modified in females are the mesotarsi and mesotibiae. The mesotibial spur is elongate as in males, but it is also thickened (*cf.* Figs. 4.19, 4.20), and females of many genera have either a patch or a row of stout pegs along the anterior distal edge of the tibia (Fig. 4.19). Furthermore, the tarsomeres are not all of the same diameter as in males, but instead the tarsus thickens proximally (*cf.* Figs. 4.19, 4.20). The mesotarsus also has a dense pad of setae, one or more lateral rows of stout pegs, or both, on the ventral surface (Fig. 4.19). When the middle legs are forcefully extended to catapult the individual, the mesotarsi, and probably also the apex of the tibiae are appressed against the substrate. The thick tibial spur probably acts as a brace, appressed against the substrate in an opposite direction to the tarsus. The various pegs probably prevent the tarsus, and thus the leg from slipping as the forces are exerted through the tarsus. The tarsal pegs, ventral pad of setae, or both, may also cushion the tarsus against the forces exerted through it by absorbing some of the shock load. Proximal thickening of the tarsus undoubtedly strengthens the tarsus against possible damage.

All aspects of contortion described in Table 4.4 were explained as a consequence of the jumping mechanism of female eupelmines, except for orientation of the mesocoxae. Individuals with a flexed or unflexed mesonotum can have the mesocoxae within the coxal fossa (Fig. 4.29), and thus the legs extended posteriorly (Fig. 4.16), or out of the coxal fossa (Fig. 4.30) and extended anteriorly with the rest of the legs (Fig. 4.22). Function of this apomorphic mesocoxal-mesopleural articulation is uncertain, but I suspect that the articulation was developed for protection of the individual upon landing. The legs can be projected straight forward when the mesocoxae are rotated out of the coxal fossa, and if so the tarsi project beyond the head. Because individuals tend to tumble on landing, I suspect that they prepare for this by extending the middle legs cephalad to protect the head and antennae. Within Eupelmidae, individuals of *Cynipencyrtus* Ishii, *Metapelma* Westwood and *Neanastatus* Girault do not have the apomorphic mesocoxal-mesopleural articulation. However, individuals of the latter two taxa have exceptionally long middle legs, which can be extended beyond the head without the mesocoxae having to be rotated out of the coxal fossa. Almost all Encyrtidae also lack the apomorphic eupelmid mesocoxal-mesopleural articulation, but encyrtids have the mesocoxal-mesopleural articulation advanced anteriorly to approximately the midline of the acropleuron. This in effect increases the distance the middle legs can be extended forward.

4.5.5 Females: jumping musculature compared with that of other eupelmids

Female eupelmines appear to have the most apomorphic jumping musculature of all eupelmids, based on the fully expanded acropleuron (**ac**, Fig. 4.30) and tendon-like reduced t_2-tr_2 muscles (17, Figs. 4.33, 4.35). In Calosotinae, the t_2-tr_2 muscles are plesiomorphic in form whether or not the acropleuron is completely expanded. Each t_2-tr_2 arises from the axilla [t_2-tr_2a (17a)] and from a large axillar phragma [t_2-tr_2b (17b)], and inserts ventrally into a large, oval, golf tee-like pedicel (**pdl**) (Fig. 4.53). Individuals of Tanaostigmatinae also have this plesiomorphic form of t_2-tr_2 (Gibson in press; a, fig. 45). However, individuals of *Metapelma* Westwood, *Neanastatus* Girault, and *Z. schwarzii* have forms of t_2-tr_2 intermediate between the apomorphic structure of female eupelmines and the plesiomorphic structures of calosotines, tanaostigmatines and male eupelmines.

In *Neanastatus* (Fig. 4.54), each t_2-tr_2 is reduced so that its pedicel (**pdl**) is at the ventral level of the scutellar-axillar complex (**sac**). The pedicel is elongate and slender and its posterior edge articulates with the scutellar-axillar complex. A thin, tendon-like ligament extends from the anterior edge of the pedicel ventrally through the body cavity. T_2-tr_2a (**17a**) arises from the reduced axilla as a thin band-like muscle, whereas t_2-tr_2b (**17b**) is a short tubular muscle that arises from the apex of the reduced axillar phragma (**axp**). Individuals of *Z. schwarzii* have the same structure, exept that t_2-tr_2 is as a single, small, band-like muscle that originates from the ventral edge of the lateral axillar surface. The reduced t_2-tr_2 of individuals of *Metapelma* is quite different in form. The lateral axillar surface (**las**) has a triangular plate (**axpl**) extended ventrally from its inner surface so that a narrow channel is formed between the two (Fig. 4.56). The apex of the inner plate is connected to the small pedicel (**pdl**) of t_2-tr_2 by t_2-tr_2b (**17b**) (Fig. 4.56). Part of t_2-tr_2b apparently also extends from the pedicel into the channel formed between the outer and inner lateral axillar surfaces, as does t_2-tr_2a (**17b**, **17a**, Fig. 4.55). The pedicel lies freely within the body cavity and a tendon-like ligament extends ventrally from near its center (Figs. 4.55, 4.56).

Individuals [illegible] *Metapelma* do not have horizontally-produced axillar phragmata. It is therefore possible [illegible] the inner plate of the lateral axillar surface (**axpl**, Fig. 4.56) is a modified phragma [illegible] has been reflexed ventrally from the plesiomorphic horizontal alignment. The different form of t_2-tr_2 in individuals of *Metapelma* and *Neanastatus* and *Z. schwarzii*, indicates that there were two independent reductions from a common ancestor with the plesiomorphic form of t_2-tr_2. This will be justified further in a subsequent paper. The tendon-like t_2-tr_2 muscle of female eupelmines most likely represents a third independent reduction. However, how the apomorphic female form of the muscle evolved can not be hypothesized because there are no known intermediate states in the subfamily.

Mesothoracic musculature of calosotines and tanaostigmatines indicates reduction of t_2-tr_2 (17) was not simultaneous with enlargment of pl_2-t_2c (5). Rather, it appears these latter muscles were initially enlarged to aid the t_2-tr_2 muscles in jumping, and only after the pl_2-tr_2c muscles were completely, or almost completely expanded were the t_2-tr_2 muscles reduced.

4.5.6 Females: flight

It is unknown whether macropterous female eupelmines are capable of flight. I have observed males and females of *Eusandalum* Ratzeburg (Calosotinae) in the laboratory, as well as males and females of *Eupelmus* Dalman and *Brasema* Cameron (Eupelminae). Individuals of both sexes of *Eusandalum* fly, albeit poorly, as noted by Bouček (1967). Males of *Eupelmus* and *Brasema* fly readily, but I have never seen females fly. They can be induced to flap their wings if they are lifted into the air, and sometimes flap their wings during a jump. The latter may prolong descent, but apparently does not provide lift.

Crossman (1925, p. 60) also investigated whether females of *Anastatus bifasciatus* (Geoffroy, *nec* Fonscolombe) could fly. He stated that the investigations "indicated that they can not", though males were often seen flying. However, Packard (1916, p. 327) apparently observed flight in "adults" of *Eupelmus allynii* (French), stating that they "do not seem to fly more than a few feet at a time, using their wings merely to go from stem to stem". It thus appears that if macropterous female eupelmines can fly, they do so only very poorly. Probable reduction of flight capability is undoubtedly related to mesothoracic modifications for increased jumping ability, particularly increased mesonotal flexing and modifications of the axillary sclerites.

4.6 Phylogenetic Implications

Origin of the transscutal articulation, and resultant changes in the flight apparatus was a major event in the evolution of Hymenoptera. The transscutal articulation arose within Symphyta and was previously hypothesized as a synapomorphy for Xyphidriidae + Orussidae (Symphyta) + Apocrita (Gibson in press, a). Relative importance of the presumably more efficient flight mechanism to the success of Apocrita is unknown, but undoubtedly has contributed to it.

Chalcidoidea is the only known group of Apocrita that was preadapted through retention of various plesiomorphies to further modify the novel flight mechanism for an entirely different function, that of jumping. Only stephanids and most chalcidoids are known to retain both an independent prepectus (and thus a loosely connected pro- and mesothorax necessary for retraction of the mesoscutum), and a mesotergal-mesotrochanteral (t_2-tr_2) muscle (Gibson in press, a, b). Furthermore, apparently only chalcidoids retained pl_2-t_2c, which was secondarily adapted to provide power for jumping in the modified mechanism.

The selective pressure to enhance jumping ability at the expense of flight ability in some chalcidoids (those with expanded acropleura) was probably to avoid predation. Trjapitzin (1977) proposed that jumping in encyrtids serves to escape predators, such as ants and larvae of some Neuroptera. Eupelmids generally have been regarded as evolved from some cleonymine-like ancestor (Bouček 1958, Graham 1969). Most members of Cleonyminae (Pteromalidae) are parasites of wood-boring beetle (Coleoptera) larvae, as are most Calosotinae and species of *Metapelma*. The much larger subfamily Eupelminae has much more diverse host relationships, including developmental stages attacked and microhabitats the hosts are in. Though relatively few eupelmines are known parasites of wood-boring insects, I suspect that their ancestors were such parasites. Male and female eupelmines have one or more tiny, curved, stout spines at the apex of the protibiae. Such spines are characteristic of diverse and phylogenetically unrelated groups of wood-borer parasites as an adaptation for exiting the host tunnel. I suspect that the spines are a relictual character in Eupelminae, and evidence of their ancestral life-history. Females of wood-borer parasites, searching for hosts in twigs and trunks of trees, are probably relatively exposed to predators. Hence, escape by extremely rapid jumping may be selected for. Males presumably spend less time so exposed, searching only for mates, and thus may not be under the same selective pressures as females. This could explain sexual dimorphism in Eupelminae, though males of Calosotinae, Tanaostigmatinae, and Encyrtidae are similarly modified as females. It is important to determine whether female eupelmines can actually fly, whether both sexes of the other taxa listed above can fly, and with what relative efficiencies. If female eupelmines are unable to fly, or do so only very poorly, flight in males could be important to maintain gene flow. The subfamily Eupelminae is much more diverse than any of the other recognized subfamilies of Eupelmidae, and it is interesting to question whether sexual dimorphism, *i. e.*, selection of males for flight but females for jumping, has contributed to the evolution of this diversity. Reduction of flight capability for increased jumping ability certainly explains, at least in part, apparently independent evolution of brachyptery in females of many eupelmine taxa.

Figure 4.1. *Brasema* sp. (♂), lateral mesosoma.

Figure 4.2. *Lysisca* sp. (♀), lateral mesosoma.

Figure 4.3. *Brasema* sp. (♂), dorsal mesosoma.

Figure 4.4. *Epistenia* sp. (♀), sagittal section of mesosoma.

Figure 4.5. *Brasema* sp. (♂), sagittal section of mesosoma.

Figure 4.6. *Epistenia* sp. (♀), sagittal section of mesosoma.

Figure 4.7. *Brasema* sp. (♂), inner surface of mesopleuron.

Figure 4.8. *Epistenia* sp. (♀), inner surface of mesopleuron.

Scale bar = x100 μm.

Figure 4.9. *Brasema* sp. (♂), muscles of mesofurca and second phragma.

Figure 4.10. *Brasema* sp. (♂), ventral view of prepectus and anterior margin of mesoscutum.

Figure 4.11. *Brasema* sp. (♂), pre-jump configuration of body, ventral view.

Figure 4.12. *Brasema* sp. (♂), mesopleural-coxal articulation, ventral view.

Figure 4.13. *Brasema* sp. (♂), mesocoxal fossa, posterolateral view.

Figure 4.14. *Brasema* sp. (♂), mesocoxa, anterobasal view.

Figure 4.15. *Brasema* sp. (♀), pre-jump configuration of middle legs.

Figure 4.16. *Brasema* sp. (♀), post-jump configuration of middle legs.

Scale bar = x100 μm.

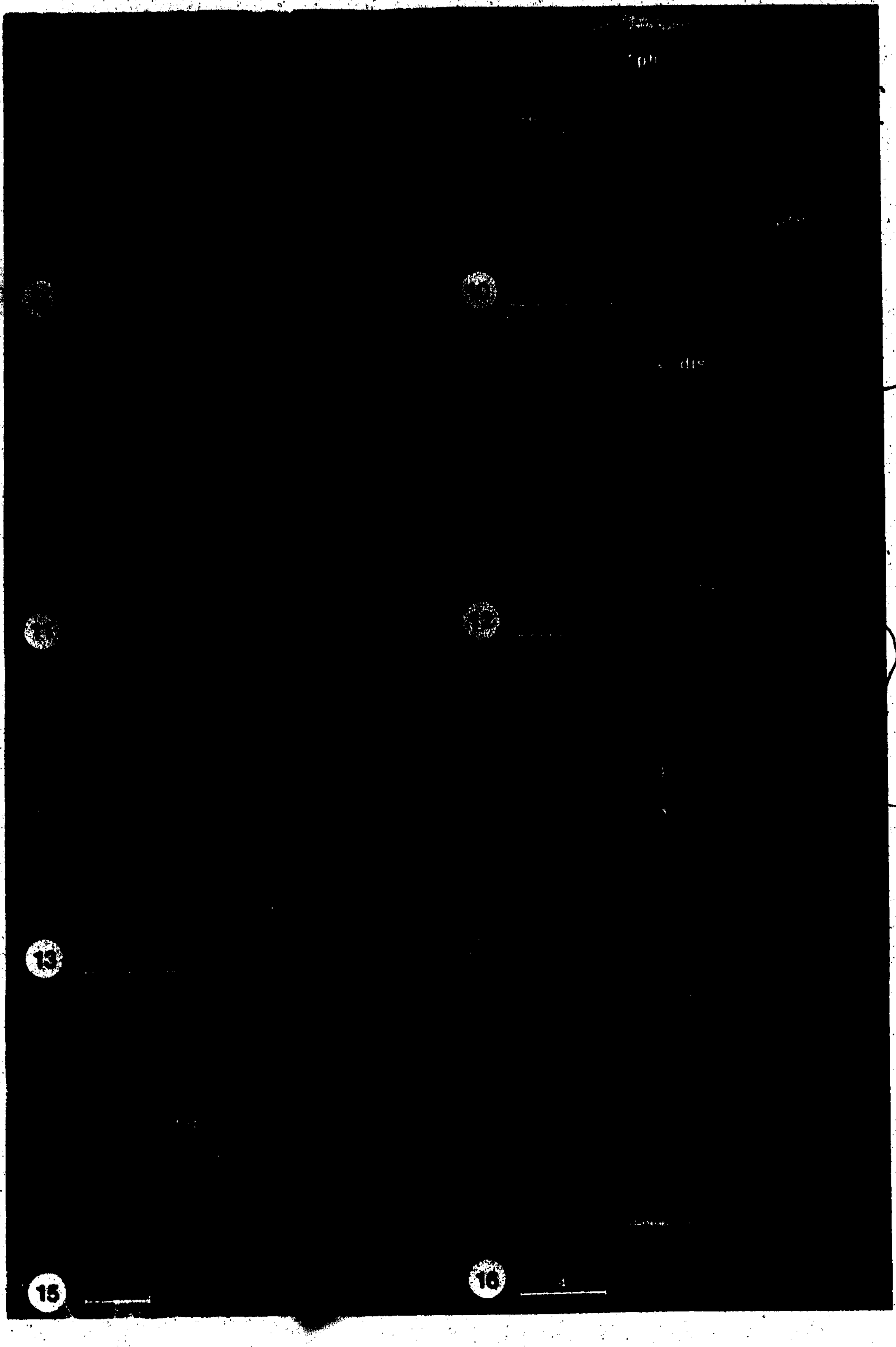
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Figure 4.17. *Eupelmus* sp. (♀), mesopleural-coxal articulation, ventral view.

Figure 4.18. *Eupelmus* sp. (♀), posterolateral view of mesocoxal fossa, coxae rotated forward.

Figure 4.19. *Eupelmus* sp. (♀), mesotarsus and apex of mesotibia.

Figure 4.20. *Eupelmus* sp. (♂), mesotarsus and apex of mesotibia.

Figure 4.21. *Arachnophaga picea* (♀) (Riley), uncontorted configuration of body.

Figure 4.22. *Arachnophaga picea* (♀) (Riley), contorted configuration of body.

Figure 4.23. *Eupelmus* sp. (♀), dorsal mesosoma.

Figure 4.24. Undescribed genus "B" of Calosotinae (♀), ventral mesosoma.

Scale bar = x100 μm.

Figure 4.25. Undescribed genus "A" (Calosotinae) (♂), lateral mesosoma.

Figure 4.26. Undescribed genus "B" (Calosotinae) (♀), lateral mesosoma.

Figure 4.27. Undescribed genus "C" (Calosotinae) (uncoated ♀), lateral mesosoma.

Figure 4.28. *Calosota acron* (Walker) (♀), lateral mesosoma of Calosotinae.

Figure 4.29. *Brasema* sp. (♀), lateral mesosoma, unflexed. (Solid arrows indicate direction of movement of sclerites with mesonotal flexing.)

Figure 4.30. *Brasema* sp. (♀), lateral mesosoma, flexed.

Figure 4.31. *Brasema* sp. (♀), lateral mesosoma, cuticle of acropleuron removed.

Figure 4.32. *Brasema* sp. (♀), inner view of acropleuron.

Scale bar = x100 μm.

[Dashed arrows in Figs. 4.29 and 4.30 indicate rotation of frontal prepectal surface (fps) with mesonotal flexing.]

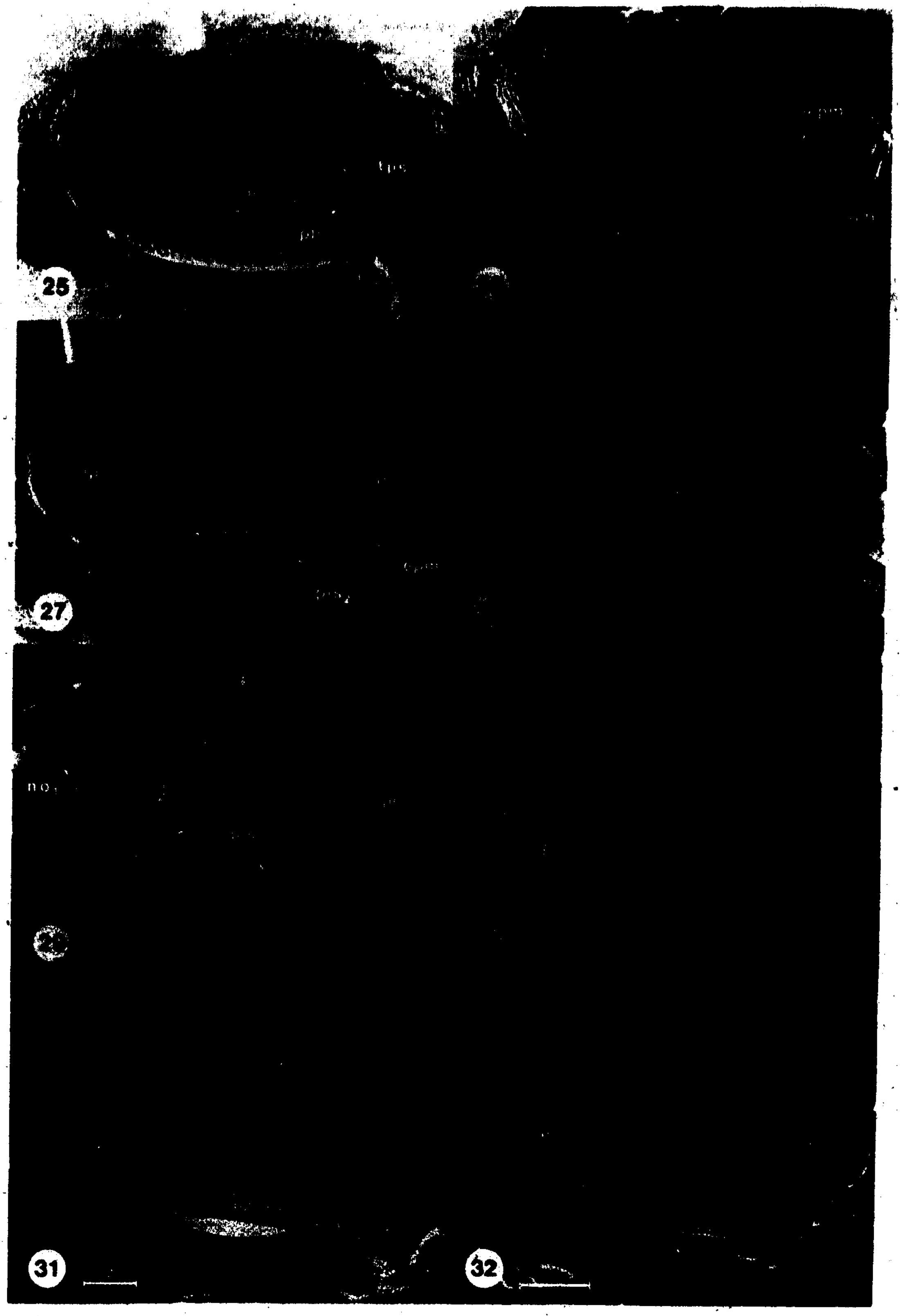
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Figure 4.33. *Eupelmus* sp. (♀), sagittal section of mesosoma: mesosoma unflexed. [Solid arrows denote rotation of lateral axillar surface (las) and movement of muscle 17 with mesonotal flexing.]

Figure 4.34. *Eupelmus* sp. (♀), sagittal section of mesosoma: mesosoma flexed.

Figure 4.35. *Eupelmus* sp. (♀), mesosoma, acropleuron removed: mesonotum unflexed. [Arrow denotes rotation of lax with mesonotal flexing.]

Figure 4.36. *Eupelmus* sp. (♀), mesosoma, acropleuron removed: mesonotum flexed.

Figure 4.37. *Eupelmus* sp. (♀), orientation of prepectus (left lateral prepectal surface removed), mesonotum unflexed. [Arrow denotes movement of mesoscu[illegible] (msc).]

Figure 4.38. *Eupelmus* sp. (♀), orientation of prepectus (left lateral prepectal surface removed), mesonotum flexed. [Dashed line indicates axis of rotation between prepectus and anterior edge of mesoscutum.]

Figure 4.39. *Eupelmus* sp. (♀), muscles of second phragma and orientation of propodeum and metasoma: mesonotum unflexed.

Figure 4.40. *Eupelmus* sp. (♀), muscles of second phragma and orientation of propodeum and metasoma: mesonotum flexed.

Scale bar = x100 μm.

[Dashed arrows in Figs. 4.33 and 4.40 indicate rotation of frontal prepectal surfaces, and large arrows in Figs. 4.39 and 4.40 indicate direction of movement of sclerites with mesonotal flexing.]

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Figure 4.41. *Brasema* sp. (♂), mesonotum and lax, lateral view. [Arrows denote directions of movement of the sclerites.]

Figure 4.42. *Brasema* sp. (♂), mesonotum and lax, dorsal view.

Figure 4.43. *Brasema* sp. (♂), lateral junction of mesoscutum and scutellar-axillar complex, dorsal view.

Figure 4.44. *Brasema* sp. (♂), axillary sclerites, dorsal view of lax and ventral view of 2ax and 3ax.

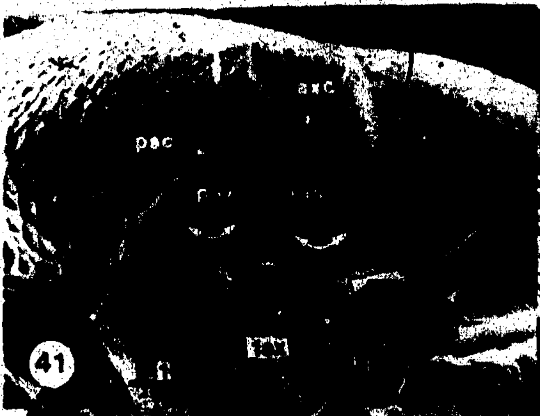
Figure 4.45. *Brasema* sp. (♂), body of lax, ventral view.

Figure 4.46. *Eupelmus* sp. (♀), lateral junction of mesoscutum and scutellar-axillar complex, dorsal view.

Figure 4.47. *Eupelmus* sp. (♀), lax, ventral view.

Figure 4.48. *Eupelmus* sp. (♀), lax connected to mesonotum, ventral view.

Scale bar = x100 μm.



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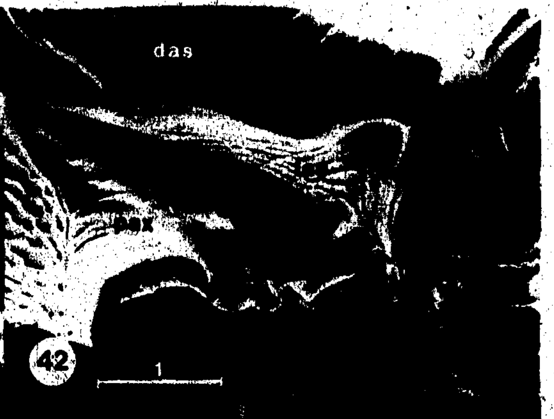

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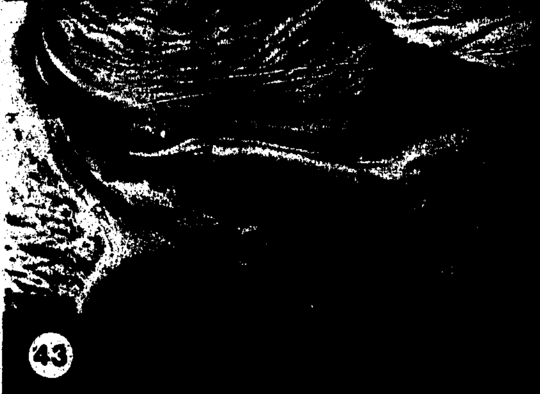

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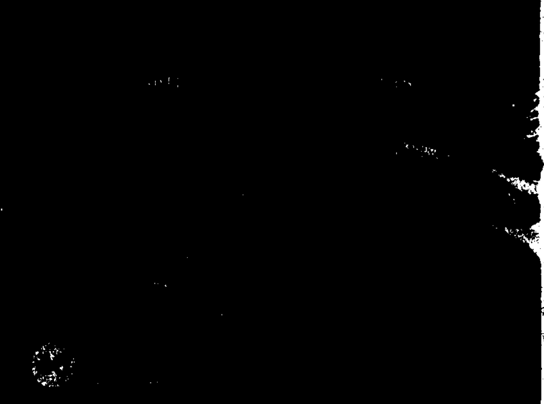

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Figure 4.49. *Eupelmus* sp. (♀), lax connected to mesonotum, lateral view.

Figure 4.50. *Eupelmus* sp. (♀), articulation of mesopleuron and 2ax, inner view.

Figure 4.51. *Metapelma spectabile* Westwood (♀), lateral mesosoma.

Figure 4.52. *Metapelma spectabile* Westwood (♀), posterior mesopleural muscles.

Figure 4.53. *Eusandalum* sp. (♀), sagittal section.

Figure 4.54. *Neanastatus* sp. (♀), dorsal region of t_2-tr_2 (**17a, 17b**), inner view.

Figure 4.55. *Metapelma spectabile* Westwood (♀) t_2-tr_2 (**17a, 17b**), outer view: complete.

Figure 4.56. *Metapelma spectabile* Westwood (♀) t_2-tr_2 (**17a, 17b**), outer view: partly removed to show inner plate (**axpl**) of lateral axillar surface (**las**).

Scale bar = x100 μm.


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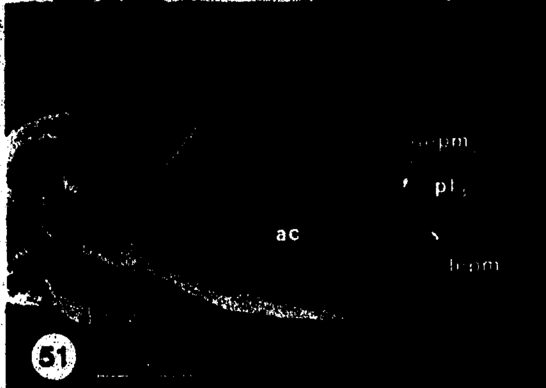
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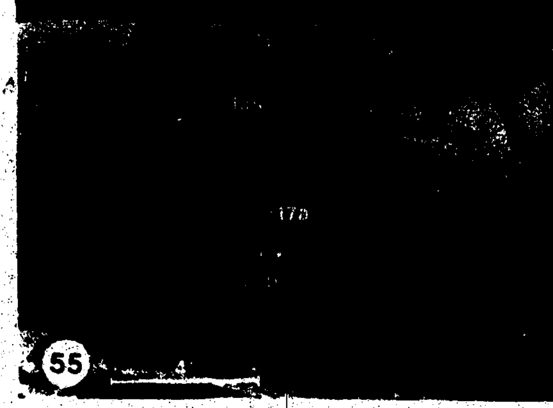
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las
axpl
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4.8 Appendix: List of abbreviations used for figures

a: margin of 1ax that articulates with the anterior lobe of the anterior notal wing process

a': anterior lobe of the anterior notal wing process

ac: acropleuron

acs: acropleural sulcus

anwp: anterior notal wing process

1ax: first axillary sclerite

2ax: second axillary sclerite

3ax: third axillary sclerite

axa: axillula

axas: axillular sulcus

axc: axillar carina

axp: axillar phragma

axpl: plate of lateral axillar surface

b: lobe of 1ax that articulates with the posterior lobe of the anterior notal wing process

b': posterior lobe of the anterior notal wing process

ba: basalare

c: lobe of 1ax that articulates within concavity of 2ax

c': concavity of 2ax for lobe c of 1ax

cxf: coxal flange

cxg: coxal groove

cxl: coxal lobe

das: dorsal axillar surface

dis: discrimen

epm$_2$: mesepimeron

eps$_2$: mesepisternum

fg: femoral groove

fps: frontal prepectal surface

iam: insertion of 3ax muscles

icm: intercoxal membrane

las: lateral axillar surface

lca: lateral mesopleural-coxal articulation

lepm$_2$: lower mesepimeron

leps$_2$: lower mesepisternum

lg: ligament

lps: lateral prepectal surface

mb: membrane

mca: median mesopleural-coxal articulation

mgr: mesopleural groove

mll: mesoscutal lateral lobe

mml: median mesoscutal lobe

mpe: median prepectal edge

msc: mesoscutum

Mt: metasoma

mtl: mesotrochantinal lobe

mtp: mesotrochantinal plate

no$_1$: pronotum

no$_2$: mesonotum

no$_3$: metanotum

not: notaulus

pax: preaxilla

pdl: pedicel of t_2-tr_2

1ph: first phragma

2ph: second phragma

pl$_3$: metapleuron

pls$_2$: mesopleural suture

pnwp: posterior notal wing process

pre: prepectus

prel: pronotal lobe

pro: propodeum

psc: parascutal carina

rsp: resilin pad

sac: scutellar-axillar complex

sap: subalar pit

scl: scutellum

sss: scutoscutellar stuture

su: subalar

tg: tegula

tps: transepimeral sulcus

tsa: transscutal articulation

tss: transepisternal sulcus

uepm$_2$: upper mesepimeron

ueps$_2$: upper mesepisternum

wp$_2$: mesopleural wing process

5. REVISION OF THE WORLD GENERA OF CALOSOTINAE BOUČEK AND METAPELMATINAE N. SUBF., WITH A PRELIMINARY ANALYSIS OF PHYLOGENETICS AND CLASSIFICATION OF THE FAMILY EUPELMIDAE (HYMENOPTERA: CHALCIDOIDEA)

5.1 Synopsis

Four subfamilies are included in Eupelmidae *s. l.* for the purposes of this study, Calosotinae Bouček, Metapelmatinae n. subf. [type genus: *Metapelma* Westwood], Eupelminae Walker, and Tanaostigmatinae Ashmead. Diagnoses of the four subfamilies are given, as is a key to distinguish members from each other and from other chalcidoids. Genera of Calosotinae and Metapelmatinae are also revised for the world, with a key to genera given for both subfamilies, and the following provided for each genus: description of structural features of males and females, synonymy, notes on known distribution and hosts, available keys to species listed by biogeographic region, and a catalog of species. Eight genera are included in Calosotinae (type species in parenthesis) - *Archaeopelma* n. gen. [*A. tropeotergum* n. sp.], *Licrooides* n. gen. [*L. umbilicatus* n. sp.], *Paraeusandalum* n. gen. [*P. chilensis* n. sp.], *Eusandalum* Ratzeburg, *Chirolophus* Haliday, *Calosota* Curtis, *Balcha* Walker, and *Tanythorax* n. gen. [*T. spinosus* n. sp.], and three genera in Metapelmatinae - *Metapelma* Westwood, *Neanastatus* Girault, and *Lambdobregma* n. gen. [*L. schwarzii* (Ashmead) n. comb.]. Representatives of the four eupelmid subfamilies, and of Cleonyminae (Pteromalidae), Encyrtidae, and Aphelinidae, are studied to determine distribution of 17 characters of adults, and observed character-state distribution used to hypothesize monophyly and relationships of the taxa. Distribution of states of another 17 characters of adults is analyzed only for adults of Calosotinae or Metapelmatinae for futher evidence of intergeneric relationships in these two subfamilies. Character states are illustrated by scanning electron photomicrographs, and distribution of states and hypotheses of groundplan states for each higher taxon are summarized in two tables. Phylogenetic relationships and hypotheses of monophyly are

proposed using inferred synapomorphic states, with hypotheses of character-state evolution and intergeneric relationships in Calosotinae and Metapelmatinae illustrated by separate cladograms. Monophyly of Eupelmidae + Encyrtidae is supported by a single character state that is not considered to be a reliable synapomorphy. No character states support monophyly of Eupelmidae; rather, Eupelmidae is indicated as a grade-level taxon, with membership determined by similar suites of apomorphic states that function to enhance jumping ability. Eupelmidae is indicated as minimally paraphyletic because monophyly of Tanaostigmatinae + Encyrtidae is supported by three character states, structure of the transscutal articulation, an elongate mesoscutal process for pl_2-t_2c, and encyrtiform eggs. The genus *Cynipencyrtus* Ishii, recently transferred from Encyrtidae to Tanaostigmatinae, is tentatively hypothesized as the sister group of Encyrtidae based on transverse dorsal axillar surfaces. Relationships between Calosotinae, Metapelmatinae, and Eupelminae, and between these and Tanaostigmatinae + Encyrtidae, remain unresolved because of insufficiency of the analysis.

5.2 Introduction

Walker (1846) first recognized Eupelmidae as a family in Chalcidoidea, but without giving reasons or characters for his taxon. He listed seven genera as consitituting the family, and another five genera, which are now assigned to Cleonyminae (Pteromalidae), were stated as "nearly allied" to Eupelmidae. Eupelmidae was first diagnosed and distinguished from the family Encyrtidae by Förster (1856), though Ashmead (1897, 1900, 1904) included eupelmids as a subfamily of Encyrtidae, along with Encyrtinae and Signiphorinae. He (1900) defined Encyrtidae on the basis of an expanded mesopleuron, saltatorial mesotibial spur, and a large triangular prepectus (mesepisternum *sensu* Ashmead), and distinguished Eupelminae from the other two subfamilies on the basis of a usually elongate marginal vein, and a usually non-convex mesoscutum with more or less distinct notauli (parapsidal furrows *sensu* Ashmead). Ashmead (1904) also recognized two tribes in Eupelminae, Eupelmini and

Tanaostigmini (*sic*), the latter tribe distinguished on the basis of a convex mesonotum and particular form of the notauli.

Other than ranking of the respective taxa, little changed in classification of eupelmids until Bouček (1958) organized the genera of Eupelminae into Eupelminae *s. s.* and his new subfamily Calosotinae. He distinguished the latter subfamily primarily on form of the mesoscutum (convex anteriorly, flattened posteriorly, and wide so as to be distinctly shoulder-like on either side of the pronotum), but also noted that in contrast to eupelmines, calosotines were always fully winged and there was little sexual dimorphism in thoracic structure. Bouček considered Calosotinae to be the more "primitive" of the two subfamilies, which seemed to be related to Cleonyminae (Pteromalidae) through several cleonymine genera, in particular *Oodera* Westwood, though the exact relationships were unknown to him.

Recognition of Calosotinae by Bouček (1958) was a major contribution toward a more natural classification of eupelmids, but for the most part our knowledge of correct phyletic relationships and classification of eupelmids is little advanced from the early works of Walker, Förster, and Ashmead. For example, similar to the thinking of Walker (1846) and Bouček (1958), Graham (1969b) stated that the genus *Oodera* forms "a link between Eupelmidae and Cleonyminae (Pteromalidae), having some characters peculiar to both", and he concluded that "these two groups must I think have originated from a common stock" (p. 36). Graham differed from Bouček (1958) in his views on the systematic position of *Oodera*. He "doubted" proper classification of *Oodera* in Cleonyminae and in his key to families of Chalcidoidea keyed the genus out in Eupelmidae. He also suggested that Eupelmidae might be united with Pteromalidae as one proposal for establishing "a more mature classification" of Chalcidoidea through reduction in number of recognized families. The views of Riek (1970) on classification of eupelmids were more similar to those of Ashmead (1904). Riek included Eupelminae (inclusive of calosotines) and Tanaostigmatinae (Tanaostigmodinae *sensu* Riek) as two of five subfamilies in Encyrtidae, the family being united on the basis of modifications of the middle legs for jumping. The classification of Burks (1979), on the other hand, is almost diametrically opposed to that of Riek (1970). Burks stated (p. 878) that "all eupelmids agree in possessing an array of characters that indicate that they and encyrtids diverged separately from the evolutionary stem of chalcidoids at a remote time in the development of the superfamily", so that he recognized eupelmids as a distinct family, with Eupelminae, Calosotinae and Tanaostigmatinae all as subfamilies.

LaSalle (1984) was the first to specifically investigate monophyly of Encyrtidae and Eupelmidae, and to examine relationships between higher taxa based on nearest common ancestor, proposed on the basis of derived character states shared between members of the taxa. He treated tanaostigmatines as a family level taxon, and hypothesized that they and Eupelmidae + Encyrtidae form a monophyletic assemblage based on three proposed synapomorphies. Tanaostigmatids (*sensu* LaSalle) were hypothesized as a monophyletic taxon based on one proposed autapomorphy, and hypothesized as more closely related to encyrtids than to eupelmids on the basis of two proposed synapomorphies. Because LaSalle knew of no autapomorphies for Eupelmidae, excluding tanaostigmatids and encyrtids, he suggested that Eupelmidae was probably paraphyletic relative to the latter two taxa, with Tanaostigmatidae + Encyrtidae not the sister group of Eupelmidae, but more closely related to some more derived subgroup of Eupelmidae. Finally, he considered aphelinids and signiphorids each as family level taxa that were not part of the eupelmid - tanaostigmatid - encyrtid lineage, but without justifying this hypothesis.

This paper has two major aims. The first is to investigate phylogenetics and classification of Eupelmidae. This is accomplished by study of character-state distribution for representatives of all chalcidoid higher taxa that are known to have at least some members with an enlarged acropleuron, the principal state used in the past to distinguish or to relate eupelmids and encyrtids, and in Cleonyminae (Pteromalidae), the purported "ancestral stock" of Eupelmidae. Observed character-state distribution is used to hypothesize the level of apomorphy of states shared between members of the higher taxa, *i. e.*, whether the states are plesiomorphic, synapomorphic, or homoplasous. Previous classifications are then tested on the basis of whether taxa are supported as monophyletic clades by any hypothesized synapomorphies, and whether taxa of increasing hierarchial rank are composed of increasingly more inclusive monophyletic clades.

Higher classification of Chalcidoidea is presently "in a state of confusion" (Heraty and Darling 1984, p. 309). Anywhere from nine (Riek 1970) to twenty-one (Peck 1963) families are recognized, and a new classification is proposed with each new catalog or major publication about chalcidoids (*cf.* Nikolskaya 1952, Peck 1963, Peck *et al.* 1964, Graham 1969b, Riek 1970, Gordh 1979, Yoshimoto 1984). I agree with Heraty and Darling (1984) that documentation of monophyletic taxa in Chalcidoidea should be a high priority prior to a revised classification of the superfamily. I therefore do not use any new familial classification based on the results of this study, but do establish a new subfamily in Eupelmidae, Metapelmatinae, for *Metapelma* Westwood, *Neanastatus* Girault, and a newly proposed genus, *Lambdobregma*. Members of these taxa were previously classified in Eupelminae, and establishing a new subfamily for them was necessary to establish Eupelminae as a monophyletic taxon. I otherwise follow the subfamilial classification of Eupelmidae presented by Burks (1979).

The second major aim of this paper is to revise the world genera of Calosotinae and Metapelmatinae. Bouček (1967) gave character states to distinguish members of some genera of Calosotinae in his revision of the Palearctic species of *Eusandalum* Ratzeburg, but gave no formal revision or key to genera. Members of Calosotinae and Metapelmatinae are very diverse in most external and internal characters of the mesothorax, on which familial and subfamilial classification of Eupelmidae is based. Consequently, it was necessary to accurately determine character states possessed by members of the two subfamilies, through revision of the genera, prior to phylogenetic analyses. Mesothoracic structure of members of Eupelminae is also exceedingly diverse, primarily because of sexual dimorphism, but I previously described differences in external and internal mesothoracic structure of male and female eupelmines (Gibson in press, c).

5.3 Materials and Methods

5.3.1 Materials

The list below details collections examined for this study, acronyms used for the collections, and curators who provided loans or access to collections in their care. The symbol "t" indicates a collection that contains primary type material of Calosotinae or Metapelmatinae, and an asterisk (*) indicates a collection that was examined. Consequently, collections designated only by a "t" were not examined, but the acronyms used in the text to indicate location of type material.

AEI (t*)	American Entomological Institute, Gainesville, Florida, USA (H. Townes).
AMUA (t)	Aligarh Muslim University, Aligarh, India.
BMNH (t*)	British Museum (Natural History), London, England (Z. Bouček and J. Noyes).
BPBM *	Bernice P. Bishop Museum, Honolulu, Hawaii, USA (G. Nishida).
CAS (t*)	California Academy of Sciences, San Francisco, California, USA (P. Arnaud and W. Pulawski).
CDAS *	California Department of Food and Agriculture, Sacramento, California, USA (M. Wasbauer).

CMP *	Carnegie Museum, Pittsburgh, Pennsylvania, USA (G. Ekis and G. Wallace).
CNC (t*)	Canadian National Collection, Agriculture Canada, Ottawa, Ontario, Canada (C. Yoshimoto).
CU (t*)	Cornell University, Ithaca, New York, USA (D. Darling and J. Schafrik).
DEI (t*)	Institute für Pflanzenschutzforschung [formerly Deutsches Entomologisches Institut], Kleinmachnow, Eberswalde, DDR (J. Oehlke).
FSCA *	Florida State Collection of Arthropods, Florida State Department of Agriculture and Consumer Services, Gainesville, Florida, USA (J. Wiley).
GPC *	M. J. Gijswijt collection (private), Ankeven, Netherlands.
IEEM (t)	Instituto Espanol de Entomologiá, Madrid, Spain.
IML (t*)	Fundación e Insituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina (P. Fidalgo).
INHS *	Illinois Natural History Survey, Champaign Illinois, USA (W. LaBerge).
IRSN *	Institut Royal des Sciences Naturelles, Brussels, Belgium (P. Dessart).
KHPC (t*)	Karl-J. Hedqvist collection (private), Stockholm, Sweden.
LACM *	Los Angeles County Museum of Natural History, Los Angeles, California, USA (R. Snelling).
MAKB (t)	Zoologisches Forschungsinstitut und Museum "Alexander Koenig", Bonn, BRD.
MBR (t)	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

MCZ *	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (N. Stone).
MHNG (t*)	Muśum d'Histoire Naturelle, Geneva, Switzerland (I. Löbl).
MLP (t*)	Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina (L. DeSantis).
MNHP (t*)	Muśum National d'Histoire Naturelle, Paris, France (S. Kelner-Pillault).
MPM (t*)	Milwaukee Public Museum, Milwaukee, Wisconsis, USA (G. Noonan).
MRAC *	Musée Royal de l'Afrique Centrale, Tervuren, Belgium (E. De Coninck).
MSNG (t*)	Museo Civico di Storia Naturale, Genoa, Italy (R. Poggi).
MSNM (t)	Museo Civico di Storia Naturale, Milan, Italy.
MSNV *	Museo Civico di Storia Naturale, Venice, Italy (A. Giordani Soika).
MSU *	Mississippi State University, Mississippi State, Mississippi, USA (R. Brown).
MSUE *	Michigan state University, East Lansing, Michigan, USA (R. Fischer).
NHMV (t)	Naturhistorisches Museum, Vienna, Austria (M. Fischer).
NMVM (t)	National Museum of Victoria, Abbotsford (formerly Melbourne), Victoria, Australia.
NRS (t*)	Naturhistoriska Riksmuseet, Stockholm, Sweden (K.-J. Hedqvist).
ODAS *	Oregon Department of Agriculture, Salem, Oregon, USA (R. Westcott).
OSU (t*)	Ohio State University, Columbus, Ohio, USA (C. Triplehorn).
QMB (t)	Queensland Museum, Brisbane, Australia.
RNHL *	Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands (C. van Achterberg).
SAMA (t)	South Australian Museum, Brisbane, Australia.

TAMU *	Texas A & M University, College Station, Texas, USA (S. Merritt).
TMB (t*)	Termszettudományi Múzeum, Budapest, Hungary. (J. Papp Jenő).
UAT (t*)	University of Arizona, Tucson, Arizona, USA (F. Werner).
UCB *.	Essig Museum of Entomology, University of California, Berkeley, California, USA (L. Caltagirone).
UCD *	University of California, Davis, California, USA (R. Schuster).
UCLA (t*)	University of California, Los Angeles, California, USA (H. Hespenheide).
UCR *	University of California, Riverside, California, USA (S. Frommer, J. Hall, J. LaSalle, J. Woolley, and J. Huber).
UGO *	University of Guelph, Guelph, Ontario, Canada (J. Heraty and D. Pengelly).
UMO (t)	University Museum, Oxford University, Oxford, England.
USNM (t*)	National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA (E. Grissell and M. Schauff).
UZIL (t*)	Universitets Zoologiska Institut, Lund, Sweden (R. Danielsson).
ZBPC (t)	Zdenek Bouček collection (personal), London, England.
ZIL (t)	Zoological Institute, Academy of Sciences, Leningrad, USSR.
ZMHB (t)	Zoologisches Museum, Humboldt-Universität, East Berlin, DDR.
ZMUC *	Zoologisk Museum, Universitets Copenhagen, Copenhagen, Denmark (B. Petersen).
ZSBS *	Zoologische Sammlungen des Bayerischen Staates, Munich, BRD (F. Bachmaier).
ZSIC (t)	Zoological Survey of India, Calcutta, India.

5.3.2 Methods

5.3.2.1 Taxonomic Analysis

Treatment of taxa. Descriptions of taxa are divided into three sections corresponding to the primary body regions of the adult, *viz.*, head, mesosoma and metasoma, and major structures or regions of the body are indicated in boldface type within each section. This format is to aid rapid comparison of parts of [illegible] between different taxa.

Only the [illegible] described for new genera, but if specimens representing other undescribed [illegible] to me this is indicated in the section on "Generic diversity". Character states that [illegible] to be of specific value and readily distinguish specimens of the undescribed species from the type species are given. Descriptions of the type species of new genera include separate descriptions of the two sexes. Description of the female is based on the holotype, whereas description of the male is based on the allotype. Known variation in character states, based on differences in the paratypes, are discussed in the section on "Variation".

A species list is given for previously described genera and includes all species that were either described in or transferred to the genus, plus *nomina nuda*. The nomenclatural history of each name is given, including the authority for transfers (comb.) or synonyms (syn.). The latter are included in the list of references, but references to original descriptions are not. Depository of primary type material is listed for each species, if known, and if type specimens were examined the species is denoted by an asterisk (*). The country the species was described from is also given, preceded by the respective biogeographic region. Biogeographic regions are indicated by the following abbreviations: N - Nearctic, Nt - Neotropical, P - Palearctic, E - Ethiopian, O - Oriental, A - Australian.

Terms for structure and sculpture. Terms used for parts of the head, including the antennae, follow Bouček (1974), except as clarified in the following section on measurements. Positional terms (dorsal, posterior, etc.) for the head are based on the head being in a hypognathous position. Terms used for parts of the mesothorax, including mesothoracic muscles, are explained in Gibson (in press a, c).

Fused to the metathorax in apocritan Hymenoptera is the **propodeum**, or first abdominal segment. Various authors presently use different terms for the thorax plus propodeum, and abdomen minus first segment. I use **mesosoma** for the thorax + propodeum, and **metasoma** for the abdomen minus first segment, for the reasons given by Johnson (1984). The propodeum is divided into two regions, the median **plical region**, and lateral **callar regions**. The plical region of many eupelmids is differentiated from the callar regions by a furrow or carina mesad of the spiracles, and is either convex or concave relative to the callar regions (Figs. 5.63-5.66). If not so delineated, the plical region [illegible] entire region between the spiracles (Fig. 5.62). The **propodeal foramen** is the variedly incurved posterior edge of the propodeum anterior to the first metasomal tergum (Mt1), the **petiole**. The metasoma is composed of eight or nine terga, abbreviated "Mt1, Mt2, Mt3 [illegible]". Mt9 is either independent or fused to Mt8 as the **syntergum** (= epipygium of some authors). Number of terga, or the tergum being referred to in the description should be determined by counting anteriorly and posteriorly from Mt7, the tergum possessing the single pair of metasomal spiracles, except for females of Eupelminae, the terga of which should be determined by counting anteriorly from Mt8, the tergum possessing the cerci. This method of counting is used because some Metapelmatinae and Calosotinae have Mt9 independent from Mt8, and the cerci on Mt9 or in the membrane between Mt8 and Mt9 (Figs. 5.108, 5.109), whereas others have Mt8 and Mt9 fused, and then the cerci on Mt8 (Fig. 5.110), but female eupelmines, which have Mt8 and Mt9 fused, have Mt7 concealed dorsally by Mt6 in some species so as to be easily overlooked (*cf.* Figs. 5.111, 512). The **hypopygium** (= subgenital plate of some authors) is the last visible **sternum**.

Most terms for sculpture have a range of meaning in literature on Hymenoptera, with the descriptor used depending partly on the magnification the sculpture was viewed at, relative differences in coarseness, and preferences of the author. "Coriaceous", "alutaceous", and "reticulate" are three terms in particular with multiple meanings (*cf.* Eady 1968, Harris 1979). I use "coriaceous" and "reticulate" to denote two main classes of sculpture. **Coriaceous** defines a mesh-like pattern (cells having multiple sides) in which the cells are flat and distinguished from each other by fine, impressed lines. **Reticulate** defines a mesh-like pattern in which the cells are shallowly concave so as to be separated by raised lineations. Either sculpture is **isodiametric** if the sides of the mesh are more or less equal, but **elongate** if the cells are longitudinal, or **transverse** if the cells are lengthened and oriented at a right-angle to the long axis of the body. Minute coriaceous sculpture appears **granulate** under lower magnifications, and if reticulations are more or less circular to oval, rather than multi-sided, the sculpture is **punctate**, or if the punctures are very small, **punctulate**. Deeply concave and relatively large reticulations are called **alveolae (alveolate sculpture)**, whereas deeply concave and relatively large punctures are called **umbilications (umbilicate sculpture)**. **Alutaceous** refers to sculpture that is similar to coriaceous, but the cells are lengthened and irregular in shape, and often impressed along one of the long sides and convex along the other so that the sculpture appears somewhat undulatory or shingle-like. **Rugulose** refers to an irregular roughened sculpture in which discrete cells are not obvious. Intermediate sculpture is denoted by hyphenating any two of the above descriptors.

Measurements. Length of specimens is given in centimeters, but all other measurements are relative, measured with an ocular grid having 100 divisions per centimeter. Measurements were taken at different magnifications, but all converted as if measured at 96X. Because all measurements are standardized, ratios can be determined between any two body parts. Length (L), width (W), and height (H) measurements are obtained by rotating the specimen so that both ends of the object measured are equidistant from the objective of the microscope, *i. e.*, both ends are equally in focus. This is important in order to avoid parallax problems encountered when measuring a three dimensional object with a microscope.

The following measurements, and abbreviations for structure or measurements, are used in descriptions (numbers correspond to measurements illustrated in figures):

1. **Head height (HH)** - maximum distance from ventral edge of clypeus to dorsal edge of head (excluding posterior ocelli), in frontal view (1, Fig. 5.3).
2. **Head width (HW)** - maximum distance across head in frontal view (2, Fig. 5.3).
3. **Head length (HL)** - maximum distance across head in lateral view (excluding sculptural protuberances of inner orbits) (3, Fig. 5.6).
4. **Eye height** - maximum distance from ventral to dorsal margin of eye in lateral view (4, Fig. 5.6).
5. **Eye width** - maximum distance at a right-angle to the long axis of the eye in lateral view (5, Fig. 5.6).
6. **Distance between eyes below** - distance between each intersection of malar sulcus and ventral eye margin, in frontal view (6, Fig. 5.3).
7. **Distance between eyes above** - minimal distance between eyes in dorsal view (7, Fig. 5.4).
8. **Ocular ocellar line (OOL)** - minimal distance between outer margin of posterior ocellus and inner eye margin (8, Fig. 5.4).
9. **Lateral ocellar line (LOL)** - minimal distance between inner margin of posterior ocellus and median ocellus (9, Fig. 5.4).
10. **Posterior ocellar line (POL)** - minimal distance between inner margins of posterior ocelli (10, Fig. 5.4).
11. **Malar space** - distance between ventral eye margin at intersection with malar sulcus to edge of oral cavity at intersection with malar sulcus (11, Fig. 5.6).
12. **Genal length** - distance from posterior or ventral margin of eye (where measured indicated in text) to posterior of head.
13. **Distance between torulus and clypeal edge** - distance between ventral edge of clypeus and carina delimiting ventral margin of torulus (13, Fig. 5.10).

14. **Distance between toruli** - minimum distance between carinae delimiting inner margin of each torulus (14, Fig. 5.10).

15. **Distance between torulus and eye margin** - minimal distance between eye margin and carina delimiting outer margin of torulus (15, Fig. 5.10).

16. **Scrobe height** - distance from carina delimiting ventral margin of torulus to dorsal limit of scrobal channel (maximum length to ventral margin of median ocellus) (16, Fig. 5.5).

17. **Scrobe width** - distance across channel where declined from inner orbits (height measurement taken at is indicated in text).

18. **Inner orbit width** - distance from lateral edge of scrobal channel to inner margin of eye (height measurement taken at is indicated in text).

19. **Antennal articles** - **scape** length is the maximum length excluding the **radicle**, and width is the maximum medial width unless otherwise indicated; measurements of all other antennal articles are maximum lengths and widths, with the latter measurement in parenthesis.

20. **Mesoscutum length** - distance from transscutal articulation to anterior edge of mesoscutum at posterolateral angle of pronotum (20, Fig. 5.20).

21. **Mesoscutum width** - maximum distance across mesoscutum when focused at dorsal edge of tegula or junction between mesoscutum and acropleuron (21, Fig. 5.19).

22. **Scutellar-axillar width** - maximum distance across scutellar-axillar complex measured between axillar carinae (22, Fig. 5.19).

23. **Dorsal axillar surface (DAS) width** - maximum distance across DAS from axillar carina to anteromedial angle (23, Fig. 5.19).

24. **Dorsellum length** - maximum medial length of metanotum.

25. **Propodeum length** - maximum medial length of plical region.

26. **Venation** - measurements of the **submarginal vein** (SMV), **marginal vein** (MV), **postmarginal vein** (PMV), and **stigmal vein** (STV) are as illustrated by Graham (1969b).

27. **Legs** - length of tibia and tibial spur is maximum length; tibial width is maximal apical width; tarsomere length is measured along ventral edge, excluding apically projected pegs or

spines, and length of ultimate tarsomere excludes pulvillus and claws.

28. **Metasomal terga (Mt)** - the posterior margins of the terga are variedly incised to outcurved so that length of a tergum is either measured along the midline (M, Fig. 5.107), or paramedially (PM, Fig. 5.107) between the apex of the tergum measured and that of the preceding tergum. The abbreviation "m" or "pm" is included in parenthesis after the measurement to indicate which method was used, and all subsequent terga are likewise measured until otherwise indicated by the alternate abbreviation.

Illustrations. Specimen preparation for scanning electron microscopy (SEM) is as described in Gibson (in press, a). Setae were usually removed during cleaning of specimens for SEM, so that most photomicrographs do not illustrate described setal patterns. SEM illustrations of structure are arranged on the pl[illegible]dy region, beginning with the head.

5.3.2.2 Phylogenetic Analysis

Basis of Analysis. For the purposes of this study, Tanaostigmatinae *s. l.* (including the genus *Cynipencyrtus* Ishii) is included with Calosotinae, Eupelminae, and Metapelmatinae as the family Eupelmidae *s. l.* Analysis of possible phylogenetic relationships between Encyrtidae, Aphelinidae, and the subfamilies of Eupelmidae *s. l.* is based on a study of character states and their distribution in adults of the above taxa and in adults of Cleonyminae (Pteromalidae). The latter taxon is used as the outgroup, and members are considered to exhibit the plesiomorphic state for each character unless otherwise stated and justified.

Because chalcidoids other than those listed above are omitted from the analysis, any evidence for relationships with these is ignored. This is an important weakness of the analysis because Eupelmidae + Encyrtidae may represent a grade of structure rather than a clade. Both families are recognized as higher taxa primarily because of structures that are similarly, distinctively modified to serve a similar function, that of jumping. In a previous study I described the skeletomuscular system of males and females of Eupelminae, and correlated differences in external mesothoracic structure with differences in musculature, and differences of musculature and structure with differences in function between the sexes (Gibson in press, c). The apomorphic mesosomal structure of female eupelmines was shown to be the result of an apomorphic jumping mechanism in which parts of the independent flight and jumping mechanisms of males are integrated into a single mechanism for improved jumping capability. Members of Calosotinae, Metapelmatinae, Tanaostigmatinae, Encyrtidae, and some members of Cleonyminae and Aphelinidae share different combinations of the apomorphic states that are correlated with jumping. However, the shared apomorphic states are not the result of newly evolved or novel structures, but merely the result of modifications to previously existing structures. Possibly, therefore, similarity in structure is not the result of common ancestry, but results from similar, independent modifications to enhance jumping ability, *i. e.*, homoplasy. Detailed analyses of the skeletomuscular system of members of each taxon might be sufficient to distinguish synapomorphy from homoplasy. However, these analyses have yet to be done, and exclusion of other chalcidoids from the analysis ignores any evidence of alternative relationships that could indicate homoplasy in the characters analyzed.

A second weakness in the analysis is the relatively superficial analysis of character-state distribution in Cleonyminae, Tanaostigmatinae, Aphelinidae, and Encyrtidae. Character-state distribution for Calosotinae, Metapelmatinae, and Eupelminae is based on extensive materials from all biogeographic regions, but that given for the first four taxa is based only on published data and on study of representative taxa. An attempt was made to examine representatives of 'unusual' genera, when known, but analyses of the latter type are prone to omit uncommon states for taxa, particularly for characters with little published information. If the uncommon states are plesiomorphic, ignorance of their existence may result in incorrect [illegible] groundplan states of a taxon, and lead to inaccurate hypotheses of transformation series, synapomorphy, and relationship.

5.4 Higher classification of Eupelmidae

Four subfamilies are included in the family Eupelmidae for the purposes of this study, Eupelminae Walker, Calosotinae Bouček, Metapelmatinae new subfamily, and Tanaostigmatinae Ashmead. This classification follows Burks (1979), except that *Metapelma* Westwood, *Neanastatus* Girault, and *Zaischnopsis schwarzii* (Ashmead) are excluded from Eupelminae. The subfamily Metapelmatinae is newly established for members of these three taxa, with the new genus *Lambdobregma* proposed for *Z. schwarzii*.

Phylogenetic analysis of relationships between the four subfamilies listed above, and Cleonyminae (Pteromalidae), Aphelinidae, and Encyrtidae, indicates that the classification used probably is indefensible. Eupelmidae is probably a paraphyletic, grade-level taxon. However, exact relationships between the taxa are not clarified in this study, and conclusions are both tentative and preliminary.

One consequence of the classification used is that Eupelmidae can not be defined by any single character state or combination of states without explicitly excluding some taxa whose members have one or more of the states, and including some taxa whose members lack one or more of the states. Though diagnosis of the family is difficult, most eupelmids can be distinguished from other chalcidoids by using the keys provided by Peck *et al.* (1964), Graham (1969b), or Yoshimoto (1984). Male eupelmines are the most difficult eupelmids to identify correctly to family because they are very similar in structure to many male pteromalids, particularly those of the subfamily Cleonyminae.

Because a new subfamily is established in Eupelmidae, comparable diagnoses of the four included subfamilies are given below, plus a key to distinguish individuals of the four subfamilies from each other and from other chalcidoids. External and internal characters are used in the key, but whenever possible external characters are listed first.

5.4.1 Key to distinguish subfamilies of Eupelmidae from other Chalcidoidea

1 Acropleuron inevident, or as small subalar region that is at most as large as mesepimeron (Figs. 5.41, 5.42, 5.58). 2

1' Acropleuron conspicuously larger than mesepimeron, which is small or absent (Figs. 5.43-5.45, 5.47-5.55, 5.57, 5.59) 4

2(1) Mesocoxal fossae as separate orifices; mesotrochantinal plate extended to metasternum (Figs. 5.81, 5.82). .... most Chalcidoidea

2' Mesocoxal fossae continuous, united by intercoxal membrane; mesotrochantinal plate not extended to metasternum (Fig. 5.83). 3

3(2') Transscutal articulation deeply V-shape, dorsal axillar surface conspicuously advanced anterior to scutellum; lower mesepisternum with small membranous region anterior to each mesocoxa (*cf.* Fig. 5.76); males and females. .... *Oodera* Westwood [Pteromalidae: Cleonyminae]

3' Transscutal articulation transverse, dorsal axillar surface not advanced anterior to scutellum (Fig. 5.39); lower mesepisternum transverse along base of mesocoxae (*cf.* Fig. 5.69); males only. .... Eupelminae [pt.]

4(1') Mesocoxal insertion at or anterior to midline of acropleuron (Figs. 5.59, 5.73, 5.74); prepectus with separate lateral prepectal surface and internal prepectal strut (Fig. 5.60), externally not protuberant anterior to mesothoracic spiracle (Fig. 5.59) .... Encyrtidae

4' Mesocoxal insertion distinctly posterior to midline of acropleuron (Figs. 5.43, 5.45, 5.47-5.55, 5.67-5.70, 5.72), or, if near midline (Figs. 5.57, 5.71), then prepectus as single sclerite that is conspicuously protuberant anterior to mesothoracic spiracle (Fig. 5.57). 5

5(4') Antenna with 9 or less articles; notauli percurrent and widely separate at transscutal articulation (Fig. 5.37); mesotrochantinal plate extended to metasternum, mesocoxal fossae separate (Fig. 5.80). .... Aphelinidae [pt.]

5' Antenna with 10-13 articles; notauli absent (Figs. 5.25, 5.27), or not extended to transscutal articulation (Figs. 5.17-5.24, 5.38), or if percurrent then contiguous or subcontiguous at transscutal articulation (*cf.* Fig. 5.31); mesotrochantinal plate not extended to metasternum, mesocoxal fossae united by intercoxal membrane.. 6

6(5') Lower mesepisternum transverse along base of mesocoxae (Figs. 5.69, 5.70, 5.72), or at most with small cavity between mesepisternum and each mesocoxa (Fig. 5.68)... 7

6' Lower mesepisternum with membranous region anterior to each mesocoxa (Figs. 5.67, 5.71, 5.75-5.79). 8

7(6) Pronotum subtriangular in dorsal view (Figs. 5.25, 5.27); lower mesepisternum distinctly longer than wide in ventral view (Figs. 5.68-5.70); mesotergal-mesotrochanteral muscle (t_2-tr_2) reduced (Figs. 5.101a, 5.102-5.104)... Metapelmatinae

7' Pronotum subrectangular in dorsal view (Fig. 5.33); lower mesepisternum wider than long in ventral view (Fig. 5.72); t_2-tr_2 large (*cf.* Figs. 5.99, 5.100)........... .... *Cynipencyrtus* Ishii [Tanaostigmatinae *s. l.*]

8(6') Prepectus conspicuously protuberant anterior to mesothoracic spiracle (Fig. 5.57); pronotum vertical, linear in dorsal view (Fig. 5.31)............................ .... Tanaostigmatinae *s. s.*

8' Prepectus not protuberant anterior to mesothoracic spiracle (Figs. 5.47-5.52), or only slightly so (Fig. 5.45); pronotum conspicuous in dorsal view (Figs. 5.17-5.23, 5.38). 9

9(8') Mesotarsus ventrally with row(s) of pegs along anterior and posterior edges (Fig. 5.98), or with dense pad of setae (Fig. 5.97); mesopleuron without exposed mesepimeron, acropleuron completely expanded to metapleuron (Fig. 5.52); mesoscutum with V-shape, furrow-like notauli in most taxa (Fig. 5.38); mesotergal-mesotrochanteral muscle (t_2-tr_2) tendon-like and extended from anteroventral angle of lateral axillar surface (Fig. 5.105); females only..Eupelminae [pt.]

9' Mesotarsus ventrally without pegs (Fig. 5.91), or with single row along posterior edge (Fig. 5.92), or with row along anterior and posterior edges (Fig. 5.93), but then with mesepimeron (Fig. 5.48) or at least lower mesepimeron (Figs. 5.49-5.51) exposed, or with notauli subparallel on dorsal surface of mesoscutum (Fig. 5.24), or both; t_2-tr_2 large, extended from within dorsal axillar surface and from axillar phragma (Fig. 5.100); males and females..................Calosotinae

5.4.2 Diagnosis of subfamilies of Eupelmidae

5.4.2.1 Metapelmatinae new subfamily

Type genus: *Metapelma* Westwood. Present designation.

Included genera: *Metapelma* Westwood, *Neanastatus* Girault, *Lambdobregma* n. gen.

Diagnosis (M = *Metapelma* Westwood, N = *Neanastatus* Girault, L = *Lambdobregma* n. gen.). **HEAD** varied in form, more or less lenticular in lateral view, with frons evenly curved to about level of posterior ocelli and vertex narrow or indistinct (M & N) (Figs. 5.13, 5.14), or oval (Fig. 5.16), with vertex distinct from frons anterior to median ocellus (L) (Fig. 5.15); vertex and temples rounded into occiput (M & L) (Figs. 5.14, 5.16), or carinate (N) (Fig. 5.13); scrobes as short vertical furrow above each torulus (M & N) (Figs. 5.13, 5.14), or Λ -shape convergent above toruli and coextensive as single depression or channel above interantennal region (L) (Fig. 5.15); upper inner orbits not distinguished by region of differentiated sculpture; ocelli in elongate to equilateral triangle; maxillary palpus 4-articled; labial palpus 3-articled. **Antenna** 13-articled with 3-articled clava (M & L), or 10-articled with 2-articled clava (N); anellus elongate-cylindrical and not differentiated from funiculars, or transverse ring-like and conspicuous from funiculars; males with filiform funicle.

MESOSOMA not sexually dimorphic in characters correlated with flight and jumping mechanisms. **Pronotum** (Figs. 5.25, 5.27) conspicuous and subtriangular in dorsal view; sides overlapping mesothorax very slightly, base of prepectus and process for pl$_2$-t$_2$c concealed; entire. **Mesoscutum** (Figs. 5.25, 5.27) not wider than posterior of pronotum, mesosoma evenly curved from base of wings to head; posterior edge straight, articulated along entire length of scutellar-axillar complex (M & L), or connected to scutellar-axillar complex by membrane (visible between separate edges of two structures when mesonotum flexed, *cf.* Figs. 5.29, 5.30) (N); sides not recurved as carinate edge or flange; process for pl$_2$-t$_2$c not extended anterior to mesothoracic spiracle (concealed by pronotum); notauli absent (most *Metapelma* with mesoscutum convex anteromedially and depressed posteromedially, with small, triangular, median mesoscutal lobe defined relative to convex lateral lobes, *cf.* females of Eupelminae); parapsidal lines absent (L & N), or as percurrent, ridge-like line of altered sculpture from transscutal articulation at basolateral angle of DAS (M) (*cf.* Figs. 5.25, 5.26). **Scutellar-axillar complex** with varied DAS, large and subtriangular with basomedial angles subcontiguous (M & L) (Figs. 5.25, 5.27), or small, elongate-triangular, and widely separate at basolateral angles of scutellum (N) (Fig. 5.30); scutellum flat to lowly convex, undivided (M & L) (Figs. 5.25, 5.27), or divided mediolongitudinally (N) (Fig. 5.30). **Prepectus** with lateral prepectal surface enlarged subcircular to subquadrate and extended to base of tegula (N) (Fig. 5.54), or subtriangular with apex extended to base of tegula, or not, when mesonotum unflexed, but extended more ventrally and projected over acropleuron when mesonotum flexed (M & L) (Fig. 5.53); frontal prepectal surface flat, or only very slightly recurved over apex of mesoscutal process for pl$_2$-t$_2$c (concealed by pronotum). **Mesopleuron** with acropleuron convexly expanded and extended to metapleuron and metacoxa (L & N) (Fig. 5.54), or with slender mesepimeron between acropleuron and metpleuron (M) (Fig. 5.53); acropleural sulcus extended anteriorly from above base of mesocoxa as subparallel sulci along ventrolateral surface of mesopleuron (L & N) (Figs. 5.68, 5.70), or straight convergent from base of mesocoxa toward discrimen near apex of procoxa (M) (Figs. 5.53, 5.69); mesepimeron absent (L & N), or present and subdivided into larger upper mesepimeron and small lower mesepimeron by transepimeral sulcus (M) (Fig. 5.53); mesepisternum without transepisternal sulcus (M & N), or with straight sulcus parallel with discrimen from midline of mesocoxa (L) (Fig. 5.68); lower mesepisternum longer than wide. **Mesotrochantinal plate** triangular (M) (Fig. 5.84) or subrectangular (N & L) (Figs. 5.85, 5.86), extended posteriorly and partly visible, with small, oblique cavity between lower mesepisternum and each mesocoxa (L) (Fig. 5.68), or, extended internally, with lower mesepisternum transverse along base of mesocoxae (M & N) (Figs. 5.69, 5.70), but with mesocoxae in members of all three taxa unable to rotate out of combined fossa. **Mesotergal-mesotrochantinal muscle** (t_2-tr_2) reduced, differently so for members of each genus as detailed in respective descriptions (Figs. 5.101-5.104). **Wings** fully developed, brachyptery unknown; fore wing setose with variedly developed linea calva (except some species of *Metapelma*); marginal vein elongate. **Legs**. Front leg with one or more short, stout, curved spines on dorsoapical edge of tibia, without denticle-like spicules along dorsal edge. Middle leg with basolateral surface of mesocoxa convexly rounded (L), or incised with distinct cavity between coxa and Λ -shape region formed between lower mesepisternum and acropleuron (Figs. 5.53, 5.54); tibia with row of pegs along anteroapical edge (Fig. 5.94); tarsus ventrally with row of spines along posterior edge and row of pegs (double row in very few species of *Metapelma*) along anterior edge, and with one or more pegs extended along anteroapical edge so that row curved distally (Fig. 5.94). **Propodeum** with plical region rectangular, entire region between spiracles (M & L) (Figs. 5.25, 5.27), or extremely reduced, narrow (Fig. 5.30) and linear between metanotum and metasoma (N) (Fig. 5.29).

METASOMA of females with Mt9 independent from Mt8 (M) (Fig. 5.108), or fused to Mt8 as syntergum (L & N), but in males fused to Mt8; ultimate tergum of females varied in shape and length, but with apex simple and in same plane as rest of tergum; ovipositor sheaths only slightly exserted beyond apex of ultimate tergum (N), or conspicuously so (M & L).

Monophyly. States of five or six characters indicate monophyly of Metapelmatinae. Absence of notauli [Table 5.1, 7(5)] and pattern of mesotarsal pegs [5(3)] are interpreted as the most reliable states. Absence of the specialized mesocoxal articulation [6(2a)] that permits rotation of the mesocoxae also indicates monophyly if absence is the result of secondary loss rather than symplesiomorphy. Structure of the pronotum [11(2a)] may also indicate monophyly of Metapelmatinae, but a more comprehensive survey of pronotal structure in Chalcidoidea is required to determine if pronotal structure is ancestral to that of tanaostigmatines and encyrtids. Presence of mesotibial pegs [12(2)] and a linea calva in the fore wing [15(2)] may also indicate monophyly, but if so, the states are convergent to those possessed by members of other higher taxa [Table 5.1] (see section 5.7.2.2).

5.4.2.2 Calosotinae Bouček

Calosotinae Bouček, 1958: 354. Type genus: *Calosota* Curtis. Original designation.

Calosotinae; Peck *et al*, 1964: 60 (key to subfamily and genera); Bouček, 1967: 261 (subfamily characters and component genera); Hedqvist, 1970: 439 (Ethiopian catalog); De Santis, 1979: 169 (Neotropical catalog); Burks, 1979: 879 (Nearctic catalog).

Diagnosis. **HEAD** (Figs. 5.3-5.12) varied in form, but vertex and temples rounded into occiput; interantennal region variedly convex, with scrobes distinctly Λ -convergent above toruli in most taxa, but at least coextensive as single depression or channel above interantennal region (Figs. 5.3-5.5, 5.7-5.12); upper inner orbits distinguished by band of differentiated sculpture along eye margin or scrobes in many taxa (Figs. 5.3-5.5, 5.7-5.9); ocelli in equilateral to elongate triangle; maxillary palpus 4-articled; labial palpus 3-articled. **Antenna** 11-articled with 1-articled clava, or 13-articled if clava 3-articled by transverse sutures; anellus elongate-cylindrical and not differentiated from funiculars, or transverse ring-like and conspicuous from funiculars; males with funicle filiform or pectinate.

MESOSOMA not sexually dimorphic in characters correlated with flight and jumping mechanisms. **Pronotum** (Figs. 5.17-5.23) conspicuous and campanulate (parallel sided posteriorly, but abruptly convergent to head anteriorly) in dorsal view; sides not overlapping prepectus or mesoscutal process for pl_2-t_2c; entire. **Mesoscutum** (Figs. 5.17-5.24) conspicuously wider than pronotum, with distinct shoulder-like angles on either side of pronotum (except in individuals of *Tanythorax* n. gen.); posterior edge straight, articulated along entire length of scutellar-axillar complex (mesonotum hinge-like bent along transscutal articulation when flexed); sides recurved as carinate or flange-like edge; mesoscutal process for pl$_2$-t$_2$c extended at most slightly anterior to mesothoracic spiracle (most conspicuously so in individuals of *Eusandalum* Ratzeburg); notauli linear, impressed or as line of differentiated sculpture, V-shape convergent within anterior 0.5 of mesoscutum (Figs. 5.17-5.21) or paramedially subparallel dorsally (Fig. 5.24), but not percurrent; parapsidal lines absent, or as line of effaced or minute sculpture near anterior edge of mesoscutum adjacent to notauli (Fig. 5.24). **Scutellar-axillar complex** with varied DAS, subtriangular with contiguous basomedial angles (Fig. 5.17), to linear and widely separate at extreme basolateral edges of scutellum (Fig. 5.23); scutellum flat to lowly convex, not medially divided. **Prepectus** with lateral prepectal surface subtriangular, apex extended posteriorly toward tegula when mesonotum unflexed (Fig. 5.43, 5.45), but more ventrally projected over acropleuron when mesonotum flexed (Fig. 5.48, 5.49), and extended to base of tegula, or not, when mesonotum unflexed (*cf.* Figs. 5.45, 5.47, 5.51); frontal prepectal surface flat, or at most very slightly recurved over apex of mesoscutal process for pl$_2$-t$_2$c (*cf.* Figs. 5.24, 5.46). **Mesopleuron** (Figs. 5.43-5.45, 5.47-5.51) with acropleuron flatly to convexly enlarged, extended at least 0.5 length mesopleuron, and in most genera extended to metapleuron at least dorsally; acropleural sulcus variedly recurved anteriorly from above mesocoxa, but abruptly angled toward prepectus as straight or posteriorly curved sulcus or line in many taxa (Figs. 5.44, 5.47, 5.67); mesepimeron present or absent, lower mesepimeron exposed in numerous taxa, but upper mesepimeron in only a few; mesepisternum without transepisternal line or sulcus, or if present directed anteriorly from anterolateral corner of mesocoxa (Fig. 5.48); lower mesepisternum quadrate to longer than wide. **Mesotrochantinal plate** (Figs. 5.67, 5.75-5.77) extended horizontally with trochantinal lobes, with membranous region anterior to each mesocoxa visible if coxae not rotated anteriorly out of combined fossa (Figs. 5.67, 5.75-5.77). **Mesotergal-mesotrochantinal muscle** (t$_2$-tr$_2$) (Fig. 5.100) large and tubular, from DAS (t$_2$-tr$_2$a) and large axillar phragma (t$_2$-tr$_2$b), inserted into golf tee-like mesotrochantinal pedicel ventrally in body cavity. **Wings** fully developed, brachyptery unknown; fore wing superficially glabrous to entirely setose, with linea calva in only very few species; marginal vein elongate in most species. **Legs.** Front leg with one or more short, stout, curved spines on dorsoapical edge of tibia (Fig. 5.89), and with denticle-like spicules along dorsal edge of tibia in many species (Fig. 5.88). Middle leg with basolateral surface of coxa convexly rounded, without cavity between coxa and mesopleuron; tibia with row of pegs along anteroapical edge in only very few species; tarsus ventrally with equally developed row of seta-like spines along anterior and posterior edges (Fig. 5.91), with row of spines along anterior edge and row of pegs along posterior edge (Fig. 5.92), or with equally developed row of pegs along anterior and posterior edges (Fig. 5.93). **Propodeum** with plical region as entire region between spiracles, undifferentiated from callar regions (Fig. 5.62), or differentiated as narrower region by furrow or carina mesad of each spiracle (Figs. 5.63-5.66).

METASOMA of females with Mt9 independent (Fig. 5.109), or fused to Mt8 as syntergum (Fig. 5.110), but in males fused to Mt8; ultimate tergum of females varied in shape and length, but with apex simple and in same plane as rest of tergum; ovipositor sheaths only slightly exserted beyond apex of ultimate tergum.

Monophyly. Two states indicate possible monophyly of Calosotinae, form of the parapsidal lines [Table 5.1, 13(2)], and mesoscutal lateral lobes abruptly angled as distinct 'shoulder' on either side of pronotum [11(1b)]. However, members of at least two genera of Cleonyminae (Pteromalidae) have the same form of the parapsidal lines as do calosotines. Consequently, the state could be symplesiomorphic rather than synapomorphic. Furthermore, relative structure of the pronotum and mesoscutum of calosotines could be ancestral to that of members of some other higher taxa (see section 5.7.2.1).

5.4.2.3 Eupelminae Walker

Eupelmidae Walker, 1846: 114. Type genus: *Eupelmus* Dalman. By inference in context from formation of family-group name.

Nomenclatural history of this subfamily is not included, but will be given in a subsequent generic revision.

Extreme sexual dimorphism, particularly of mesosomal structures, characterizes this subfamily. Structural diversity is also enhanced by a predilection toward brachyptery in females, which in many taxa is correlated with distinctive modifications of the dorsum of the mesosoma. As a result, structural diversity of Eupelminae is considerably more than in other eupelmid subfamilies. Most structures of males are also much more conservative than in females, *i. e.*, exhibiting much less structural diversity, so that generic classification is based almost entirely on females.

Sexual dimorphism in mesosomal characters, correlated with the two different flight and jumping mechanisms of males and females, is described in detail in Gibson (in press, c). The following subfamilial description describes additional regions of the body, and attempts to encompass most variation in the structures described, though this is almost impossible in any concise description of the subfamily.

Diagnosis. HEAD extremely varied in structure (differences important in recognition of some genera, and in many instances enabling generic placement of males because of a similar head structure); scrobes of females distinctly ∧ -shape convergent above toruli because of triangular interantennal region, or coextensive dorsally as single depression or channel, but some males with only short vertical furrow above each torulus; upper inner orbits not distinguished by band of differentiated sculpture; ocelli in elongate to wide triangle in most individuals, but some males with very flat ocellar triangle; maxillary palpus 4-articled; labial palpus 3-articled. **Antenna** 13-articled with 3-articled clava; anellus transverse ring-like to slightly longer than wide, differentiated from funiculars unless these reduced; males with filiform funicle, except pectinate in *Anastatus (Cladanastatus) umae* Bouček.

MESOSOMA sexually dimorphic in characters correlated with flight and jumping mechanisms (see Gibson in press, c). **Pronotum** of females with sides inconspicuously parallel beside each spiracle (convergent almost from mesoscutum) (Fig. 5.38), to elongate parallel-sided (conspicuously campanulate), and in many taxa mediolongitudinally divided or with light-colored line (declined or concave medially in many instances if divided)(Fig. 5.38), with dorsal transverse ridge or conically produced dorsomedially in some females; pronotum of males similar to females, except at most with mediolongitudinal light-colored line or sulcus, or with dorsal surface abruptly declined from mesoscutum, short to almost vertical and inapparent in dorsal view (Figs. 5.39, 5.41); sides not overlapping base of prepectus or mesoscutal process for pl_2-t_2c in either sex. **Mesoscutum** at most slightly wider than posterior of pronotum, without distinct shoulder-like angles (Fig. 5.38); posterior edge straight in females, slightly convex in some males, but articulated along entire length of scutellar-axillar complex in both sexes; lateral edge abruptly reflexed as distinct flange in females (Fig. 5.38), but only parascutal edge slightly recurved as carina in males; mesoscutum of males relatively evenly convex, notauli obscure in some taxa, but distinctly impressed, percurrent, and widely separate at transscutal articulation in most (Fig. 5.39), without parapsidal lines; females much more varied in mesoscutal structure, most alate individuals with variedly convex triangular median mesoscutal lobe defined by shallow, posteriorly convergent furrows in positions homologous with notauli, and with region posterior to median lobe flat or variedly concave relative to more convex or ∧ -shape angulate lateral lobes (Fig. 5.38), but few alate females with distinct, impressed, linear notauli; most alate females with parapsidal lines as ridge-like line or more pronounced ∧ -shape angulation extended anteriorly from transscutal articulation from near center or outer angle of DAS (Fig. 5.38); brachypterous females as described above, or with dorsal surface of mesoscutum almost flat, with or without parapsidal lines or angulations, or with lateral lobes, median lobe, or both, variedly Λ -shape angulate to abruptly knife-like ridged. **Scutellar-axillar complex** of males (Fig. 5.39) with DAS triangular, somewhat longer than wide, conspicuously declined posteriorly, and with basomedial angles contiguous to separate by up to 0.5 width of DAS; scutellum or entire dorsal surface of complex distinctly convex, with scutellum entire; females (Fig. 5.38) also with triangular DAS of similar dimensions and separation described for males, but with dorsal surface of complex or at least DAS flattened in most alate individuals, many brachypterous females with DAS and scutellum conspicuously elongate-narrow, either flat or with DAS, scutellum, or both, mediolongitudinally, Λ -shape carinately angled; scutellum entire. **Prepectus** with lateral prepectal surface subtriangular in males (Fig. 5.41), and subtriangular to subrectangular in females (Fig. 5.52), with apex extended to base of tegula in both sexes when mesonotum unflexed (in most females extended more ventrally over acropleuron when mesonotum flexed); frontal prepectal surface distinct from lateral surface in females. **Mesopleuron** (♂: Fig. 5.41, ♀: Fig. 5.52), mesotrochantinal plate (♂: Fig. 5.83, ♀: Figs. 5.78, 5.79), and **mesotergal-mesotrochantinal muscle** (♂: *cf.* Fig. 5.99, ♀: Fig. 5.105) for each sex as described in Gibson (in press, c). **Wings.** Males fully winged, females winged or variedly brachypterous; alate individuals with fore wing setose, with or without linea calva in females, but with at most large glabrous band below parastigma in males; marginal vein of fore wing elongate in both sexes. **Legs.** Front leg with one or more short, stout, curved spines on dorsoapical edge of tibia in both sexes, but without denticle-like spicules on dorsal edge of tibia. Middle leg with basolateral surface of coxa convexly rounded, without cavity between coxa and mesopleuron; mesotibia of males without differentiated pegs or robust spines at apex (Fig. 5.90), most females with row or patch of pegs (Fig. 5.98), or robust spines, along anteroapical edge, in some females pegs isolated above tibial spur by oblique groove extended from anteroapical edge between tibial spur and basitarsus; mesotibial spur elongate in both sexes, distinctly thickened and setose only in females; mesotarsus of males not differentiated from pro- and metatarsus, tarsomeres subequally cylindrical and with only row of elongate setae along anterior and posterior ventral edges (Fig. 5.90), females with mesotarsus conspicuous from pro- and metatarsus, tarsomeres increased in thickness or compressed toward tibia, and ventrally with row of pegs along anterior and posterior edges (more than one on basitarsus in some species) (Fig. 5.98), or some species with pegs reduced in number, robustness, or both, but then ventral surface of at least basitarsus densely setose as cushion-like pad (Fig. 5.97) (latter correlated with brachyptery in most species). Propodeum of males relatively long, with plical region as entire region between spiracles, undifferentiated from callar regions; extremely varied in females, and with structure of metanotum and apex of scutellum important for recognition of genera, but most females with plical region differentiated from callar regions by plical furrow distinctly mesad of each spiracle.

METASOMA 8-segmented in both sexes, Mt9 fused to Mt8 as syntergum; females with apex of syntergum unmodified, or circularly incised to surround sclerotized disk-like anal sclerite above base of ovipositor sheaths (Figs. 5.111, 5.112), or reflexed as varied flange over base of ovipositor sheaths, or W-like extended on either side of base of ovipositor sheaths; ovipositor sheaths variedly exserted beyond apex of ultimate tergum, in some species for 2-3 times length of body.

Monophyly. Eupelminae is supported as a monophyletic taxon by sexual dimorphism of mesothoracic structures [Table 5.1, 1(2)], and by the tendon-like reduced mesotergal-mesotrochantinal (t_2-tr_2) muscle of females [16(6)] (see section 5.7.2.3).

5.4.2.4 Tanaostigmatinae Ashmead

Tanaostigmatini Ashmead, 1904: 291. **Type genus**: *Tanaostigma* Howard. By inference in context from formation of family-group name. [As tribe of Eupelminae within Encyrtidae.]

Taneostigminae (!); Girault, 1915: 39 [as subfamily of Encyrtidae] (fauna of Australia).

Tanaostigmatidae; Peck, 1951: 331 (Nearctic catalog); De Santis, 1979: 167 (Neotropical catalog); La Sallè, 1984 (revision of New World fauna).

Tanaostigmodinae (!); Riek, 1970: 924 [as subfamily of Encyrtidae] (diagnosis).

Tanaostigmatinae; Burks, 1979: 878 [as subfamily of Eupelmidae] (Nearctic catalog).

Diagnosis (T = Tanaostigmatinae *s. s.*, C = *Cynipencyrtus* Ishii). **HEAD** more or less lenticular with frons curved to posterior ocelli, vertex very narrow; vertex and temples rounded (T) or carinately angled to occiput (C); scrobes separate above toruli by varied interantennal region, coextensive above as shallow depression to deep channel, and extended to median ocellus, or partly so; upper inner orbits not distinguished by region of differentiated sculpture; ocelli in almost straight line or flat triangle, with median ocellus anterior to posterior ocelli by twice or less diameter of ocellus (T), or in wide but distinct triangle, with median ocellus conspicuously anterior to posterior ocelli (C); maxillary palpus 4-articled; labial palpus 3-articled. **Antenna** 13-articled with 3-articled clava; anellus transverse ring-like, and with ful (T) or ful and fu2 (C) also ring-like reduced; males with funicle filiform, pectinate, or with short dorsal projections on funiculars.

MESOSOMA not sexually dimorphic in characters correlated with flight and jumping mechanisms. **Pronotum** vertical, almost inapparent in dorsal view (Fig. 5.31), and on inner side of prepectus (Figs. 5.31, 5.57) (T), or, with horizontal, transverse-rectangular dorsal surface (Fig. 5.33), with side over base of prepectus and apex of mesoscutal process for pl_2-t_1c (Fig. 5.55) (C); entire. **Mesoscutum** not conspicuously wider than posterior of pronotum, except if prepectus anteriorly protuberant (Figs. 5.31, 5.57) (T); posterior edge straight (C) or sinuate (T), but articulated only laterally with anterior edge of scutellar-axillar complex, edges inconspicuously (Fig. 5.33) (C) to conspicuously (Fig. 5.32) (T) separate when mesonotum flexed; sides recurved as carinate edge; process for pl_2-t_1c extended conspicuously anterior to mesothoracic spiracle; notauli absent (C, some T), or as sinuately convergent sulci that extend at least 0.5 medial length of mesoscutum (T), sulci separate posteriorly, and then slightly recurved posteriorly in most species (Figs. 5.31, 5.32), or united posteriorly, and in some species extended to transscutal articulation as median sulcus; parapsidal lines absent. **Scutellar-axillar complex** with DAS large and equilateral to elongate-triangular (Figs. 5.31, 5.32) (T), or relatively small and transverse-triangular (Fig. 5.33) (C), but with basomedial angles contiguous; scutellum flat to lowly convex, not divided. **Prepectus** with lateral surface extended to base of tegula, position unaltered by flexed or unflexed condition of mesonotum; frontal prepectal surface conspicuously recurved over apex of mesoscutal process for pl_2-t_1c and distinctly protuberant anterior to mesothoracic spiracle, with latter externally evident (Figs. 5.31, 5.57) (T); or concealed by pronotum (*cf.* Figs. 5.55, 5.56) (C). **Mesopleuron** (Figs. 5.55, 5.57) with acropleuron convexly expanded and extended to metapleuron and metacoxa; acropleural sulcus extended anteriorly from above base of mesocoxa toward posteroventral angle of lateral prepectal surface, where abruptly angled dorsally as much finer, posteriorly curved sulcus or line in most species; mesepimeron absent; mesepisternum without transepisternal line or sulcus; lower mesepisternum transverse. **Mesotrochantinal plate** rectangular and internally reflexed (Fig. 5.87), with lower mesepisternum transverse along base of mesocoxa, trochantinal lobes not exposed, no membranous region anterior to each mesocoxa, and latter unable to rotate out of combined fossa (Fig. 5.72) (C), or, trochantinal plate extended somewhat posteriorly as medially concave plate (*i. e.*, surface V-shape declined to median), with trochantinal lobe at posterolateral angle of plate and fitted into coxal groove at base of prominent median coxal lobe, with membranous region anterior to each mesocoxa, and latter able to rotate anteriorly (Fig. 5.71) (T). **Mesotergal-mesotrochantinal muscle** (t_2-tr_2) (*cf.* Fig. 5.100) large and tubular, from DAS (t_2-tr_2a) and large axillar phragma (t_2-tr_2b), both inserted into large golf tee-like mesotrochantinal pedicel ventrally in body cavity. **Wings** fully developed, brachyptery unknown; fore wing setose, without distinctly defined linea calva, but with large glabrous region below parastigma; marginal vein elongate. **Legs.** Front leg without curved spine on dorsoapical edge of tibia, though cuticle denticle-like produced in many taxa (state unknown for "C"), without denticle-like spines along dorsal edge. Middle leg with basolateral surface of mesocoxa convexly rounded, without cavity between coxa and mesopleuron; tibia with row of pegs along anteroapical edge (Fig. 5.96) (C), or without pegs (T); tarsus ventrally with row of seta-like spines along anterior and posterior edges, or with row of more peg-like spines along posterior edge (Fig. 5.95) (T), or with row of pegs along anterior edge and row of spines (plus 1-3 pegs per tarsomere) along posterior edge (Fig. 5.96) (C). **Propodeum** with plical region as entire region between spiracles, undifferentiated from callar regions, or as narrower region differentiated from callar regions by conspicuous carinae.

METASOMA of both sexes 8-segmented, with Mt9 fused to Mt8 as syntergum; syntergum almost horizontal and in similar plane as preceding terga (C), or almost vertical except for abruptly reflexed, convex extension over ovipositor sheaths (Fig. 5.107) (T); ovipositor sheaths at most slightly exserted beyond apex of ultimate tergum.

Monophyly. Tanaostigmatinae *s. s.* is indicated as a monophyletic taxon based on structure of the pronotum [Table 5.1, 11(3a)], structure of the mesonotal articulation (edges of mesoscutum and scutellar-axillar complex widely separate when mesonotum flexed, *cf.* Figs.

5.31, 5.32), and phytophagy of the larvae. However, monophyly of Tanaostigmatinae *s. l.* is uncertain. A sister-group relationship between *Cynipencyrtus* and Tanaostigmatinae may be indicated by the gall-inhabiting habitat of the larvae, but a sister-group relationship between *Cynipencyrtus* and Encyrtidae is indicated by the transverse shape of the dorsal axillar surfaces [10(2b)], and possibly by presence of mesotibial pegs [12(2)]. If the latter relationship is correct, Tanaostigmatinae *s. l.* is paraphyletic (see section 5.7.2.3).

5.5 Revision of the genera of Calosotinae of the world

5.5.1 Key to genera of Calosotinae of the world

1 Dorsal axillar surfaces contiguous basally, scutellum acutely angled at transscutal articulation (Fig. 5.17). 2

1' Dorsal axillar surfaces separate basally, scutellum transverse along transscutal articulation (Figs. 5.18-5.23).. 3

2(1) Acropleuron convexly expanded and (sub)contiguous with metapleuron dorsally, upper mesepimeron inevident (Fig. 5.44) or linear; mesotarsus ventrally with row of seta-like spines along anterior edge and row of peg-like spines along posterior edge (*cf.* Fig. 5.92); females with apex of Mt7 extended to level of cerci, Mt8 at least inevident dorsally if independent from Mt9. .... *Paraeusandalum* new genus

2' Acropleuron flat or slightly concave medially and not extended to metapleuron, triangular upper mesepimeron present (Fig. 5.43); mesotarsus with equally developed row of seta-like spines along anterior and posterior edges (Fig. 5.91); females with Mt7 not extended to level of cerci, Mt8 independent and subequal in length to Mt9.. *Archaeopelma* new genus

3(1') Notauli V-shape convergent and posteriorly contiguous, or nearly so (Figs. 5.17-5.21); scutellum laterally acarinate distal to dorsal axillar surface (Figs. 5.17-5.21); middle tarsus ventrally with row of seta-like spines along anterior edge and row of peg-like spines along posterior edge (Fig. 5.92), or, if rows of spines equally developed (Fig. 5.93), then acropleuron not extended to metapleuron (Fig. 5.48). 4

3' Notauli separate and subparallel dorsally (Figs. 5.24); scutellum laterally carinate distal to dorsal axillar surface (Figs. 5.22, 5.23); middle tarsus ventrally with equally developed row of pegs along anterior and posterior edges, and acropleuron extended to metapleuron at least dorsally, with at most lunate to triangular, convex lower mesepimeron (Figs. 5.49-5.51). 6

4(3) Acropleuron not extended to metapleuron, lunate mesepimeron extended to base of hind wing (Fig. 5.48); mesotarsus ventrally with equally developed row of peg-like spines along anterior and posterior edges (Fig. 5.93); protibia non-spiculate dorsally.. *Licrooides* new genus

4' Acropleuron extended to metapleuron at least dorsally (Figs. 5.45, 5.47); mesotarsus ventrally with row of seta-like spines along anterior edge and row of peg-like spines along posterior edge (Fig. 5.92); protibia with one or more spine-like or denticle-like spicules on dorsal edge in most species (*cf.* Fig. 5.88).. 5

5(4') Scutoscutellar sulcus straight convergent or slightly concave to transscutal articulation, scutellum subovate (Fig. 5.21); mesopleural suture extended posterodorsally as distinct sulcus from anterolateral corner of mesocoxa toward apex of acropleuron (Fig. 5.47); Mt8 and Mt9 indistinguishably fused dorsally in females (Fig. 5.110); males with conspicuously compressed, asetose rami on antennal funicular articles 1-5, with all rami extended to about apex of fu7....... .... *Chirolophus* Haliday

5' Scutoscutellar sulcus convexly curved to transscutal articulation, scutellum of distinctive gourd-shape with more or less petiolate base (Figs. 5.19, 5.20); mesopleural suture inevident (Fig. 5.45), or as obscure furrow or line of effaced sculpture extended dorsally from anterolateral corner of mesocoxa to ventral edge of acropleuron; Mt8 and Mt9 of females dorsally divided by transverse suture between cerci (not externally evident in all specimens) (Fig. 5.109); males with filiform antennae, or, if pectinate, then not as described above....................... ....*Eusandalum* Ratzeburg

6(3') Mesoscutum as long as wide, or slightly longer; middle legs very long, mesotibia about 1.7 times as long as maximum width of head; mesotibia with robust elongate spines along dorsal and anterior surfaces; prepectus not extended to tegula; mesoscutum with fine coriaceous sculpture.. ....*Tanythorax* new genus

6' Mesoscutum about 1.2-1.7 times wider than long (Figs. 5.22, 5.23); middle legs relatively short, mesotibia at most 1.25 times maximum width of head; mesotibia without robust spines; prepectus either extended to tegula (Fig. 5.50), or mesoscutum with coarse umbilicate sculpture at least laterally (Fig. 5.51)........ 7

7(6') Prepectus distinctly separate from tegula (Fig. 5.51); mesoscutum of most species at least black between notauli and along parapsidal lines, in distinct contrast to brilliantly metallic colored and umbilicately sculptured lateral lobes.... .... *Balcha* Walker

7' Prepectus extended to tegula (Fig. 5.50), or only slightly separate; mesoscutum uniformly black or of dull metallic color, or finely sculptured, or both............. .... *Calosota* Curtis

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5.5.1.1 *Archaeopelma* new genus

(Figs. 5.3, 5.4, 5.17, 5.43, 5.75, 5.88, 5.91)

Type-species. *Archaeopelma tropeotergum* new species, by present designation.

Derivation of generic name. Combination of greek word "archaios", meaning "primitive", or "from the beginning", and root of family name; referring to presumed early split of clade during evolution of Eupelmidae. Gender: neuter.

Description. HEAD (Figs. 5.3, 5.4). Inner orbits of females not differentiated, evenly sculptured; inner orbits of males as for females, or upper inner orbits slightly raised along edge of eye and here with minute transverse-reticulate sculpture. Scrobal cavities separated ventrally by triangular interantennal region; coextensive above as relatively deep, parallel-sided channel; shallowed to median ocellus; narrower and more distinctly defined by declivous sides in females than in males. Ocelli in very wide, almost flat triangle; median ocellus at upper edge of scrobal cavity; posterior ocellus approximately one ocellar diameter from eye orbit. Eye glabrous. **Antenna** 11-articled in both sexes; inserted close together, distance between inner edges of toruli subequal to width of torulus and about 0.33 distance between outer edge of torulus and inner eye margin. Scape extended to vertex. Anellus short, wider than long in females and distinctly transverse in males. Flagellum of females relatively long and slender, not conspicuously tapered or expanded distally, with scattered multiporous plate sensilla; funiculars slightly compressed (subcylindrical), decreased in length distally, fu1 about 4 times longer than wide but fu7 only about 2 times as long as wide; clava moderately differentiated from funiculars, not divided by transverse sutures, but distinctly longer than fu7. Flagellum of males long and filiform, with dense multiporous plate sensilla; funiculars and clava markedly compressed; clava inconspicuously differentiated from funiculars, only slightly longer than fu7.

MESOSOMA. Pronotum (Fig. 5.17) campanulate and conspicuously narrower than mesoscutum. **Mesonotum** (Fig. 5.17). Mesoscutum relatively broad, at least 1.6 times wider than long; distinctly 'shoulder-like' on either side of pronotum, with anterior margin almost right-angled to side; relatively evenly convex, but with dorsum flattened anterior to transscutal articulation. Notauli linear, V-shaped convergent within anterior 0.5 mesoscutum; obscure as subeffaced line of sculpture in females, but more distinct as line of regular sculpture in males; not contiguous posteriorly in most male specimens, either effaced before midline, or abruptly curved posteriorly near midline and subparallel distally. Parapsidal line short, as impressed band of minute and fine sculpture near anterior margin of mesoscutal lateral lobe adjacent to notaulus. Scutellar-axillar complex with almost straight convergent (slightly sinuate) scutoscutellar sulci, DAS triangular with basomedial angles subcontiguous; scutellum relatively flat with acute basomedial angle at transscutal articulation. **Prepectus** (Fig. 5.43) large, but apex slightly to distinctly separate from base of tegula in some specimens; lateral surface evenly curved to frontal surface, not anteriorly protuberant beneath mesothoracic spiracle. **Mesopleuron** (Fig. 5.43). Acropleuron not extended to metapleuron, relatively small and flat, or even slightly concave medially as femoral groove; acropleural sulcus distinct posteriorly as oblique, arcuate sulcus, ventrally recurved anteriorly for short distance and then abruptly reflexed to anterodorsal edge of pleuron at base of tegula as much finer sulcus (obscurely so in some males). Mesopleural suture distinct, recurved to metapleuron as transepimeral sulcus below acropleural sulcus. Mesepimeron as small, triangular, upper mesepimeron, and larger, rectangular, lower mesepimeron. Mesepisternum without transepisternal line, except in some male specimens as oblique line demarking abrupt change in sculpture between upper and lower mesepisterna; upper mesepisternum as relatively large triangular region between prepectus and acropleuron, and between acropleuron and mesopleuron; lower mesepisternum not deeply incurved anterior to mesocoxae, with only widely spaced, transverse membranous region anterior to each coxae; trochantinal lobes widely separate (Fig. 5.43). **Metathorax.** Metanotum (Fig. 5.17) with distinctly differentiated transverse dorsellum between scutellar apex and propodeum.. Metapleuron elongate-triangular. **Legs.** Fore leg (Fig. 5.88) with denticle-like spicules along dorsal edge of tibia, and with 1 or 2 slightly smaller dorsoapical spicules. Middle leg (Fig. 5.91) without peg-like spines along anterodistal edge of tibia; tibial spur slightly thickened and setose, 1.5-2.0 times as long as apical width of tibia; tarsus long, subequal in length to mesotibia in females and about 0.8 times as long in males, not differentiated from pro- and metatarsi, tarsomeres equally slender; basitarsus slightly longer than 0.5 length of tibia and longer than combined length of tarsomeres 2-5 in females, and about 0.40 length of tibia and subequal in length to tarsomeres 2-4 in males; tarsomeres ventrally with equally developed row of spine-like setae along anterior and posterior edges. Hind leg with spine-like spicules along dorsal edge of tibia, and with dorsoapical spicules. **Wings.** Fore wing of females setose, except about basal 0.33 glabrous beneath costal cell, with basal vein and base of m+cu vein indicated by narrow bands of setae; SMV about 2-4 times as long as MV; PMV longer than MV (though depigmented and obscure distally in some males); and STV expanded distally, with uncus. Fore wing of males similar to that of females, or superficially glabrous, but with very sparse, inconspicuous discal setae. Hind wing with short spike-like basal vein. **Propodeum** of females subrectangular in dorsal view, sides subparallel and foramen shallowly, evenly incurved over almost entire posterior width; median length about 3.0-4.0 times that of metanotum or petiole; plical region as entire region between spiracles, inconspicuously differentiated from callar regions by shallowly obscure plical furrow posterior to each spiracle, without median carina; callar region setose. Propodeum of males trapezoidal in dorsal view, sides posteriorly convergent with foramen relatively much narrower than in females; median length about 3 times that of metanotum; otherwise similar to that of female.

METASOMA of females 9-segmented; long and subcylindrical, with sides parallel or slightly divergent to apex of Mt5. Mt1 (petiole) transverse-cresentic, almost as wide as basal width of Mt2; Mt2 with posterior margin very slightly incised medially; Mt3-Mt5 with posterior margins entire and transverse; Mt6 with posterior margin very shallowly incurved; Mt7 with shallow, subbasal transverse furrow, and with posterolateral margins sinuately convergent to small rounded apex; Mt8 and Mt9 independent; Mt8 exposed dorsally, large, with median length equal to that of Mt9, triangular in cross-section distal to apex of Mt7, with sides abruptly, concavely narrowed and with dorsolongitudinal median ridge, posterior ventrolateral corners acutely protruded lateral to base of Mt9, and with ventrolateral longitudinal furrow beneath lateral margins of Mt5-Mt7 from apex of hypopygium to apex of Mt7; Mt9 moderately narrow, long, and evenly convex in dorsal view. Cercus peg-like, at extreme basolateral corner of Mt9.

Metasoma of males 8-segmented; relatively much shorter than in females; either elongate-lanceolate with dorsum flattened (subtriangular in cross-section), or cylindrical. Petiole much narrower than in females but longer, trapezoidal; postpetiolar terga with posterior margins entire and transverse. Mt8 + Mt9 indistinguishably fused as syntergum.

Distribution. Known from Nearctic (southwestern USA) and Neotropical (northwestern Mexico) regions.

Hosts. Unknown, but most likely xylophagous beetles (Coleoptera).

Generic diversity. In addition to the type species, I saw a single male specimen [Mexico, Sinaloa, Mazatlan, 10.V.1961, Howden & Martin, at light (NRS)], which represents a second species. Striking character states that differentiate this specimen from males of the type species include color (head and mesosoma greenish; PMV entirely pigmented and distinctly longer than MV), structure (upper inner orbits of head not differentiated from rest of inner orbits; antennal funiculars relatively much longer; metasoma cylindrical with different relative lengths of terga), sculpture (metasoma transverse-coriaceous dorsally), and setation (fore wings distinctly setose).

Monophyly and relationships. Monophyly of *Archaeopelma* is indicated by structure of Mt8 and Mt9 in females; hypotheses of relationships are illustrated in figures 5.1a and 5.1b, and justified in section 5.7.2.1.

5.5.1.2 *Archaeopelma tropeotergum* new species

(Figs, 5.3, 5.4, 5.17, 5.43, 5.75, 5.88, 5.91)

Type material. HOLOTYPE - Female.Texas , Starr Co., 31.III.1960; D.J. & J.N. Knull Collrs. (OSU). ALLOTYPE - Male.Arizona , 17 mi. SW Cortaro, 2600', 8.V.1961, R.H. & E.M. Painter (UAT). PARATYPES - 6 ♂♂, 1 ♀, 5 ♂♂, same data as allotype; 1 ♀, Texas, Hidalgo Co., 26.III.1957, D.J. & J.N. Knull Collrs. (OSU); 1 ♂, Mexico Baja Calif. Sur, 10 mi. SE La Paz, 3.VIII.1966; P.D. Hurd Collector, *Colubrina glabra* (UCB, deposited in CAS by request).

Condition of holotype. Entire; mesoscutum in unflexed position but obliquely pinned through mesoscutum and acropleuron; left side of mesosoma broken and distended, with large axillar phragmata and t_2-tr_2 muscle, and first axillary sclerite, exposed.

Derivation of specific epithet. From latin words "*tropeos*", meaning "keel", and "*tergum*", meaning "back"; referring to shape of Mt8 of females.

Description. FEMALE. Length = 0.92 cm. HEAD (*cf.* Figs. 5.3, 5.4) green, but with irregular region on inner orbits from malar sulcus to near ocelli, and oval region between ocelli, coppery-colored; relatively evenly convex in lateral view with frons gradually rounded into convex vertex; inner orbits slightly, convexly protuberant lateral to interantennal region, but not distinctly narrowed above toruli, width about 1.75 times as wide as scrobes (measured at midheight); relative measurements, HW = 16.2, HH = 14.1, HL = 9.9. Interantennal region, and clypeus below, granulate; rugulose-reticulate below toruli, but increasingly isodiametric-reticulate over inner orbits (maximum size of cells about 0.5), reticulations smaller dorsally near ocelli and on vertex; occipit more reticulate-alutaceous. Setae white, unmodified, and relatively long on occiput, vertex, and genae; translucent-whitish, flattened-spatulate to lanceolate on frontal aspect of head and on inner orbits, and inserted at juncture of cells. **Mouthparts.** Labrum yellow; maxilla and labium dark brown, except stipes greenish. **Antenna** with scape and pedicel yellowish, flagellum dark brown with obscure metallic luster at some angles; inserted in line with ventral margin of eyes, distance between lower edge of toruli and clypeal edge compared with malar space = 4.0:4.9; scape elongate-cylindrical and curved; fu1 widened slightly to apex, and fu2 and fu3 expanded slightly dorsobasally; relative measurements, scape = 9.6(0.9), pedicel = 2.0(1.1), anellus = 0.7(0.9), funiculars = 4.8(1.3), 5.0(1.4), 4.2(1.5), 3.5(1.2), 3.1(1.0), 2.6(1.0), 2.4(1.1), clava = 3.5(1.4). **Ocelli** with POL = 2.8, LOL = 1.0, OOL = 1.0; median ocellus faced anteriorly at upper edge of scrobal cavity; posterior ocelli faced dorsally on vertex. **Eyes** oval, H:W = 9.1:6.7; distance between eyes below = 12.2, above = 6.8. **Scrobes** (*cf.* Figs. 5.3, 5.4) elongate-slender, H:W = 9.2:2.0; isodiametric-reticulate within channel above interantennal region, cells much smaller than on inner orbits.

MESOSOMA primarily dull greenish but with coppery-violaceous regions (particularly dorsum of pronotum and along notauli), more bluish-violaceous on propodeum, and tegula yellow; relatively evenly setose with unmodified white setae, except following glabrous: metanotum, plical region of propodeum, acropleuron, and mesepimeron. **Pronotum** (*cf.* Fig. 5.17) with isodiametric-reticulate sculpture on sides, but isodiametric-coriaceous dorsolaterally to reticulate medially; shallowly, transversely concave subapically. **Mesothorax** (*cf.* Figs. 5.17, 5.43) with mesonotum and prepectus isodiametric-reticulate, cells of similar size throughout and of similar size to those on inner orbits; lower mesepisternum alutaceous to coriaceous; upper mesepisternum reticulate to rugulose-reticulate; acropleuron punctate-reticulate centrally, but more punctulate along edges; acropleural sulcus and mesopleural suture costate; upper mesepimeron smooth and shining; lower mesepimeron isodiametric-reticulate ventrally, but graduated to coriaceous dorsally, and smooth and shining near dorsal edge. Scutellar-axillar complex quadrate, medial length of scutellum to width of complex = 9.2:9.0. **Metathorax** with pleuron rugulose-reticulate, similar to callar region of propodeum; dorsellum rugulose, length to medial length of propodeum = 0.7:3.1. **Propodeum** with plical region costulate along basal edge, but otherwise isodiametric-reticulate, cells deeper and smaller than those on mesonotum and much smaller laterally near spiracle, punctulate-rugulose; callar regions rugulose-reticulate. **Wings** hyaline, with brownish trace veins, and yellowish-brown venation; fore wing with SMV = 24.0, MV = 8.6, PMV = 16.2, STV = 3.0. **Legs** yellowish, except coxae green and outer femoral surfaces with slight bluish luster. Protibia (*cf.* Fig. 5.88) with 4 (left tibia), and 5 (right tibia) denticle-like spicules on dorsal edge. Middle leg with tibia = 16.8; tarsomeres = 9.3, 2.2, 1.5, 1.2, 0.9. Metatibia with 2 spine-like spicules on dorsal edge.

METASOMA dark with Mt8, base of Mt7, and sides coppery-violaceous, elsewhere mostly with greenish to bluish luster at different angles; relatively evenly setose with unmodified white setae, except petiole to Mt3 glabrous dorsally. Mt1 (petiole) transversely costulate along base, length to width = 1.0:7.3; Mt2 smooth and shining dorsally, except obscurely coriaceous laterally and rugulose-reticulate on sides; Mt3 mostly concealed dorsally under Mt2 and very difficult to distinguish (see section on variation), but sides rugulose-reticulate; Mt4 smooth along base and apex, but about medial 0.5 punctate-reticulate to isodiametric-reticulate, and sides rugulose-reticulate; Mt5 isodiametric-reticulate, except smooth along apex and with sides rugulose-reticulate; Mt6 punctate-reticulate basally, but graduated to coriaceous apically, with apical edge smooth, and sides rugulose-reticulate; Mt7-Mt9 isodiametric-coriaceous dorsally and ventrally, except concave sides of Mt8 distal to Mt7 vertically wrinkled; Mt9 with sides subparallel over most of length, relatively elongate-~~slender,~~ 3.3 times as long as basal width; relative length of terga = 1.0(m), 8.2(pm), 1.3(m), 5.6, 7.8, 15.0, 16.5, 7.0, 7.0. **Hypopygium** small, extended to about midway between apices of Mt4 and Mt5. **Ovipositor sheaths** dark brown, slightly (3.0) exserted beyond Mt9.

MALE. Length = 0.49 cm. **HEAD** (Figs. 5.3, 5.4) bluish with violaceous reflections; similar to females in setation except setae on frontal aspect less conspicuously flattened; similar also in structure except inner orbits only about 0.75 as wide as scrobes at midheight and upper orbits with conspicuously differentiated elongate-rectangular region along inner margin of eye, region black, slightly convex and protuberant anterior to posterior ocellus, and minutely transverse-reticulate or somewhat imbricate; relative measurements, HW = 10.7, HH = 9.4, HL = 7.1 **Antenna** black, except radicle yellowish-brown and scape with bluish luster; inserted distinctly above line drawn between ventral margin of eyes, distance between lower edge of toruli and clypeal edge compared with malar space = 3.8:2.9; scape cylindrical, but much stouter than in females; relative measurements, scape = 4.0(1.0), pedicel = 1.0(1.0), anellus = 0.3(0.8), funiculars = 3.0(1.8), 4.5(2.0), 4.7(2.0), 4.0(1.9), 3.5(1.8), 3.2(1.7), 2.8(1.5), clava = 3.2(1.4). **Ocelli** with POL = 3.0, LOL = 1.3, OOL = 0.7.**Eyes** oval, H:W = 6.4:3.9. **Scrobes** (Figs. 5.3, 5.4) similar to females, except relatively shorter and wider, H:W = 5.3:2.5.

MESOSOMA bluish with violaceous reflections, similar to head, but with tegula yellow; setation similar to females except longer. **Mesothorax** (Figs. 5.17, 5.43) with sculpture similar to females, except as follows: dorsum of pronotum same isodiametric-reticulate as rest of mesonotum; acropleuron isodiametric-reticulate, except posterodorsal region smooth and shining; and upper mesepimeron obscurely coriaceous. Scutellar-axillar complex relatively much longer than in females, length of scutellum to width of complex = 7.8:6.2. **Propodeum** most conspicuously costulate basolaterally; plical region isodiametric-reticulate, with cells much shallower than on mesoscutum, almost coriaceous; medial length of dorsellum to propodeum = 0.9:2.6. **Wings** superficially glabrous, but with very sparse and short discal setae; hyaline, without trace veins; venation dark brown, except PMV depigmented distally, gradually whitened and difficult to measure accurately (see section on variation); fore wing with SMV = 15.2, MV = 4.7, PMV = 5.0, STV = 1.5. **Legs** with coxae and femora bluish, similar to mesosoma; trochanters and tibiae brownish with slight bluish luster, except tibial-femoral joints yellowish; each tarsus with basitarsus mostly white, but apex and subsequent tarsomeres brownish. Protibia (Fig. 5.88) with 6 (left tibia) and 5 (right tibia) denticle-like spicules on dorsal surface. Middle leg with tibia = 9.3; tarsomeres = 3.5, 1.1, 1.0, 0.6, 0.9. Hind tibia with two subbasal, and one more apical spine-like spicule on dorsal edge.

METASOMA with dorsum of Mt2 dark brown, sides of metasoma dark brown with brassy luster, Mt7 coppery-colored, Mt8 green, otherwise metasoma with bluish luster dorsally. Mt1 (petiole) smooth and shining; Mt2 shining dorsally and almost smooth, but with very fine coriaceous sculpture; Mt3-Mt6 isodiametric-reticulate, with cells more distinctly defined toward median than laterally, and with terga narrowly smooth along apex; Mt7 coriaceous; and syntergum (Mt8 + Mt9) very finely coriaceous; Mt2 to syntergum with sides alutaceous; relative length of terga = 1.0(m), 5.1, 2.0, 4.3, 5.0, 5.6, 4.0, 1.5.

Variation. The single female paratype is broken and lacks the antennae and middle legs. It is slightly larger than the holotype (approximately 1 cm in length), but is similar in structure, sculpture, and color except that the entire body is more distinctly coppery in color, each fore tibia has 4 dorsal denticles, and Mt3 is more conspicuously exposed (slightly greater than 0.5 length of Mt4 and about 0.4 length of Mt2), asetose, and with only obscure coriaceous sculpture.

Males, similar to females, have Mt3 overlapped by Mt2 to differing extents so that the dorsal length of Mt3 is varied, but it is distinctly shorter than Mt2 or Mt4. The smallest male is 0.35 cm, whereas the largest is 0.55 cm. Variation occurs in pigmentation of the postmarginal vein, so that if only the 'brownish' part is measured the vein is superficially shorter than the marginal vein, but actually is up to 1.25 times as long as the latter vein. Number of denticles on the protibia varied from 4 to 7, with the number usually different on each tibia by 1 or 2.

Distribution. Southwestern USA and Baja California, Mexico.

5.5.2 *Licrooides* new genus

(Figs. 5.8, 5.9, 5.18, 5.48, 5.62, 5.76, 5.93)

Type-species. *Licrooides umbilicatus* new species, by present designation.

Derivation of generic name. From greek words "likros", meaning "antler", and "eidos", meaning "like"; referring to antler-like antennae of males. Gender: masculine.

Description. HEAD (Figs. 5.8, 5.9). Upper inner orbits moderately raised, with single row of coarse cristae along inner eye margin. Scrobal cavities separated ventrally for about half length by elongate-triangular interantennal region; coextensive above as relatively deep parallel-sided channel that is medially divided by low carinate ridge; extended to median ocellus. Ocelli in low, almost flat triangle; median ocellus immediately above scrobal cavity in depression between raised inner orbits; posterior ocellus contiguous with dorsal eye orbit. Eye inconspicuously setose. **Antenna** 11-articled in both sexes; inserted close together, distance between inner edge of toruli subequal to width of torulus and 0.30-0.50 distance between outer edge of torulus and inner eye margin. Scape extended to ventral edge of median ocellus. Anellus quadrate in females and transverse in males. Flagellum of females relatively short and compact, with scattered elongate multiporous plate sensilla; funiculars slightly compressed (subcylindrical), increased very slightly in width and decreased slightly in length distally, with fu1 only about 2 times as long as wide and fu7 subquadrate; clava not distinctly wider than funiculars nor divided by distinct sutures, but subequal in length to fu6 + fu7 and differentiated from funiculars. Flagellum of males pectinate; funiculars and rami with dense multiporous plate sensilla, hence appearing longitudinally or obliquely strigose; fu1-fu5 or fu1-fu6 each with basal ramus; rami asetose, compressed, lanceolate, and decreased slightly in length distally, not extended more than two subsequent funicular articles in length; clava similar to that of females.

MESOSOMA. Pronotum (Fig. 5.18) campanulate and conspicuously narrower than mesoscutum. **Mesonotum** (Fig. 5.18). Mesoscutum broad, about 1.8-2.0 times wider than long; distinctly 'shoulder-like' on either side of pronotum, with anterior margin of lateral lobes almost right-angled to side; conspicuously flattened dorsally, and slightly, paramedially depressed anterior to inner edges of DAS. Notauli linear, V-shaped convergent within anterior 0.33 mesoscutum, not impressed and obscure as line of slightly altered, finer sculpture. Parapsidal line inevident or obscure as small region of finer sculpture near anterior margin of mesoscutal lateral lobe adjacent to notaulus. Scutellar-axillar complex with straight convergent scutoscutellar sulci; DAS triangular with basomedial angles separate, distance between inner angles about equal to or slightly less than own basal width; scutellum flat or moderately convex with basal edge transverse along transscutal articulation. **Prepectus** (Fig. 5.48) separate from base of tegula by distal width to length of tegula; lateral surface evenly curved to frontal surface, not anteriorly protuberant beneath mesothoracic spiracle. **Mesopleuron** (Fig. 5.48). Acropleuron large, but not extended to metapleuron, evenly, though relatively flatly convex; acropleural sulcus distinct for entire length, or shallowed and more obscure anterodorsally, but smoothly extended to anterodorsal edge of pleuron at point midway between apex of prepectus and base of tegula. Mesopleural suture distinct, extended vertically immediately behind acropleural sulcus, and slightly recurved posteriorly as transepimeral sulcus in some specimens (Figs. 5.48, 5.76). Mesepimeron narrowed dorsally to base of hind wing, not differentiated into upper and lower mesepimera except obscurely so in specimens with mesopleural suture posteriorly recurved. Mesepisternum segregated into upper and lower mesepisterna by fine but distinct transepisternal sulcus; upper mesepisternum as relatively large triangular region between prepectus and acropleuron, and linear posterior region between acropleuron and mesepimeron; lower mesepisternum not deeply incurved anterior to mesocoxae, with only moderately sized, widely separate subcircular membranous region anterior to each mesocoxa; trochantinal lobes widely separate (Fig. 5.76). **Metathorax.** Metanotum (Fig. 5.62) with distinct transverse-rectangular dorsellum between scutellar apex and propodeum. Metapleuron triangular, dorsally narrowed. **Legs.** Fore leg with tibia non-spiculate dorsally, but with 2 tiny dorsoapical spicules. Middle leg (Fig. 5.93) without peg-like spines along anterodistal edge of tibia; tibial spur thickened and setose, 1.5-1.7 times as long as apical width of tibia; tarsus relatively long, about 0.6 times or slightly less than length of mesotibia, and slightly thickened proximally; basitarsus short, about 0.25 times length of tibia and slightly shorter than combined length of tarsomeres 2-4; tarsomeres 1-4 ventrally with equally developed row of more or less peg-like spines along anterior and posterior edges, except seta-like proximally on basitarsus. Hind leg with inconspicuous spine-like spicules along dorsal edge of tibia, and with dorsoapical spicules. **Wings.** Fore wing glabrous beneath costal cell to about apex of submarginal vein, setose distally, but more sparsely so in males than in females; SMV 1.5-2.5 times as long as MV; MV about 3.5-5 times as long as short PMV; PMV subequal in length to about 3 times as long as STV; and STV short, straight, and not expanded distally nor with uncus. Hind wing with short spike-like basal vein. **Propodeum** of females with foramen relatively widely and shallowly incurved, edge recurved as carina; median length about twice that of metanotum; plical region entire region between spiracles, at most inconspicuously differentiated from callar regions, plical furrows absent or extended for short distance from propodeal foramen slightly mesad of each spiracle, with fine median carina. Propodeum of males (Fig. 5.62) with foramen relatively much narrower and more deeply incurved than in females, but median length about 2.5-5.0 times that of dorsellum; plical region not differentiated from callar regions, without plical furrows, but with fine median carina or sulcus at least distally.

METASOMA 8-segmented in both sexes; elongate-ovate to lanceolate and more or less flattened in air-dried females, but prone to collapse or compress in air-dried males, thus varied in appearance. Mt1 (petiole) wide in females, narrower in males, but transverse-arcuate to linear in both sexes. Mt2 with posterior margin deeply incised medially; Mt3-Mt6 with posterior margins entire and transverse or very slightly incised to emarginate medially in females, but distinctly emarginate in males; Mt7 with posterior margin evenly rounded and not extended to level of cerci; Mt8 and Mt9 indistinguishably fused as syntergum dorsally, but with oblique sulcus below cercus indicating lateral line of fusion; syntergum with sides convergent to apex, triangular in dorsal view. Cercus button-like.

Distribution. Known from Nearctic (southwestern USA) and Neotropical (Mexico, Costa Rica, Argentina) regions.

Hosts. Unknown, but most probably xylophagous beetles (Coleoptera); one specimen reared from oak (*Quercus*).

Generic diversity. In addition to the type species, I saw single specimens representing at least two additional species: (♀) Mexico, Lower Cal., Cedros Id., 3.VI.1925, H.H. Keifer Collector (CAS); (♂) Costa Rica, S. Rosa Park, Guan., 21.III.1978, D.H. Janzen, riparian (HTC); (♀) Argentina, La Rioja, Guayapa, 4.X.1954, Coll. Hayward (IML). The latter female lacks the head and antennae, but the meso- and metasoma are very similar in structure, and there are only slight differences in color and sculptural features from females of the type species. The specimen may be conspecific with the type species, but the head and antenna are needed to be certain. The male from Costa Rica is differentiated from males of the type species most conspicuously by antennal characters (only fu1-fu5 with rami and these longer); whereas the female from Mexico is distinguished from females of the type species by numerous character states, including sculpture (frontal aspect of the head lacking umbilications), structure (scutellum conspicuously convex), setation (much denser on callar regions of propodeum, and metasoma dorsally setose), color (legs yellowish distal to coxae), and venation (marginal vein relatively much longer).

Monophyly and relationships. Monophyly of *Licrooides* is indicated by presence of a transepisternal sulcus (Fig. 5.48), which is autapomorphic for Calosotinae [Table 5.2, 25(2)]. *Licrooides* is hypothesized as the sister taxon of *Calosota* + *Balcha* + *Tanythorax*, as illustrated in figures 5.1a, 5.1b, and justified in section 5.7.2.1.

5.5.2.1 *Licrooides umbilicatus* new species

(Figs. 5.8, 5.9, 5.18, 5.48, 5.62, 5.76, 5.93)

Type material. HOLOTYPE - Female. **Arizona** , Chiricahua M., 20.VII.1953; D.J. & J.N. Knull Colls. (OSU). ALLOTYPE - Male. **Arizona** , SW Res. Sta., 5 mi. W Portal, 12.IX.1959, 5400', H.E. Evans; on honeydew on *Populus* (CU). PARATYPES - 5 ♀♀, 48 ♂♂, 1 ♀, 17 ♂♂, same data as allotype; 15 ♂♂, same data as allotype, except collected 13.IX.1959; 3 ♀♀, 13 ♂♂, same data as allotype, except collected 9.IX.1959; 1 ♂, same date as allotype, except collected 10.VIII.1959 by H.E. & M.A. Evans; 1 ♂, same data as allotype, except collected 29.VIII.1959; 1 ♂, **Arizona**, Cochise Co., Cave Ck. Cyn., Chiricahua Mts., Sunny Flat, 5100', 31° 53'N 109° 10'W, 4.VI.1982, H. A. Hespenheide, *Quercus* (UCLA); 1 ♀, Texas, Davis Mts., 14.VII.1957, D.J. & J.N. Knull Collrs. (OSU); 1 ♂, Texas, Brewster Co., Big Bend National Park, trailhead to Pine Canyon, 4700'-5200', 11.VII.1982, G. Gibson (CNC).

One female and two males paratypes each desposited in CNC and USNM by permission of CU.

Condition of holotype. Entire, mesothorax in unflexed position; point-mounted.

Derivation of specific epithet. From latin word "*umbilicatus*", meaning navel; referring to thimble-like, or umbilicate punctation of frontal aspect of head of individuals.

Description. FEMALE. Length = 0.45 cm. HEAD (*cf.* Figs. 5.8, 5.9) dark with umbilicate punctures of frontal aspect reflecting blue, occiput violaceous, but otherwise black. Head with frontal aspect relatively flat in lateral view, with vertex abruptly declined at posterior ocelli, and at acute angle to frons; inner orbits wider than scrobes ventrally, but distinctly narrowed dorsally, width of scrobes to width of inner orbits (measured below median ocellus) = 1.7:1.1; cristae along inner eye margin, origin 0.33 length of eye from ventral margin of eye (in lateral view), widened dorsally from denticle-like protrusions to transverse, anteriorly arcuate ridges; relative measurements, HW = 10.2, HH = 8.5, HL = 5.6. Frontal aspect of head with large subcircular umbilications; interstices distinct and flat, but of varied width; median of clypeus and interantennal region minute isodiametric-coriaceous (granulate), with interstices between umbilications of similar sculpture but more distinctly coriaceous; vertex reticulate-coriaceous; occiput alutaceous. **Setae** white and unmodified, except flattened-lanceolate on frontal aspect, setae inserted within umbilications. **Mouthparts.** Labrum brown; maxilla and labium dark brown with slight violaceous luster. **Antenna** dark brown, except scape with bluish luster; inserted about in line with ventral margin of eyes, distance between lower edge of toruli and clypeal edge compared with malar space = 1.7:3.5; scape elongate-cylindrical and curved; fu1-fu3 with dorsal edges slightly convex; relative measurements, scape = 5.7(0.7), pedicel = 1.5(0.7), anellus = 0.5(0.5), funiculars = 2.2(0.9), 1.9(0.9), 1.7(0.8), 1.7(0.8), 1.5(0.9), 1.4(1.0), 1.3(1.1), clava = 3.0(1.2). **Ocelli** with POL = 2.2, LOL = 0.9, OOL =0; median ocellus faced anterodorsally at upper edge of scrobal cavity; posterior ocelli faced posterodorsally on declined vertex. **Eyes** oval, H:W = 6.1:4.5; distance between eyes below = 8.3, above =3.7. **Scrobes** (*cf.* Figs. 5.8, 5.9) elongate, H:W = 6.3:1.7; coriaceous within channels above interantennal region.

MESOSOMA with dorsum of pro-, meso- and metanotum primarily brassy in color, but pronotum and mesonotum bluish laterally; propodeum bluish medially, brilliant green laterally; tegula dark brown; prepectus, upper mesepisternum, and mesopleuron violaceous; acropleuron black; and lower mesepisternum bluish-violaceous. Mesosoma with unmodified white setae, with following glabrous: metanotum, propodeum between spiracles (except for patch of setae basal to and along inner edge of spiracle), acropleuron and mesepimeron; scutellar-axillar complex with scattered, sparse setae; setae longest and most conspicuous on callar regions of propodeum, but cuticle and color readily visible. **Pronotum** (*cf.* Fig. 5.18) isodiametric-reticulate, similarly to mesoscutum. **Mesothorax** (*cf.* Figs. 5.18, 5.48) with mesoscutum isodiametric-reticulate, cells larger on dorsum than on convex sides of lateral lobes; DAS isodiametric-reticulate, cells similar in size to those on sides of mesoscutal lateral lobes; scutellum reticulate, with cells distinctly longitudinal, except more isodiametric and smaller toward edges; prepectus and upper mesepisternum reticulate-coriaceous; acropleuron finely, but distinctly isodiametric-coriaceous, except smooth posterodorsally; mesepimeron granulate ventrally, and dorsally smooth; lower mesepisternum very finely coriaceous. Medial length of scutellum to width of scutellar-axillar complex = 5.6:6.6; width of DAS to distance between DAS = 2.5:1.8; scutellar-axillar complex flat. **Metathorax** with pleuron roughened by setal origins, similarly to callar region of propodeum; dorsellum (*cf.* Fig. 5.62) minute isodiametric-reticulate; length to medial length of propodeum = 0.9:1.6. **Propodeum** (*cf.* Fig. 5.62) with fine, percurrent median carina, obscurely costulate basally; plical region isodiametric-reticulate, cells similar in size to those on DAS; callar regions very finely alutaceous-coriaceous, but roughened by setal origins; plical furrow short, recurved anteriorly from along propodeal foramen mesad of spiracle and directed toward, but not extended to spiracle. **Wings** hyaline, with brownish venation; fore wing with SMV = 10.9, MV = 5.1, PMV = 1.5, STV = 0.5. **Legs** with coxae violaceous; femora dark brown with violaceous reflection; tibiae dark brown, except tibial-femoral joints and apex of meso- and metatibiae yellowish-brown; tarsi with basitarsi yellowish-white, but increasingly brownish distally. Middle leg with tibia = 9.3; tarsomeres = 2.5, 0.9, 0.6, 0.5, 0.9.

METASOMA dark laterally, with varied metallic luster at different angles; dorsally with base of Mt2 reflecting bright green and syntergum with slight bluish tinge, dorsum otherwise coppery in color and shining; relatively evenly setose on sides, and on dorsum of Mt7 and syntergum (Mt8 + Mt9), but glabrous, or almost so on dorsum of Mt2-Mt6; sides of metasoma coriaceous; Mt1 (petiole) transverse-linear; Mt2 almost smooth, with only very obscure coriaceous sculpture; Mt3-Mt5 coriaceous basally (isodiametric laterally, but more transverse and finer medially), with about apical 0.33 of each tergum smooth; Mt6 and Mt7 isodiametric-coriaceous to isodiametric-reticulate; syntergum finely coriaceous, with sides concavely convergent to apex, 0.83 times as long as basal width; relative length of terga (begining with Mt2) = 4.0(pm), 2.5, 3.5, 4.0, 4.2(m), 6.0, 3.3. **Hypopygium small**, extended to about apex of Mt4. **Ovipositor sheaths** dark brown, slightly (2.7) exserted beyond syntergum.

MALE. Length = 0.24 cm. **HEAD** (Figs. 5.8, 5.9) similar to that of female in color, structure, and sculpture, except umbilications not concave, only very slightly depressed and conspicuous by their color rather than as distinct punctures; relative measurements, HW = 7.2, HH = 5.8, HL = 3.8; POL = 2.4, LOL = 1.0, OOL = 0; eye height = 4.0, width = 2.8, distance between below = 5.8, above = 3.4. **Antenna** inserted distinctly above line drawn between lower margin of eyes, distance between lower edge of toruli and clypeal edge compared with malar space = 2.2:2.0; flagellum with basal rami on fu1-fu6, rami curved and each projected approximately to apex of subsequent funicular; fu1 and fu2 cylindrical, with subsequent funiculars increasingly compressed, but all rectangular except for subtriangular fu7, latter conspicuously widened distally with straight ventral edge and curved dorsal edge, and with small dorsoapical projection; relative measurements, scape = 3.0(0.5), pedicel = 0.6(0.6), anellus = 0.1(0.4); funiculars = 1.8(0.5), 1.8(0.6), 2.0(0.8), 2.1(0.9), 2.0(0.9), 2.0(0.8), 1.5(1.1), clava = 3.1(1.0). **Scrobes** (Figs. 5.8, 5.9) relatively shorter and wider than in females, with L:W = 3.7:1.5.

MESOSOMA (Figs. 5.18, 5.48) similar in color to females, except acropleuron with violaceous luster, and propodeum entirely bluish-green; sculpture similar to females, but finer on plical region of propodeum so as to be isodiametric-coriaceous; setation similar to that of females; and structure similar to that of females, except propodeum without plical furrows; relative measurements, length of scutellum to width of scutellar-axillar complex = 4.0:4.8, width of DAS to distance between DAS = 1.8:1.2, length of dorsellum to medial length of propodeum = 0.3:1.5. **Wings** hyaline, with brownish venation; superficially glabrous, but with very sparse, short setae; fore wing with SMV = 7.5, MV = 3.1, PMV = 0.6, STV = 0.3. **Legs** with coxae, femora, and tibiae violaceous, but otherwise similar to females; middle leg with tibia = 6.2, tarsomeres = 1.5, 0.5, 0.4, 0.4, 0.5.

METASOMA similarly colored to females, but green of Mt2 and coppery color of dorsum of other terga not as conspicuous; similar in setation and sculpture to females, except with generally finer sculpture [structure can not be accurately described because of compressed condition distal to Mt3 (see section on variation)].

Variation. The female paratypes are all very similar to the holotype, 0.35-0.50 cm in length, differing primarily in that the propodeum is entirely bright green and the dorsal edges of fu1-fu3 are not distinctly convex in all specimens.

Males are also similar to the allotype, 0.20-0.30 cm in length, but most have the propodeum brilliant green in distinct contrast to the mesothorax and metasoma, and there is some variation in length of the antennal rami. Each ramus extends at least half the length of the subsequent funicular, and at most slightly beyond the apex of the subsequent funicular. The metasoma is variedly compressed, or collapsed-flattened, but lanceolate when flattened, and then the posterior margins of Mt2-Mt6 are roundly incised (those of Mt3-Mt6 somewhat more broadly than Mt2). Mt2 is about 0.3-0.4 length of the metasoma, Mt3-Mt6 are transverse-rectangular and increased slightly in length distally, and Mt7 has sides distinctly convergent towards apex and is subequal with, to about 1.5 times longer than Mt6, and about 1.5-1.9 times as long as semicircular syntergum.

Distribution. Southwestern USA (Arizona and Texas).

5.5.3 *Paraeusandalum* new genus

(Fig. 44)

Type-species. *Paraeusandalum chilensis* new species, by present designation.

Derivation of generic name. Combination of greek word "para", meaning "near", and generic name *Eusandalum* Ratzeburg; referring to presumed close phylogenetic affinity of the two taxa. Gender: neuter.

Description. HEAD. Inner orbits raised, with coarse cristae along scrobal cavity. Scrobal cavities separated ventrally by very narrow interantennal region; coextensive above as narrow, deep channel, with sides abrubtly declivous, and with carinate dorsal edge subcontiguous with median ocellus. Ocelli in relatively flat triangle; median ocellus on conical tubercle slightly behind carinate edge of scrobal cavity; posterior ocellus subcontiguous with upper eye orbit. Eye almost glabrous. **Antenna.** Two known females lack complete antennae, but probably 11-articled; inserted subcontiguously, with distance between inner edge of toruli slightly less than width of torulus and about 0.17 distance between outer edge of torulus and inner eye margin. Scape extended slightly beyond vertex. Anellus elongate-cylindrical, about 2 times as long as wide. Flagellum probably conspicuously elongate-slender, with distal articles possibly slightly compressed (subcylindrical); fu1 about 8 times as long as wide; clava probably inconspicuously differentitated from funicular articles, not divided by transverse sutures, and about equal in length and width to fu7.

MESOSOMA. Pronotum campanulate and conspicuously narrower than mesoscutum. **Mesonotum.** Mesoscutum relatively broad, about 1.6 times wider than long; distinctly 'shoulder-like' on either side of pronotum, with anterior margin of lateral lobes almost right-angled to side; relatively evenly convex, but slightly flattened dorsally or paramedially depressed anterior to DAS. Notauli V-shaped convergent within anterior 0.5 mesoscutum, linear and obscure as subeffaced line of sculpture. Parapsidal line obscure as small region of granulate sculpture near anterior margin of mesoscutal lateral lobe adjacent to notaulus. Scutellar-axillar complex with almost straight convergent (slightly sinuate) scutoscutellar sulci; DAS triangular with basomedial angles subcontiguous; scutellum relatively flat, with acute basomedial angle at transscutal articulation. **Prepectus** extended to base of tegula; lateral surface evenly curved to frontal surface, not anteriorly protuberant beneath mesothoracic spiracle. **Mesopleuron** (Fig. 5.44). Acropleuton dorsally, extended almost to metapleuron, separate by only very slender or linear upper mesepimeron, evenly convex; acropleural sulcus distinct posteriorly, and ventrally for about 0.5 distance between mesocoxa and anteroventral angle of prepectus, then abruptly reflexed to anterodorsal edge of pleuron slightly distad of middle of prepectus as much finer sulcus. Mesopleural suture distinct, extended dorsally to acropleural sulcus and here recurved posteriorly to metapleuron as transepimeral sulcus (best observed from posteroventral angle). Mesepimeron as linear upper mesepimeron and relatively large, rectangular to rhomboidal lower mesepimeron, or only latter region. Mesepisternum without transepisternal line; upper mesepisternum with relatively large triangular region between prepectus and acropleuron, and between acropleuron and lower mesepimeron; lower mesepisternum deeply incurved anterior to mesocoxae, with relatively large, separate, subcircular membranous regions anterior to each mesocoxa; trochantinal lobes separate. **Metathorax**. Metanotum U-shape behind scutellum, dorsellum short to linear, with apex of scutellum almost extended to propodeum. Metapleuron triangular, narrowed dorsally. **Legs**. Fore leg with spine-like spicules on dorsal edge of tibia, and with 2 slightly more robust dorsoapical spicules. Middle leg without peg-like spines along anterodistal edge of tibia; tibial spur thickened and setose, about 1.33 times apical width of tibia; tarsus relatively long, about 0.66 times length of mesotibia, and not thickened proximally; basitarsus short, only about 0.25 times length of tibia and subequal in length to tarsomeres 2-4; tarsomeres 1-4 ventrally with row of slender spines along anterior edge and row of peg-like spines along posterior edge, except spine-like proximally on basitarsus. Hind leg without spicules on dorsal edge of tibia nor with dorsoapical spicules. **Wings.** Fore wing setose; SMV about 1.75 times longer than MV; PMV gradually attenuated, but at least as long as elongate PMV; and STV expanded distally, with uncus. Hind wing with short spike-like basal vein. **Propodeum** with foramen relatively widely but shallowly incurved, edge recurved as carinae; median length subequal to that of relatively long petiole; plical region entire region between spiracles, but conspicuously differentiated from callar regions by prominent, percurrent, plical carina contiguous with inner edge of each spiracle, without or with only very fine and obscure median carina; callar region setose; edge of propodeal foramen recurved as carina.

METASOMA 8-segmented (?); elongate-lanceolate with long slender apex. Mt1 (petiole) relatively long and wide; Mt2 to Mt5 with posterior margins shallowly incised medially; Mt6 with posterior margin broadly incurved; Mt7 with posterior margin evenly rounded and extended slightly beyond level of cerci; Mt8 and Mt9 separate at least laterally by suture below cercus, but not possible to determine if independent dorsally in two available specimens; ultimate tergum elongate-narrow in dorsal view. Cercus button-like.

Distribution. Known only from Neotropical region (Chile).

Host. Unknown, but most likely xylophagous beetles (Coleoptera).

Generic diversity. The type species is the only known member of the genus.

Monophyly and relationships. Monophyly of *Paraeusandalum* is not supported by known autapomorphic states for Calosotinae, and the genus could be ancestral to *Eusandalum*, *Chirolophus*, or both; hypotheses of relationships with the latter two genera are illustrated in figures 5.1a, 5.1b, and discussed in section 5.7.2.1.

5.5.3.1 *Paraeusandalum chilensis* new species

(Fig. 44)

Type material. HOLOTYPE - Female.Chile , Linares, San Pablo, Cord. Parral, 17.XI.1960, Pẽna (CNC). PARATYPE - 1 ♀. Chile, Santiago, El Canelo, XI-XII.1978, Luis Pe˜na (HTC). **Condition of holotype.** Entire, except for antennae, which are missing beyond ful; glued by mesopleuron to pin.

Derivation of specific epithet. Based on type-locality.

Description. FEMALE. Length = 1.05 cm. **HEAD** dark with coppery reflection on vertex and face, and isolated blue or green reflections at some angles, particularly along edges of scrobal cavity. Head markedly convex in lateral view, inner orbits abruptly raised, much wider than scrobes ventrally, but distinctly narrowed dorsally, with width of scrobes to width of inner orbits (measured below median ocellus) =2.6:2.6; vertex abruptly declined from raised inner orbits and at distinct angle to frons, with region posteromedial to ocelli distinctly concave; origin of cristae along inner orbits slightly above ventral edge of eye, denticle-like and in single line ventrally, but dorsally wider, anteriorly arcuate, and in 2 or 3 slightly offset rows as oblong region; relative measurements, HW = 17.2, HH = 14.5, HL = 11.5 (not including height of cristae). Frontal aspect of head isodiametric-reticulate, with cells relatively large (maximum 0.7), except granulate below interantennal region, and inner orbits lateral to and somewhat below oblong patch of cristae abruptly rugulose, or reticulate but with very small cells; vertex with raised posterior surface of inner orbits (between lateral ocelli and cristae) tiny isodiametric-reticulate, between inner orbits and median ocellus smooth and shining, and reticulate posterior to posterior ocelli, with size of cells intermediate between those on frontal aspect of head and on posterior surface of inner orbits; occiput coriaceous. **Mouthparts.** Labrum brown; maxilla and labium dark brown, except stipes with green reflection. **Antenna**

dark brown, except scape with obscure bluish reflection at some angles; inserted very close to anterior edge of head capsule, distinctly below level of ventral margin of eyes, with distance between lower edge of toruli and clypeal edge compared with malar space = 1.6:6.0; scape elongate-slender, straight; relative measurements, scape = 11.4(1.1), pedicel = 2.1(1.0), anellus = 2.0(0.9), funiculars = 8.0(1.1) [antenna missing distally]. **Ocelli** with POL = 4.3, LOL = 2.4, OOL = 0.1; median ocellus faced dorsally on conspicuous conical tubercle posteromedial to raised inner orbits; posterior ocelli faced posteriorly on declined vertex. **Eye** oval, H:W = 9.0:7.1; distance between eyes below = 13.4, above = 7.0. **Scrobes** elongate-slender, H:W = 12.9:3.5; smooth and shining within channel.

MESOSOMA dark with coppery luster, with greenish reflection at some angles, particularly along extreme anterior edge of mesoscutum and scutellum; tegula dark brown with greenish reflection; relatively evenly setose with unmodified white setae, except following glabrous: metanotum, plical region of propodeum, and acropleuron. **Pronotum** isodiametric-reticulate on sides, rugulose-reticulate dorsally; with shallow and obscure mediolongitudinal furrow extended from posterior edge. **Mesothorax** with mesonotum minute isodiametric-reticulate along extreme anterior edge posterior to pronotum, dorsally isodiametric-reticulate with larger cells similar in size to those on frontal aspect of head, cells slightly smaller over convex sides of lateral lobes; scutellar-axillar complex isodiametric-reticulate, cells somewhat smaller than those dorsally on mesoscutum; prepectus and acropleuron (Fig. 5.44) isodiametric-reticulate, cells about same size as on scutellum, but decreased in size posteriorly on acropleuron, abruptly so near posterior angle, and isodiametric-coriaceous to elongate-coriaceous along extreme posterior edge; upper and lower mesepisterna coriaceous-reticulate to alutaceous; upper mesepimeron very slender (0.5), but visible between acropleuron and metapleuron; lower mesepimeron coriaceous. Scutellar-axillar complex elongate, length of scutellum to width of complex = 11.2:10.0. **Metathorax** with pleuron reticulate-coriaceous; dorsellum minute-coriaceous (granulate), length to medial length of propodeum =0.5:2.0. **Propodeum** with plical region reticulate posterolaterally near plical carina, but obliquely strigrose over fine coriaceous sculpture medially, with very fine and obscure median carina; callar regions reticulate. **Wings** slightly embrowned, venation brown; fore wing with SMV = 24.6, MV = 13.4, PMV gradually attenuated, with apex difficult to discern, but at least as long as MV and extended to near apex of wing, STV = 2.8. **Legs** with coxae dark brown, but with lateral surfaces of pro- and metacoxae coppery and lateral surface of mesocoxa greenish; femora dark brown with slight coppery luster on outer surface at some angles; tibial-femoral joints yellowish, tibiae otherwise dark brown basally and gradually lightened to yellowish brown apically; tarsi yellowish-brown with distal tarsomeres brown. Middle leg with tibia = 20.4; tarsomeres = 5.7, 2.8, 1.7, 1.3, 1.6.

METASOMA dark with slight coppery or greenish luster at different angles, except ultimate tergum with distinct greenish-blue luster; relatively evenly setose with conspicuous white setae laterally, and with Mt7 and ultimate tergum less conspicuously setose with shorter, brown setae. Mt1 (petiole) transversely costate; Mt2-Mt7 alutaceous laterally; Mt2 dorsally shining and almost smooth, with only very fine coriaceous sculpture; Mt3 almost indistinguishable as very thin and translucent cuticle, only slightly projected paramedially beyond apex of Mt2; Mt4-Mt6 finely transverse-alutaceous basally to finely coriaceous apically; Mt7 transverse-rugulose roughened; ultimate tergum entirely rugulose-reticulate; ultimate tergum highly convex with sides parallel over most of length, 10.2 times as long as basal width; relative length of terga = 1.5(m), 11.2(pm), 1.6, 6.4, 7.7, 8.1(m), 17.1, 24.6. **Hypopygium** long, extended slightly beyond apex of Mt6. **Ovipositor sheaths** dark brown, slightly (3.0) exserted beyond ultimate tergum.

MALE. Unknown.

Variation. The single female paratype is similar to the holotype except for the following: approximately 0.7 cm in length; acropleuron only linearly separated from metapleuron, as is apex of scutellum from propodeum; upper mesepisternum more distinctly reticulate, similar to prepectus; and Mt1 (petiole) conspicuously coriaceous, though less conspicuously costate. The antennae of the paratype are also broken, but the basal 5 funiculars of the right antenna are present; relative measurements, scape = 9.1(0.9), pedicel = 2.0(0.9), anellus = 1.5(0.7), funiculars = 5.6(0.7), 4.6(0.6), 4.1(0.7), 3.4(0.8), 2.9(0.8).

Distribution. Chile.

5.5.4 *Eusandalum* Ratzeburg

(Figs. 5.5-5.7, 5.19, 5.20, 5.45, 5.46, 5.63, 5.67, 5.89, 5.92, 5.100, 5.109)

Stenocera Curtis, 1836: 596. Preoccupied by *Stenocera* Brullé, 1834. **Type species:** *S. walkeri* Curtis. Monotypy. **Type depository:** NMVM.

Eusandalum Ratzeburg, 1852: 199. **Type species:** *E. abbreviatum* Ratzeburg. Subsequent designation by Ashmead, 1904: 288. **Type depository:** NHMV.

Polymoria Förster, 1856: 31. **Type species:** *P. coronata* Thomson, 1876. Subsequent monotypy by Thomson, 1876: 111. **Type depository:** UZIL. Synonymy by Bouček, 1967: 262.

Ratzeburgia Förster, 1856: 31, 145. **Type species:** *Eusandalum abbreviatum* Ratzeburg, 1852: 200. Subsequent designation by Gahan and Fagan, 1923: 128. **Type depository:** NHMV. Isogenotypic *vide* Gahan and Fagan, 1923: 128.

Stenoceroides Dalla Torre, 1897: 88. New name for *Stenocera* Curtis 1836, nec Brullé 1834. Synonymy by Bouček, 1967; reestablished as valid genus by Bouček, 1970; **synonymy reestablished.**

Meseusandalum Girault, 1915: 34. **Type species:** *M. cyaneiventris* Girault. Original designation. **Type depository:** QMB. Synonymy by Girault, 1917b: 35.

Polymorioides Masi, 1941: 154. **Type species:** *P. tessellatus* Masi. Monotypy and original designation. **Type depository:** MSNG. Synonymy by Bouček, 1967: 262.

Notosandalum De Santis, 1968: 145. **Type species:** *N. filicornis* De Santis. Monotypy and original designation. **Type depository:** MLP. **New synonymy.**

Description. HEAD (Figs. 5.5-5.7) more or less lenticular in lateral view in most species, but quadrate or rectangular in some species from Australia; upper inner orbits raised in at least narrow band adjacent to eye, and with fine to coarse cristate sculpture in most species, but inner orbits flattened and without differentiated sculpture in some species. Scrobal cavities separated ventrally by triangular interantennal region, coextensive above in most species as subparallel to parallel-sided, deep channel (conspicuously deeper and narrower in females than in males of many species, *cf.* Figs. 5.5, 5.7); gradually shallowed to median ocellus in most species. Ocelli in very wide, almost flat triangle; median ocellus at upper margin of scrobal cavity; posterior ocellus within one ocellar diameter of eye orbit, but not contiguous with orbit. Eye inconspicuously setose to apparently glabrous. **Antenna** 11-articled in both sexes (see below for rare exception); inserted subcontinguously, distance between inner edge of toruli less than or subequal in width to torulus, and 0.25 or less than distance between outer edge of torulus and inner eye margin. Scape subcylindrical in most species, but markedly compressed-rectangular in few; extended to vertex or beyond. Anellus elongate-cylindrical to subquadrate or transverse in females, but short to transverse in males and difficult to distinguish in some specimens. Flagellum of females conspicuously elongate-slender in most species, with proximal articles slightly to strongly compressed and flagellum distally tapered in many species; funiculars decreased in length distally, but minimally twice as long as wide and at least apical funiculars slightly compressed (subcylindrical); clava inconspicuously differentiated from funicular articles, not distinctly divided by sutures and much smaller than or subequal in width and length to fu7. Flagellum of males filiform in most species, but pectinate in few; pectinate antennae with basal four flagellomeres, or as many as all 7 flagellomeres each having basal, variedly long ramus; rami cylindrical and conspicuously setose, or markedly compressed with numerous and conspicuous multiporous plate sensilla, hence appearing longitudinally or obliquely strigose; flagellum as long as metasoma to longer than entire body, not or only slightly tapered toward apex and with articles cylindrical to markedly compressed; clava inconspicuously differentiated from funicular articles, not distinctly divided by sutures nor wider than fu7, but in most species slightly to distinctly longer than fu7 (three specimens seen from Caribbean islands with compact antennae similar to species of *Calosota* Curtis, with clava 3-articled by transverse sutures and subequal in length to fu6 + fu7!)

MESOSOMA. **Pronotum** (Figs. 5.19, 5.20) campanulate, narrower than mesoscutum and in some species with transverse, possibly carinate ridge. **Mesonotum** (Figs. 5.19, 5.20). Mesoscutum broad, about 1.3-1.7 times wider than long; lateral lobes with anterior margin almost right-angled relative to side, as small to wide 'shoulder' on either side of pronotum; moderately convex to relatively flat, but paramedially depressed to varied degrees anterior to inner angles of DAS. Notauli linear, impressed, or as line of differentiated sculpture or color; V-shaped convergent within anterior 0.5 mesoscutum, but in many individuals obscure posteriorly, effaced before midline, or posteriorly recurved near midline and subparallel distally. Parapsidal lines inevident in most species, at best as obscure band or region of finer or subeffaced sculpture near anterior margin of mesoscutal lateral lobe adjacent to notaulus. Scutellar-axillar complex with convex scutoscutellar sulci, parallel or subparallel basally, but divergent distally; DAS subtriangular, with basomedial angles separate; scutellum flat and of distinctive 'gourd' shape, with wide to narrow petiolate base. **Prepectus** extended to base of tegula (Fig. 5.45) or conspicuously separate from tegula; anteriorly protuberant beneath mesothoracic spiracle as small, acutely pointed lobe (*cf.* Figs. 5.46, 5.47, 5.67). **Mesopleuron** (Figs. 5.45, 5.67). Acropleuron extended to metapleuron, and in many species to mesocoxa, evenly and conspicuously convex; acropleural sulcus distinct ventrally to point about in line with base of tegula, here abruptly reflexed toward anterodorsal edge of pleuron as posteriorly arcuate line of subeffaced or differentiated sculpture in most species (Figs. 5.45, 5.67), but as deeply impressed, straight sulcus in few species, and in most species sulcus extended almost horizontally from near base of metapleuron (Fig. 5.45), but in very few species with sulcus distinctly sinuate, similar to some species of *Chirolophus* Haliday (*cf.* 5.47). Mesopleural suture inevident if acropleuron expanded to mesocoxa, or as obscure furrow or short line of altered or effaced sculpture extended from anterior of mesocoxa dorsally to acropleuron, *i. e.*, not extended to apex of acropleuron as in *Chirolophus* species. Mesepimeron inevident, or with only small, elongate-rectangular to rhomboidal lower mesepimeron. Mesepisternum with transepisternal line as depigmented line or line of altered sculpture; lower mesepisternum deeply incurved anterior to mesocoxae, with large, oval, membranous region anterior to each mesocoxa (Fig. 5.67); trochantinal lobes widely separate. **Metathorax.** Metanotum variedly developed, in most species dorsellum broadly U-shape or transverse-rectangular, with scutellum distinctly separate from propodeum, but V-shape linear in few species, with scutellum extended almost to propodeum (Fig. 5.63). Metapleuron narrow, subtriangular to lunate. **Legs.** Fore leg with denticles or spine-like spicules on dorsal edge of tibia in most species (*cf.* Fig. 5.88), and with 2-4 small dorsoapical spicules (Fig. 5.89). Middle leg (Fig. 5.92) without peg-like spines along anterodistal edge of tibia; tibial spur thickened and setose, but only subequal in length to apical width of tibia; tarsus relatively short, about 0.7 times or less than length of mesotibia in most species, and not, or only slightly thickened proximally; basitarsus short, in most species about 0.25 times or less length of tibia and subequal in length or shorter than tarsomeres 2 + 3; tarsomeres 1-4 ventrally with row of slender spines along anterior edge and row of peg-like spines along posterior edge. Hind leg with spine-like or more robust spicules on dorsal edge of tibia in most species, and with dorsoapical spicules. **Wings.** Fore wing highly varied in setation and venation; conspicuously setose in some species, with only extreme base and elongate-band beneath parastigma glabrous, but in most species basal cell also glabrous and in many species setation further reduced to absent (many specimens with conspicuously setose wings have MV half as long as SMV or longer, PMV at least twice as long as STV to as long as MV, and STV relatively long, curved, distally expanded and with uncus, whereas most specimens with reduced setation or glabrous wings have reduced venation, particularly PMV and STV, which may be very short to punctiform and subequal in length). Hind wing with short spike-like basal vein. **Propodeum** of females (Fig. 5.63) with foramen relatively widely, roundly to rectangularly incurved, edge carinate or not; short medially, but subequal to or slightly longer than petiole, and distinctly longer than metanotum in most species; plical region in most species relatively narrow, convex, and conspicuously differentiated from callar regions by percurrent plical furrow distinctly mesad of each spiracle (Fig. 5.63), with fine median carina in some species; callar region partly to entirely setose. Propodeum of males (Fig. 5.20) with foramen relatively much narrower and more deeply incurved than in females, but median length relatively much longer, at least twice that of petiole or metanotum; plical and callar regions inconspicuously differentiated in most species by short, deep fovea at anterior margin of propodeum mesad of spiracle, or by shallowly obscure groove or carina extended anteriorly from propodeal foramen toward posterior margin of spiracle, or both; plical region with fine median carina in only few species.

METASOMA of females 9-segmented; lanceolate to elongate-lanceolate with long slender apex in many species. Mt1 (petiole) wide, very slender to subcresentic or subtriangular; sculpture similar to that of plical region in most species. Mt2-Mt5 with posterior margins medially incised to varied degrees, or in some species posterior margins of Mt3-Mt5 entire and transverse; Mt6 with posterior margin broadly incurved; Mt7 with posterior margin rounded and extended almost to or slightly beyond level of cerci (Fig. 5.109); Mt8 and Mt9 independent or only partly fused, dorsally with distinct transverse suture between cerci (not externally visible if Mt7 extended beyond level of cerci), and laterally with oblique suture below cercus; Mt9 short and stubby to elongate-slender in dorsal view, evenly convex to triangular in cross-section and with median longitudinal ridge or carina in many species. Cercus button-like.

Metasoma of males 8-segmented; subcylindrical to ovate or lanceolate. Petiole slender, but much narrower than in females and smooth and shining in most species. Mt2-Mt7 with posterior margins entire and transverse; Mt8 and Mt9 indistinguishably fused as syntergum, this very short with posterior edge rounded and in many species with dorsal or dorsoapical surface angled ventrally or almost vertical, 'hood-like'.

Synonymy. Bouček (1967) justified the synonyms of *Eusandalum* listed above, except for the later described genus, *Notosandalum* De Santis (1968). This genus was established for a South American species, females of which differed from the generic description given by Bouček (1967) for *Eusandalum* in having an elongate anellus and a postmarginal vein that is slightly longer than the marginal vein. Individuals also have the inner orbits evenly convex, without raised or differentiated sculpture. However, these character states are of specific value only, and I consequently synonymize the name *Notosandalum* with *Eusandalum*.

Bouček (1967) first synonymized the name *Stenoceroides* Dalla Torre with *Eusandalum*, but later (1970) resurrected *Stenoceroides*, primarily on the basis of males of the monotypic type species having pectinate antennae. Males of other species from the Ethiopian, Oriental, and Australian regions also have pectinate antennae (with 4, 5 or 7 rami) and I consider this to be of only specific value. I therefore reestablish synonymy of the names *Stenoceroides* and *Eusandalum*, as first proposed by Bouček (1967).

Distribution. Known from all biogeographic regions.

Hosts. Xylophagous beetles (Coleoptera) of the families Anobiidae, Bostrichidae, Buprestidae, Cerambycidae, Curculionidae, Lyctidae and Scolytidae.

Monophyly and relationships. Monophyly of *Eusandalum* is indicated by shape of the dorsal axillar surfaces (DAS) (Figs. 5.19, 5.20) [Table 5.1, 10(3b)], and possibly by the elongate mesoscutal process for pl$_2$-t$_2$c [9(2a)]. However, distribution of this latter state in members of the genus has to be documented more comprehensively. Hypotheses of relationships of *Eusandalum* in Calosotinae are illustrated in figures 5.1a, 5.1b, and discussed in section 5.7.2.1.

Keys to species. Girault 1917a (Nearctic); Ruschka 1921 (Palearctic); Bolivar y Pieltain 1923a, 1926 (Spain); Nikolskaya 1952 (USSR); Erdös 1960 (Hungary); Bouček 1967 (Palearctic); Hedqvist 1970 (Ethiopian).

Catalog of taxa. *E. abbreviatum* Ratzeburg, 1852; NHMV; P - Germany. = *E. inerme* (Ratzeburg), syn. by Bouček (1967).

**E. acmaeoderae* Girault, 1917a; USNM; N - USA.

**E. affine* (Hedqvist, 1970); BMNH, KHPC; E - South Africa. As *Polymoria* Ratzeburg, comb. by Bouček (1976).

E. afganum Bouček, 1967; MAKB, ZBPC; P - Afghanistan.

E. alfierii (Bolivar, 1925); (lost *vide* Bouček 1967); P - Egypt. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. alpinum* Girault, 1917a; USNM; N - USA.

**E. amphicerovorum* (Ashmead, 1888); USNM; N - USA. As *Ratzeburgia* Förster, comb. by Dalla Torre (1898).

E. arboris Girault, 1922; QMB; A - Australia.

**E. arizona* Girault, 1917a; USNM; N - USA.

**E. bambeyi* Risbec, 1951; MNHP; E - Senegal.

E. barteli (Gourlay, 1928); CIN; A - New Zealand. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. bicristatum* Risbec, 1951; MNHP; E - Senegal.

E. brevistylus Girault, 1922; QMB; A - Australia.

E. brevistylus var. aereifemora Girault, 1922; QMB; A - Australia.

E. bucklei Girault, 1925; QMB; A - Australia.

E. calabrum (Masi, 1941); MSNM; P - Italy. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. californicum* Girault, 1917a; USNM; N - USA.

E. cavifrons (Nikolskaya, 1952); ZIL; P - Russia. As *Polymoria* Ratzeburg, = *E. flavipenne* Ruschka; comb. and syn. by Bouček (1967).

E. chrysideum* (Ashmead, 1900); BMNH; Nt - West Indies, St. Vincent. As *Calosoter* Walker, **n. comb.

E. compressiscapus (Girault, 1915); QMB; A - Australia. As *Meseusandalum* Girault, comb. by Girault (1917b).

E. compressistylus Girault, 1922 (and 1923!); QMB; A - Australia.

**E. coquillettii* (Ashmead, 1896); USNM; N - USA. As *Ratzeburgia* Förster, comb. by Dalla Torre (1898).

**E. coronatum* (Thomson, 1876); UZIL; P - Sweden. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. curculionis* (Risbec, 1951); MNHP; E - Senegal. As *Polymoria* Ratzeburg, transferred to *Calosota* Curtis by Bouček (1976).

E. cyaneiventre (Girault, 1915); QMB; A - Australia. As *Meseusandalum* Girault, comb. by Girault (1917b).

**E. cyaneum* (Ashmead, 1896); USNM; N - USA. As *Ratzeburgia* Förster, comb. by Dalla Torre (1898).

**E. cyaneum* (Hedqvist, 1970); BMNH; E - South Africa. As *Polymoria* Ratzeburg, comb. by

Bouček (1976).

E. dalmatica (Ruschka, 1921); NHMV; P - Yugoslavia. As *Polymoria* Ratzeburg, = *E. flavipenne* Ruschka; comb. and syn. by Bouček (1967).

**E. desmanthusae* Risbec, 1952; MNHP; E - Madagascar.

E. dezorti Bouček, 1967; NMP; P - Czechoslovakia.

E. elongatum (Ruschka, 1921); NHMV; P - Germany. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. elongatum* (Hedqvist, 1970); BMNH, KHPC; E - South Africa. As *Polymoria* Ratzeburg, comb. by Bouček (1976); see *E. hedqvisti* Bouček.

**E. excavatum* (Hedqvist, 1970); BMNH; E - South Africa. As *Polymoria* Ratzeburg, comb. by Bouček (1976).

**E. filicornis* (De Santis, 1968); MLP; Nt - Argentina. As *Notosandalum* De Santis, n. comb.

E. flavipenne Ruschka, 1921; NHMV; P - Germany.

E. fucus (Nikolskaya, 1952); ZIL; P - USSR. As *Polymoria* Ratzeburg, = *E. merceti* (Bolivar); comb. and syn. by Bouček (1967).

**E. gardneri* (Mani & Kaul, 1973); USNM; O - India. As *Macromesus* Walker (Pteromalidae), comb. by Bouček *et al.* (1978).

**E. georgia* Girault, 1917a; USNM; N - USA.

E. gomezi (Bolivar, 1926); IEEM; P - Spain. As *Polymoria* Ratzeburg, = *E. coronatum* (Thomson); comb. and syn. by Bouček (1967).

**E. halyomorphae* (Risbec, 1951); MNHP; E - Senegal. As *Polymoria* Ratzeburg, transferred to

Calosota Curtis by Hedqvist (1970).

E. hedqvisti Bouček, 1976. New name for _E. elongatum_ (Hedqvist, 1970).

*_E. hubbardii_ (Ashmead, 1896); USNM; N - USA. As _Ratzeburgia_ Förster, comb. by Dalla Torre (1898).

*_E. hyalinipenne_ (Ashmead, 1896); USNM; N - USA. As _Ratzeburgia_ Förster, comb. by Dalla Torre (1898).

E. ibericum (Bolivar, 1923a); IEEM; P - Spain. As _Polymoria_ Ratzebu[illegible]comb. by Bouček (1967).

E. impressifrons Girault, 1922; QMB; A - Australia.

E. inerme (Ratzeburg, 1848); NHMV; P - Germany. As _Eupelmus_ Dalman (Eupelminae), comb. by Ratzeburg (1852).

*_E. koebelei_ (Ashmead, 1896); USNM; A - Australia. As _Chirolopus_ Haliday, **n. comb.**

*_E. latifrons_ (Hedqvist, 1970); BMNH; E - South West Africa. As _Polymoria_ Ratzeburg, comb. by Bouček (1976).

E. lepus Girault, 1918 (and 1921!); ?; A - Australia.

E. longiannulum Girault, 1929; ?; A - Tasmania.

E. longistylus Girault, 1922; QMB; A - Australia.

E. longivena Bouček, 1967; ZIL, ZBPC; P - USSR.

*_E. menozzii_ (Masi, 1940); MSNG; P - Italy. As _Polymoria_ Ratzeburg, = _E. inerme_ (Ratzeburg); comb. and syn. by Bouček (1967).

E. merceti (Bolivar, 1926); IEEM; P - Spain. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. obscurum* Girault, 1917a; USNM; N - USA.

E. pici Schrottky, 1906; destroyed; Nt - Paraguay.

E. puella (Nikolskaya, 1952); ZIL; P - USSR. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

E. sanguinipes Girault, 1925; QMB; A - Australia.

E. segurensis (Bolivar, 1926); IEEM; P - Spain. As *Polymoria* Ratzeburg, = *E. coronatum* (Thomson); comb. and syn. by Bouček (1967).

E. seyrigi (Bolivar, 1926); IEEM; P - Spain. As *Polymoria* Ratzeburg, comb. by Bouček (1967).

**E. striatum* Risbec, 1952; MNHP; E - Madagascar.

E. stylatum (Girault, 1915); QMB; A - Australia. As *Meseusandalum* Girault, comb. by Girault (1917b).

**E. stylatum* (Hedqvist, 1970); BMNH, KHPC; E - South West Africa, South Africa. As *Polymoria* Ratzeburg, comb. by Bouček (1976).

**E. tessellatum* (Masi, 1941); MSNG; E - Somalia. As *Polymorioides* Masi, comb. by Bouček (1967).

E. tridens Ratzeburg, 1852; destroyed; P - Germany. = *E. inerme* (Ratzeburg), syn. by Bouček (1967).

E. usingeri Yoshimoto & Ishii, 1965; BPBM; O - Guam.

E. walkeri (Curtis, 1836); NMVM; P - Britain, Germany. As *Stenocera* Curtis, comb. by Bouček (1967).

5.5.5 *Chirolophus* Haliday

(Figs. 5.21, 5.47, 5.64, 5.110)

Chirolophus Haliday, 1862: 117. **Type species:** *C. eques* Haliday. Monotypy. **Type depository:** NHMV.

Charitolophus Förster, 1878: 69. **Type species:** *C. coerulescens* Förster. Monotypy and original designation. **Type depository:** NHMV. Synonymy by Ruschka, 1921: 251.

Description. HEAD. Inner orbits wide, flattened, without differentiated sculpture in most species, but slightly raised along upper inner orbits in some species, and here with minute and fine sculpture in contrast to coarser sculpture of rest of orbits. Scrobal cavities of females separated ventrally by triangular interantennal region; coextensive above as narrow, relatively deep channel with abruptly declivous, margined, subparallel sides; shallowed toward but not extended to median ocellus. Scrobal cavities of males separated ventrally by only small, lowly convex interantennal region; coextensive above as broad, shallowly concave region; not extended to median ocellus. Ocelli in low triangle; median ocellus faced more or less anteriorly and distinctly above scrobal cavity; posterior ocellus one or more ocellar diameters from eye margin. Eye inconspicuously setose. **Antenna:** 11-articled, or 13-articled if clava divided by transverse sutures; inserted close together, distance between inner edge of toruli subequal to width of torulus and about 0.33 distance between outer edge of torulus and inner edge of eye margin. Scape extended to dorsal edge of median ocellus. Anellus slightly longer than wide, and dorsally with conspicuous white setae in females of some species; short and wider than long in males, without differentiated setae. Flagellum of females relatively slender to compact, ful about 3-5 times longer than wide, but other funiculars only about 2 times longer than wide, or shorter; funiculars cylindrical or slightly compressed, and all of equal diameter or increased slightly in width distally; fu1 or fu1-fu3 dorsally with dense long white setae in distinct contrast to subsequent funiculars in most species; clava slightly to distinctly wider than fu7, only slightly shorter than to longer than fu6 + fu7, and in *C. hyalinus* Hedqvist, divided by distinct transverse sutures. Flagellum of males pectinate, fu1-fu5 each with [illegible] ramus; rami compressed, spatulate, and very long, all extended to about apex of fu7, or slightly beyond; rami asetose, but with numerous and conspicuous multiporous plate sensilla, hence appearing strigose; clava inconspicuously differentiated from funicular articles in known males, not divided by distinct sutures, and subequal in width but slightly longer than fu7.

MESOSOMA. **Pronotum** (Fig. 5.21) campanulate and much narrower than mesoscutum [illegible] (Fig. 5.21). Mesoscutum broad, about 1.5-1.6 times wider than long; distinctly [illegible]ike' on either side of pronotum, with anterior margin of lateral lobes almost [illegible]ed to side; relatively evenly convex, but somewhat flattened dorsally or paramedially depressed anterior to inner angles of DAS. Notauli linear, sinuately V-shaped convergent within anterior 0.5 mesoscutum; obscure in females as subeffaced line of sculpture, but more distinct as line of minute and fine sculpture in males. Parapsidal line as short band of minute and fine sculpture near anterior margin of mesoscutal lateral lobe adjacent to notaulus. Scutellar-axillar complex with straight convergent ~~or very~~ slightly concave scutoscutellar sulci; DAS elongate-subtriangular with basomedial angles widely separate, distance between inner angles greater than width of DAS; scutellum ovate, very slightly, evenly convex. **Prepectus** (Fig. 5.47) separate from base of tegula by about length of tegula to length of prepectus; lateral surface relatively evenly curved to frontal surface, not distinctly protuberant beneath mesothoracic spiracle. **Mesopleuron** (Fig. 5.47). Acropleuron expanded to metapleuron dorsally, evenly and conspicuously convex; acropleural sulcus distinct ventrally to point about in line with base of tegula, where abruptly reflexed toward anterodorsal edge of pleuron near apex of prepectus as shallow, fine, posteriorly arcuate sulcus, and in most species acropleural sulcus curved anteroventally from about middle of metapleuron, sinuately so in some species, with relatively large episternal + epimeral region between acropleuron and mesocoxae (Fig. 5.47). Mesopleural suture fine, distinct, and extended posterodorsally from anterior of mesocoxa to apex of acropleuron (Fig. 5.47). Mesepimeron as conspicuous triangular lower mesepimeron. Mesepisternum with transepisternal line obscure as line of effaced sculpture; lower mesepisternum deeply incurved anterior to mesocoxae, with large, oval, membranous region anterior to each mesocoxa (*cf.* Fig. 5.67); trochantinal lobes widely separate. **Metathorax.** Metanotum (Fig. 5.64) V-like, scutellar apex extended over dorsellum to propodeum. Metapleuron subrectangular to triangular. **Legs.** Fore leg with denticle-like spicules on dorsal edge of tibia, and with 2 dorsoapical spicules. Middle leg (*cf.* Fig. 5.92) without peg-like spines along anterodistal edge; tibial spur thickened and setose but only subequal in length to apical width of tibia; tarsus relatively long, about 0.75 times length of mesotibia, and slightly thickened proximally; basitarsus short, in most species about 0.25 times length of tibia and subequal in length to tarsomeres 2-4; tarsomeres 1-4 ventrally with row of slender spines along anterior edge and row of peg-like spines along posterior edge. Hind leg with spine-like or more robust spicules on dorsal edge of tibia, and with dorsoapical spicules. **Wings.** Fore wing of females with about distal 0.66 setose, but sparsely setose or glabrous in males; SMV much longer than MV; MV distinct to punctiform; and PMV and STV subequal in length, short to punctiform. Hind wing with short spike-like basal vein. **Propodeum** of females (Fig. 5.64) with foramen very widely and shallowly incurved, edge carinate; median length about 4 times that of petiole; plical region relatively narrow, not conspicuously differentiated from callar regions, but asetose (except in *C. seyrigi*) and slightly convex relative to concave, setose, callar regions (Fig. 5.64), without, or with only very fine median carina. Propodeum of males similar to that of females, except foramen relatively much narrower and more deeply incurved.

METASOMA 8-segmented in both sexes; ovate-lanceolate. Mt1 (petiole) very slender, with transverse carinate ridge; wide in females, but relatively narrower in males; smooth and shining. Mt2 with posterior margin deeply incised medially; Mt3-Mt5 with posterior margins entire and transverse, or slightly emarginate medially; Mt6 with posterior margin broadly incurved; Mt7 with posterior margin rounded and extended to, or almost to level of cerci; Mt8 and Mt9 indistinguishably fused as syntergum dorsally, but with lateral oblique sulcus below cercus indicating line of fusion (Fig. 5.110); syntergum evenly convex and tapered distally in dorsal view. Cercus button-like.

Distribution. Known only from Palearctic and Ethiopian regions.

Hosts. Unknown, except two specimens seen with data, "ex. *Paraxylotinus israelsoni*" (Coleoptera: Scolytidae).

Monophyly and relationships. Monophyly of *Chirolophus* is indicated by the posterodorsally directed mesopleural suture of individuals (Fig. 5.47), and by the following combination of character states that are shared with members of one or more calosotine genera: small prepectus [Table 5.2, 22(2)]; pectinate antennae in males [21(2)]; reduced fore wing setation in males; and short to punctiform, subequal PMV and STV of individuals. Hypotheses of relationships of *Chirolophus* are illustrated in figures 5.1a, 5.1b, and discussed in section 5.7.2.1.

Keys. none available.

Catalog of taxa. *C. coerulescens* (Förster, 1878); NHMV; P - Europe. As *Charitolophus* Förster, = *C. eques* Haliday; comb. and syn. by Ruschka (1921).

C. eques Haliday, 1862; NHMV; E - Algeria.

C. halidayi Walker, 1873; lost; P - Italy. Probably congeneric with *Eusandalum* Ratzeburg, *vide* Bouček (1967).

*C. *hyalinus* Hedqvist, 1970; BMNH; **E** - South Africa.

*C. *incertus* Masi, 1923; MSNG; **P** - Italy.

*C. *koebelei* Ashmead, 1896; USNM; **A** - Australia. Transferred to *Eusandalum* Ratzeburg, **n. comb.**

*C. *seyrigi* (Risbec, 1952); MNHP; E - Madagascar. As *Oodera* Westwood (Pteromalidae), comb. by Bouček (1976).

5.5.6 *Calosota* Curtis

(Figs. 5.11, 5.12, 5.22-5.24, 5.49, 5.50, 5.65, 5.77)

Calosota Curtis, 1836: 596. **Type species:** *C. vernalis* Curtis. Original designation. **Type depository:** NMVM.

Calosoter Walker, 1837: 358. **Type species:** *C. vernalis* Walker. Subsequent designation by Westwood, 1839: 72. *Pteromalus eneubulus* Walker designated by Ashmead, 1904: 288, incorrect; species not originally included. **Type depository:** BMNH. Synonymy by Gahan and Fagan, 1923: 26.

Metacalosoter Masi, 1917: 167. **Type species:** *M. frequens* Masi. Monotypy. **Type depository:** BMNH, MSNG. **New synonymy.**

C. (Paracalosota) Masi, 1922: 142. **Type species:** *C. (P.) viridis* Masi. Monotypy. **Type depository:** MSNG. **New synonymy.**

C. (Hylephila) Masi, 1926: 330. **Type species:** *C. (H.) stenogastra* Masi. Monotypy. **Type depository:** DEI. **New synonymy.**

Description. **HEAD** (Figs. 5.11, 5.12) more or less oval in lateral view in most species, but in one species appearing subtriangular or wedge-like, with face angled to extensive, flattened, frontovertex. Inner orbits flattened or evenly convex, but without raised, differentiated sculpture. Scrobal cavities separated ventrally by low convex or triangular interantennal region; coextensive above as single channel, latter wide and shallow in most species (Fig. 5.11), but with subparallel carinate edges in some species (Fig. 5.12); not extended to median ocellus.

Ocelli in low to equilateral triangle; median ocellus distinctly above scrobal cavity; posterior ocellus about 0.5-1.5 times ocellar diameter from eye orbit. Eyes glabrous to setose. **Antenna** 13-articled in both sexes; inserted widely apart, distance between inner edge of toruli greater than width of torulus and distinctly greater than 0.5 distance between outer edge of torulus and inner eye margin. Scape elongate-subcylindrical in most species, but markedly compressed and widened distally in one species; extended to ventral margin of median ocellus, or shorter. Anellus short and subquadrate to more than twice as long as wide and only slightly shorter than fu1. Flagellum not sexually dimorphic, relatively short and compact in most species; funiculars cylindrical, subequal in diameter or only slightly increased in width toward apex, and of subequal length or decreased in length distally, but with at least apical funiculars subquadrate in most species; fu1 shorter than to only slightly longer than pedicel, or subequal in length to distinctly shorter than clava, or both, in most species; clava 3-articled by transverse sutures, subequal in width or wider than fu7, and at least as long, if not distinctly longer than fu6 + fu7 in almost all species.

MESOSOMA. **Pronotum** (Figs. 5.22, 5.23) campanulate and much narrower than mesoscutum. **Mesonotum** (Figs. 5.22-5.24). Mesoscutum relatively broad, about 1.2-1.7 times wider than long; lateral lobes with anterior margin distinctly, if not almost right-angled to side, as small to wide 'shoulder' on either side of pronotum; moderately convex to relatively flat, but lowly to quite abruptly and highly raised behind pronotum; not distinctly patterned by contrasting areas of different color and sculpture. Notauli (Fig. 5.24) obscure in most species and only evident on convex anterior part of mesoscutum in many species, but if evident dorsally then lines widely separate and subparallel to parallel. Parapsidal line (Fig. 5.24) present in most species, as short sublateral band of minute and fine sculpture near anterior margin of mesoscutal lateral lobe. Scutellar-axillar complex with DAS linear along edge of scutellum (Fig. 5.23), to more distinctly triangular with straight or concave scutoscutellar suture (Fig. 5.22), but basomedial angles separate by at least slightly more than basal width of DAS, and scutoscutellar sulcus carinately extended to near apex of scutellum (Figs. 5.22, 5.23);

scutellum flat (Fig. 5.49) to conspicuously convex (Fig. 5.50), with median longitudinal line in very few species. **Prepectus** (Figs. 5.49, 5.50) extended to base of tegula; lateral surface evenly curved to frontal surface, not anteriorly protuberant beneath mesothoracic spiracle (Fig. 5.24). **Mesopleuron** (Figs. 5.49, 5.50). Acropleuron extended to metapleuron at least dorsally, evenly and conspicuously convex, and relatively evenly and finely sculptured in most species (Fig. 5.49), but more grossly punctate anteriorly than posteriorly in some species (Fig. 5.50); acropleural sulcus distinct for most of length, evenly curved from above mesocoxa to near anterodorsal edge of pleuron (Fig. 5.50), or in many species obscurely recurved toward anteroventral angle of prepectus (Fig. 5.49). Mesopleural suture inevident, or as very short furrow extended anterodorsally from anterior of mesocoxa to acropleuron. Mesepimeron inevident or as variedly large lower mesepimeron; lower mesepimeron convex, on same plane as acropleuron, lunate to subtriangular, and setose or asetose (Figs. 5.49, 5.50). Mesepisternum with transepisternal line only as line of altered sculpture or color in some species; lower mesepisternum deeply incurved anterior to mesocoxae, with large membranous region anterior to each mesocoxa (Fig. 5.77); trochantinal lobes separate. **Metathorax.** Metanotum (Fig. 5.65) with dorsellum expanded over apex of scutellum, longer medially than paramedially in most species, and in females distinctly longer than plical region of propodeum. Metapleuron triangular to subrectangular, but dorsally narrowed. **Legs:** Fore leg with tibia non-spiculate dorsally, but with 1-3 dorsoapical spicules. Middle legs relatively short, mesotibia only slightly longer than maximum width of head, without robust spines along dorsal and anterior surfaces, but with variedly developed spines or row of pegs along anterodistal edge in some species; tibial spur thickened and setose, relatively short, subequal in length or slightly longer than apical width of tibia; mesotarsus relatively long, about 0.7-0.8 times length of mesotibia, thickened proximally and with basitarsus short, about 0.3 times or less length of tibia and subequal in length to tarsomeres 2-4; tarsomeres 1-4 ventrally with equally developed row of pegs along anterior and posterior edges, except spine-like proximally on basitarsus, or, in very few species basitarsus without pegs, or pegs reduced in number along both edges, but then ventral surface of tarsomeres densely setose, pad-like (*cf.* Fig. 5.97). Hind leg with spine-like spicules on dorsal edge of tibia in some species, and with dorsoapical spicules. **Wings.** Fore wing setose except for anal area, and in some species with elongate glabrous area below parastigma and base of MV; venation well developed, SMV vein at least slightly longer than elongate MV in all but very few species; PMV shorter than MV, but relatively long; and STV relatively long and slender, either with distinct uncus, or evenly curved distally (single Australian species seen with very sparse and inconspicuous discal setae, and with PMV and STV punctiform reduced). Hind wing with short spike-like basal vein in many species, but this unpigmented and obscure or inevident in some. **Propodeum** of females (Fig. 5.65) with foramen conspicuously incurved, expanded or reflexed as shiny, subtriangular to lunate medial carinate strip in most species; short to linear medially, but at least distinctly shorter than dorsellum; plical region relatively narrow, differentiated from callar regions by percurrent, variedly distinct plical furrow, carina, or both, distinctly mesad of spiracle, and in many species variedly concave relative to callar regions, without distinct median carina, unless strigose or costulate; callar regions setose at least laterally to spiracle. Propodeum of males similar to that of females, except foramen much narrower and more deeply incurved, plical region longer.

METASOMA 8-segmented in both sexes. Mt1 (petiole) relatively wide, but short to almost linear in females; much narrower and longer in males; smooth and shining. In females, Mt2 with posterior margin medially incised, Mt3-Mt5 with posterior margins medially incised to shallowly emarginate, Mt6 with posterior margin broadly incurved, and Mt7 with posterior margin transverse to rounded; in males, Mt2-Mt7 with posterior margins entire and transverse, or with Mt2 medially incised. Mt8 and Mt9 indistinguishably fused as syntergum, without median ridge; syntergum extremely varied in shape and relative length in females, short to elongate-subtriangular in most females, but expanded medially in some females, with base more or less petiolate; syntergum of males short with posterior edge broadly rounded. Cercus button-like.

Synonymy. Masi (1917) established *Metacalosoter* for a species from the Seychelles that was similar to species of *Calosota*, except for structure of the head and antennae of females, and an elongate marginal vein that was distinctly longer than the submarginal vein. The scape of females is markedly compressed and distally expanded, and the antenna is very robust, with all funicular articles transverse. The head is also somewhat wedge-like in lateral view, with the combined frontovertex flattened, extensive, and distinctly angled to the face. These states are not as conspicuously developed in males, the scape is only moderately compressed and the funicular articles are quadrate or slightly longer than wide. Though the type species of *Metacalosoter*, *M. frequens* Masi, is very distinctive, it is merely a conspicuously modified species of *Calosota*, and I hereby synonymize the name *Metacalosoter* with *Calosota*.

Masi (1922) differentiated *Paracalosota* as a subgenus of *Calosota* based on females of a species that has an elongate glabrous region on the fore wing beneath the parastigma, and that has the ventral surface of the mesotarsus densely, pad-like setose, but lacks pegs on the basitarsus. This latter state is most unusual for species of *Calosota*, though I have seen a few other species with the same state, and it has been derived numerous independent times in various genera of Eupelminae. Reduction of the mesotarsal pegs, with a concomitant increase in development of the ventral setae, is undoubtedly secondarily derived in *Calosota*, as it is in Eupelminae, and I do not recognize *Paracalosota* as a subgenus of *Calosota*.

Masi (1926) differentiated *Hylephila* as a subgenus of *Calosota* for females of a species that has a transverse furrow across the inner orbits of the head, at about the dorsal level of the interantennal region, and that has an elongate metasoma with an acute apex. Unfortunately, the head and metasoma are now missing from the unique type-specimen. The mesosoma remaining is similar in structure to such species as *C. testaceipes* Hedqvist and *C. ferrieri* Heqvist, which have the mesoscutum and anterior of the acropleuron relatively coarsely punctate, and the lower mesepimeron setose. These species may eventually be shown to be more closely related to species of *Balcha* Walker than to other species of *Calosota*, but I presently do not recognize *Hylephila* as a subgenus of *Calosota*.

Distribution. Known from all biogeographic regions.

Hosts. Diverse taxonomically and biologically. Individuals have been reared from beetles (Coleoptera: Anobiidae, Cerambycidae, Cleridae, Scolytidae); as primary parasites of other insects (Chalcidoidea, Diptera, and Lepidoptera), or hyperparasites of chalcidoids in grass stems; from nests of solitary bees (Apoidea: *Osmia* Panzer, *Megachile* Latreille) and wasps (Vespoidea: *Odynerus* Latreille; Sphecoidea: *Pison* Jurine); from a gall on pine (*Pinus*); and from eggs of Pentatomidae (Hemiptera).

Monophyly and relationships. Monophyly of *Calosota* + *Balcha* + *Tanythorax* is supported by four hypothesized synapomorphies, a 3-articled antennal clava [Table 5.1, 2(3)], structure of the lateral mesopleuron [3(3b)], paramedially parallel notauli [7(3)], and scutoscutellar suture carinate to near apex of scutellum [Table 5.2, 20(2)] (Figs. 5.1a, 5.1b). However, monophyly of *Calosota* is not supported by known autapomorphic states, and the genus may be paraphyletic relative to *Balcha*, *Tanythorax*, or both. Paraphyly relative to *Balcha* is indicated by what appears to be intermediate forms of mesothoracic sculpture in individuals of *C. testaceipes* Hedqvist, *C. ferrieri* Hedqvist, and *C. stenogastra* Masi, between the relatively fine sculpture of most species of *Calosota* and the gross mesoscutal sculpture that characterizes species of *Balcha*. Alternate hypotheses of character-state evolution and relationships between *Calosota*, *Balcha*, and *Tanythorax*, are illustrated in figures 5.1a, 5.1b, 5.1c, and discussed in section 5.7.2.1.

Keys. Ruschka 1921 (Palearctic); Bolivar y Pieltain 1923b, 1929 (Spain); Nikolskaya 1952 (USSR); Hedqvist 1956 (Palearctic); Erdős 1960 (Hungary); Graham 1969a (Great Britain); Hedqvist 1970 (Ethiopian); Burks 1973 (Nearctic).

Catalog of taxa. **C. acron* (Walker, 1848); BMNH; P - Europe. As *Eupelmus* Dalman (Eupelminae), comb. by Bouček (1968).

C. aestivalis Curtis, 1836; NMVM; P - Britain.

**C. aestivalis* (Walker, 1837); BMNH; P - Europe. As *Calosoter* Walker, = *C. vernalis* Curtis; comb. by Ruschka (1921), syn. by Graham (1969a).

**C. affinis* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

C. agrili Nikolskaya, 1952; ZIL; P - USSR.

C. albitarsis* (Ashmead, 1904); USNM; P - Japan. As *Calosoter* Walker, transferred to *Neanastatus* Girault (Metapelmatinae), **n. comb.

C. anemetus* (Walker, 1896); BMNH; O - Philippines. As *Calosoter* Walker, comb. by Baltzar (1966); transferred to *Balcha* Walker, **n. comb.

C. anguinalis Ruschka, 1921; NHMV; P - Austria. = *C. acron* (Walker), syn. by Bouček (1968).

C. ariasi Bolivar, 1929; IEEM; P - Spain.

**C. aristidae* (Risbec, 1951); MNHP; E - Senegal. As *Calosoter* Walker, comb. by Hedqvist (1970).

**C. beharae* (Risbec, 1952); MNHP; E - Madagascar. As *Calosoter* Walker, comb. by Hedqvist (1970).

**C. bifasciatus* (Walker, 1862); BMNH; P - Europe. As *Calosoter* Walker, hereby removed from genus to uncertain generic placement in Eupelminae, near *Ischnopsis* Ashmead.

**C. capensis* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

C. cecidobius (Joergensen & Kieffer, 1910); ?; Nt - Argentina. As *Calosoter* Walker, comb. by De Santis (1967).

C. chrysideus* (Ashmead, 1900); BMNH; Nt - West Indies, St. Vincent. As *Calosoter* Walker, comb. by De Santis (1979); transferred to *Eusandalum* Ratzeburg, **n. comb.

C. coleopterorum (Girault, 1913); SAMA; A - Tasmania. As *Calosoter* Walker, to *Anastatus* Motschulsky (Eupelminae) by Girault (1915).

C. coerulea Nikolskaya, 1952; ZIL; P - USSR. = *C. viridis* Masi, syn. by Bouček (1970).

C. contractus (Walker); BMNH; P - Europe. As *Trigonoderus* Westwood, = *C. acron* (Walker); comb. and syn. by Graham (1969a).

**C. curculionis* (Risbec, 1951); MNHP; E - Senegal. As *Polymoria* Ratzeburg, comb. by Bouček (1976).

**C. cyanea* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

C. dodone (Walker, 1839); BMNH; A - Australia. As *Calosoter* Walker, transferred to *Anastatus* Motschulsky, **n. comb.**

C. dusmeti Bolivar, 1929; IEEM; P - Spain.

**C. eneubulus* (Walker, 1838); BMNH; N - Canada [Am.: Charles Is.]. As *Pteromalus* Swederus (Pteromalidae), comb. by Walker (1846); hereby removed from genus to uncertain generic placement in Eupelminae.

**C. ferrierei* Hedqvist, 1970; BMNH, KHPC; E - Uganda.

**C. flavostylus* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

C. frequens* (Masi, 1917); BMNH, MSNG; E - Seychelles. As *Metacalosoter* Masi, **n. comb.

C. fumipennis Bolivar, 1923b; IEEM; P - Spain.

**C. grylli* Erdős, 1955; TMB; P - Hungary.

**C. halyomorphae* (Risbec, 1951); MNHP; E - Senegal. As *Polymoria* Ratzeburg, comb. by Hedqvist (1970).

C. herodoti Girault, 1934; ?; A - Australia.

C. hirsutioculus Girault, 1934; nomen nudum.

C. incognita Nikolskaya, 1952; ZIL; P - USSR.

Metacalosoter ivondroi* Risbec, 1952; MNHP; E - Madagascar. Transferred to *Ischnopsis* Ashmead (Eupelminae), **n. comb.

**C. kentra* Burks, 1973; USNM; N - USA.

**C. ligniphila* (Risbec, 1952); MNHP; E - Madagascar. As *Cerambycobius* Ashmead (Eupelminae), comb. by Bouček (1976).

**C. lixobia* Erdős, 1946; TMB, MSNG; P - Hungary.

C. lixobia var. hyperparasita Erdős, 1946; TMB, MSNG; P - Hungary.

**C. longiventris* (Ashmead, 1896); USNM; N - USA. As *Calosoter* Walker, comb. by Peck (1951).

Metacalosoter madagascariensis* Risbec, 1952; MNHP; E - Madagascar. Transferred to *Anastatus* Motschulsky (Eupelminae), **n. comb.

**C. mateui* Ferrière, 1966; MHNG; E - Algeria.

C. matritensis Bolivar, 1929; IEEM; P - Spain.

*C. *melanoptera* (Risbec, 1952); MNHP; E - Madagascar. As *Calosoter* Walker, transferred to *Ischnopsis* Ashmead (Eupelminae), **n. comb.**

*C. *metallica* (Gahan, 1922); USNM; N - USA. As *Calosoter* Walker, comb. by Packard (1928).

C. *modesta* Bolivar, 1929; IEEM; P - Spain.

*C. *montana* Burks [as *Cecidostiba montana*, lapsus !], 1973; USNM; N - USA.

C. *obscura* Ruschka, 1921; NHMV; P - Austria.

C. *olierae* (Brethés, 1916); MBR; Nt - Argentina. As *Calosoter* Walker, transferred to *Eupelmus* Dalman (Eupelminae) by De Santis (1967).

C. *parva* Girault, 1932; ?; A - Australia.

C. *plutarchi* Girault, 1932; ?; A - Australia.

*C. *pseudotsugae* Burks, 1973; USNM; N - USA.

*C. *punctata* Hedqvist, 1970; BMNH; E - South Africa.

*C. *purpurata* Hedqvist, 1970; BMNH; E - South Africa.

C. *reticulata* Nikolskaya, 1952; ZIL; P - USSR.

C. *risbeci* Bouček, 1976. New name for C. *viridis* (Risbec, 1952).

*C. *robusta* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

*C. *rugosopunctata* Hedqvist, 1970; BMNH; E - South Africa. Transferred to *Balcha* Walker by Bouček (1976).

**C. saharensis* Ferrière, 1966; MHNG; E - Algeria.

**C. septentrionalis* Hedqvist, 1956; KHPC; P - Sweden.

C. seyrigi* (Risbec, 1952); MNHP; E - Madagascar. As *Calosoter* Walker, transferred to *Brasema* Cameron (Eupelminae), **n. comb.

C. silvai (Brethés, 1917); MBR; Nt - Chile. As *Calosoter* Walker, comb. by De Santis (1979).

**C. sinensis* Ferrière, 1935; BMNH; P - China.

C. splendida Girault, 1927; QMB; O - Philippines.

**C. (Hylephila) stenogastra* Masi, 1926; DEI; O - Taiwan (Formosa).

**C. subaenea* Masi, 1925; MSNG; E - Tunisia.

**C. testaceipes* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

C. tullii Girault, 1934; ?; A - Australia.

**C. turneri* Hedqvist, 1970; BMNH, KHPC; E - South Africa.

C. varipunctata Girault, 1932; ?; A - Australia.

C. vernalis Curtis, 1836; NMVM; P - Britain.

**C. vernalis* (Walker, 1837); BMNH; P - Europe. As *Calosoter* Walker, = *C. aestivalis* Curtis; comb. by Ruschka (1921), syn. by Graham (1969a).

**C. versicolor* (Risbec, 1951); MNHP; E - Senegal. As *Calosoter* Walker, comb. by Hedqvist (1970).

**C. violascens* Masi, 1922; MSNG; P - Italy.

*_C. (Paracalosota) viridis_ Masi, 1922; MSNG; P - Italy.

*_C. viridis_ (Risbec, 1952); MNHP; E - Madagascar. As _Oodera_ Westwood (Pteromalidae), comb. by Bouček (1976); see _C. risbeci_ Bouček.

C. worcester Girault, 1934; nomen numdum.

5.5.7 *Balcha* Walker

(Figs. 5.10, 5.51, 5.66)

Balcha Walker, 1862: 394. Type species: *B. cylindrica* Walker. Monotypy. **Type depository:** BMNH. = *Eusandalum* Ratzeburg *vide* Ashmead, 1904 and Hedqvist, 1961; reestablished as valid genus by Bouček, 1967; = *Polymoria* Förster *vide* Hedqvist, 1970; **status reestablished.**

Elmba Cameron, 1908: 151. Type species: *E. levicollis* Cameron. Monotypy. **Type depository:** BMNH. Synonymy by Hedqvist, 1961.

Sauteria Masi, 1926: 333. Type species: *S. exima* Masi. Original description. **Type depository:** DEI, MSNG. **New synonymy.**

Description. HEAD (Fig. 5.10). Inner orbits flattened or evenly convex, without raised or differentiated sculpture. Scrobal cavities separated ventrally by elongate-triangular interantennal region; coextensive above as relatively deep channel with subparallel, abruptly declivous and carinate sides; shallowed to ventral margin of median ocellus, or almost so. Ocelli in low to equilateral triangle; median ocellus within or slightly above scrobal cavity; posterior ocellus one ocellar diameter or less from inner eye margin. Eye glabrous. **Antenna** 13-articled in both sexes; inserted widely apart, distance between inner edge of toruli slightly greater than width of torulus and 0.5-1.0 distance between outer edge of torulus and inner eye margin. Scape extended to ventral margin of median ocellus or beyond. Anellus quadrat[illegible] most species, but about twice as long as wide in some; about 0.25-0.33 as long as ful. Flagellum filiform and relatively long in both sexes; funiculars cylindrical, decreased in length distally but all distinctly longer than wide and of subequal width; fu1 distinctly longer than pedicel and about twice length of pedicel in most species, subequal in length or longer than clava; clava 3-articled by transverse sutures, slightly wider than fu7 in most species and subequal in length or shorter than fu6 + fu7.

MESOSOMA. Pronotum campanulate and much narrower than mesoscutum. **Mesonotum.** Mesoscutum relatively broad, about 1.25-1.50 times wider than long; distinctly 'shoulder-like' on either side of pronotum, with anterior margin of lateral lobes almost right-angled to side; abruptly convex anteriorly, highly raised behind pronotum but slightly flattened or paramedially depressed anterior to transscutal articulation in few species; variedly patterned by darkly colored, relatively finely sculptured regions, and brilliant chromatic, grossly umbilicate sculptured regions (Fig. 5.51). Notauli obscure in many species, but widely separate and subparallel within anterior half of mesoscutum (*cf.* Fig. 5.24). Parapsidal lines long and conspicuous, as sublateral band of minute and fine sculpture near anterior margin of mesoscutal lateral lobe (*cf.* Fig. 5.24). Scutellar-axillar complex with DAS linear at extreme basolateral corner of scutellum(*cf.* Fig. 5.23), to elongate-triangular, but with scutoscutellar suture carinately extended to near apex of scutellum; scutellum subquadrate or rectangular (*cf.* Fig. 5.23), convex with distinct median longitudinal line or fine carina in some species. **Prepectus** (Fig. 5.51) separate from base of tegula by about apical width to length of tegula; lateral surface evenly curved to frontal surface, not anteriorly protuberant beneath mesothoracic spiracle. **Mesopleuron** (Fig. 5.51). Acropleuron extended to metapleuron dorsally, conspicuously convex in most species; acropleural sulcus distinct for entire length, evenly curved from above mesocoxa to anterodorsal edge of pleuron at about apex of prepectus. Mesopleural suture inevident or as very short furrow extended anterodorsally from anterior of mesocoxa to acropleuron. Mesepimeron as lower mesepimeron, convex, on same plane as acropleuron, subtriangular, and setose. Mesepisternum with transepisternal line only as line of altered sculpture or color in some species; lower mesepisternum deeply incurved anterior to mesocoxae, with large membranous region anterior to each mesocoxa (*cf.* Fig. 5.77);

trochantinal lobes separate. **Metathorax.** Metanotum (Fig. 5.66) with dorsellum expanded over apex of scutellum, longer medially than paramedially in many species, and in females distinctly longer than plical region of propodeum. Metapleuron triangular to subrectangular, but dorsally narrowed. **Legs.** Fore leg with tibia non-spiculate dorsally, but with 3-6 dorsoapical spicules. Middle leg relatively short; tibia only slightly longer than maximum width of head, without robust spines along dorsal and anterior surfaces, but with spines along anterodistal edge; tibial spur thickened and setose, relatively short, subequal in length or slightly longer than apical width of tibia; tarsus relatively long, about 0.6-0.7 times length of tibia, and thickened proximally; basitarsus short, about 0.20-0.25 times length of tibia and subequal in length to tarsomeres 2-4; tarsomeres 1-4 ventrally with equally developed row of pegs along anterior and posterior edges, except spine-like proximally on basitarsus. Hind leg with tibia non-spiculate dorsally, but with dorsoapical spicules. **Wings:** Fore wing setose except for anal area; venation well developed, SMV longer than elongate MV; PMV 0.66 to subequal in length with MV; and STV relatively long and slender, either with distinct uncus, or evenly curved distally. Hind wing with short spike-like basal vein in some species, but in many species reduced or inevident near SMV, and then somewhat globose and more conspicuous distally than proximally. **Propodeum** of females (Fig. 5.66) with foramen conspicuously incurved, medially expanded in many species as shiny, subtriangular to lunate strip; short medially; plical region relatively narrow and obliquely angled to almost vertical in many species, differentiated from callar regions by distinct percurrent plical furrow, carina, or both, distinctly mesad of each spiracle, and longitudinally costate in most species, but at least with median carina; callar region setose lateral to spiracle. Propodeum of males similar to that of females, except foramen much narrower and more deeply incurved, and plical region longer, subequal in length to dorsellum.

METASOMA 8-segmented in both sexes; subcylindrical basally and tapered to apex in both sexes, or in some males expanded and flattened distally so as to appear slightly petiolate. Mt1 (petiole) in females wide and relatively slender, cresentic, but relatively much narrower and longer in males, subcresentic to almost semicircular; transversely sulcate in few species, but smooth and shining in most, with variedly prominent subbasal to medial transverse carina or ridge. In females, Mt2 and Mt3 with posterior margins medially incised and Mt4-Mt6 incised or transverse; in males, Mt2-Mt6 with posterior margins entire and transverse and Mt7 with posterior margin entire, transverse to rounded; Mt8 and Mt9 indistinguishably fused as syntergum, without median ridge or carina; syntergum varied in relative length in females, but with sides evenly convergent to apex and somewhat compressed in most species, and in males short with posterior margin broadly rounded. Cercus button-like.

Synonymy. Study of the type-specimens of *Balcha* Westwood, *Elmba* Cameron, and *Sauteri* Masi shows the species to be congeneric, and I hereby synonymize the latter two generic names with *Balcha*.

Distribution. Most diverse and speciose in the Oriental region, with numerous undescribed species; one valid species also known from South Africa (Ethiopian).

Hosts. Mostly unknown, but two individuals seen labelled as reared from larvae of *Agrilus* (Coleoptera: Buprestidae).

Monophyly and relationships. Monophyly of *Balcha* is indicated by pattern of mesoscutal color and sculpture [Table 5.2, 23(3)]. Possible relationships of *Balcha* are discussed in the respective section under *Calosota* and in section 5.7.2.1, and illustrated in figures 5.1a, 5.1b, and 5.1c.

Keys. none available.

Catalog of taxa. **B. anemeta* (Walker, 1896); BMNH; O - Phillipines. As *Calosoter* Walker, **n. comb.**

**B. cylindrica* Walker, 1862; BMNH; O - South Africa.

B. elegans* (Masi, 1926); DEI; O - Taiwan (Formosa). As *Sauteria* Masi, **n. comb.

B. exima* (Masi, 1926); DEI, MSNG; O - Taiwan (Formosa). As *Sauteria* Masi, **n. comb.

B. indica* (Mani & Kaul, 1973); USNM; O - India. As *Thaumasura* Westwood (Pteromalidae: Cleonyminae), **n. comb.

B. levicollis* (Cameron, 1908); BMNH; O - Borneo. As *Elemba* Cameron, **n. comb.

**B. rugosopunctata* (Hedqvist, 1970); BMNH; E - South Africa. As *Calosota* Curtis, = *B. cylindrica* Walker; comb. and syn. by Bouček (1976).

5.5.8 *Tanythorax* new genus

Type-species. *Tanythorax spinosus* new species, by present designation.

Derivation of Generic name. From greek words, "tany", meaning "long", and "thorax"; referring to elongate mesothorax that characterizes individuals of this genus. Gender: masculine.

Description. HEAD. Inner orbits flattened and without differentiated sculpture. Scrobal cavities separated ventrally by narrow rectangular interantennal region, latter shallowly concave, furrow-like; inner orbits roundly protuberant ventrolaterally above each torulus, but otherwise scrobal cavities shallowly obscure, not distinctly coextensive, and distant from median ocellus. Ocelli in equilateral triangle; median ocellus distinctly above scrobal cavities; posterior ocellus slightly less than ocellar diameter from eye orbit. Eye glabrous. **Antenna** 13-articled (flagellum missing distal to fu4 in single known male); inserted widely apart; distance between inner edge of toruli greater than width of torulus and slightly greater than distance between outer edge of torulus and inner eye margin. Scape extended to median ocellus. Anellus elongate-cylindrical, about twice as long as wide, and about 0.4 length of fu1. Flagellum elongate, females with conspicuous multiporous plate sensilla, but densely setose in males; funiculars cylindrical and of subequal diameter, decreased in length distally but all distinctly longer than wide; fu1 distinctly longer than pedicel and slightly longer than clava (unknown for males); clava 3-articled by transverse sutures, slightly wider than fu7 and about as long as fu6 + 0.5 fu7 (unknown for males).

MESOSOMA. Pronotum campanulate and narrower than mesoscutum. **Mesonotum.** Mesoscutum relatively long, length subequal to or slightly greater than width; lateral lobes relatively narrow, only obscurely 'shoulder-like' on either side of pronotum, with anterior margin gradually curved to side; convex laterally and slightly depressed dorsally anterior to transscutal articulation; only very lowly and gradually raised anteriorly, in same approximate plane as pronotum; not patterned by contrasted regions of color and sculpture. Notauli very obscure as slightly differentiated lines of sculpture, convergent near anterior margin of mesoscutum but widely separate and parallel over most of length. Parapsidal line obscure as sublateral line of minute, fine, or subeffaced sculpture in anterior 0.5 mesoscutal lateral lobe. Scutellar-axillar complex with DAS as only very slender arcuate region at extreme basolateral corner of scutellum; scutoscutellar suture carinately extended to near apex of scutellum; scutellum subquadrate and lowly convex, but with apex quite abruptly depressed and conically extended beneath dorsellum. **Prepectus** separate from base of tegula by slightly less than length of tegula; lateral surface evenly curved to frontal surface, not anteriorly protuberant beneath mesothoracic spiracle. **Mesopleuron.** Acropleuron extended to metapleuron, evenly convex; acropleural sulcus distinct for entire length, evenly curved from above mesocoxa toward anterodorsal edge of pleuron, but distally recurved to anteroventral edge of prepectus. Mesopleural suture as very short furrow extended anterodorsally from anterior of mesocoxa to acropleuron. Mesepimeron as lower mesepimeron, convex, on same plane as acropleuron, triangular, and sparsely setose. Mesepisternum without transepisternal line; lower mesepisternum deeply incurved anterior to mesocoxae, with large membranous region anterior to each mesocoxa; trochantinal lobes separate. **Metathorax.** Metanotum with dorsellum expanded over conically produced scutellar apex, relatively large and slightly protuberant medially into V-shape depression of plical region of propodeum. Metapleuron subtriangular, dorsally narrowed. **Legs.** Fore leg with tibia non-spiculate dorsally, but with 2 dorsoapical spicules. Middle leg conspicuously elongate; tibia about 1.7 times longer than maximum width of head, with robust, elongate spines aligned in single row along anterovental edge and in double row along anterodorsal edge, with latter row expanded distally as patch of spines at apex; tibial spur elongate-slender, subequal in length or slightly longer than twice apical width of tibia; tarsus relatively long, about 0.5 times length of tibia, and thickened proximally; basitarsus short, about 0.25 times length of tibia, and subequal to combined length of tarsomeres 2-5; tarsomeres 1-4 ventrally with equally developed row of pegs along anterior and posterior edges, except spine-like proximally on basitarsus. Hind leg with spine-like spicules on dorsal edge of tibia, and with dorsoapical spicules. **Wings.** Fore wing setose except for anal area; venation well developed, elongate MV slightly longer than SMV; PMV elongate; and STV relatively long and slender, but apex slightly expanded and distally curved by distinct uncus. Hind wing without evident basal vein. **Propodeum** with foramen very deeply and roundly incurved, plical region conspicuously differentiated from callar regions as relatively long, narrow, longitudinally to somewhat obliquely strigose region, with sides of region subparallel in males and anteriorly convergent in females, but mesad of spiracles by distance about equal to basal width of plical region; callar regions very large and conspicuous, lateral length subequal to combined medial length of scutellum + dorsellum, finely coriaceous, and sparsely setose lateral to spiracle.

METASOMA 8-segmented in both sexes; elongate-slender, subcylindrical proximally and tapered distally. Mt1 (petiole) slightly longer than plical region in both sexes, but much wider in females (transverse rhomboidal) than in males (longer than wide with anteriorly convergent sides). In females, Mt2-Mt4 with posterior ~~margins incised~~ medially, Mt5 and Mt6 with posterior margins emarginate, and Mt7 with posterior margin rounded; in males, Mt2-Mt7 with posterior margins entire and transverse; Mt8 and Mt9 indistinguishably fused as syntergum, latter elongate, tapered distally, and moderately compressed in females, but flattened with subparallel sides in males. Cercus button-like.

Distribution. Known only from Oriental region (Philippines and New Guinea).

Host. Unknown, but most probably xylophagous beetles (Coleoptera).

Generic diversity. The type species is the only known species.

Monophyly and relationships. Monophyly of *Tanythorax* is indicated by relative structure of the pronotum and mesoscutum [Table 5.1, 11(1a)], as well as by the relatively elongate mesothorax, and presence of elongate spines on the mesotibia of individuals. *Tanythorax* is hypothesized to form a monophyletic assemblage with *Calosota* and *Balcha* (see respective section in treatment of *Calosota*), but further relationships are unresolved. Alternate hypotheses of character-state evolution and relationships are illustrated in figures 5.1a, 5.1b, and 5.1c, and discussed in section 5.7.2.1.

5.5.8.1 *Tanythorax spinosus* new species

Type material. HOLOTYPE - Female [Philippines], Negros, Cuernos Mts., Baker (USNM). ALLOTYPE - Male. [Papua] New Guinea (NE), Bulolo, 885 m, 17.VIII.1956; E.J. Ford, Jr. Collector (BPBM). PARATYPES - 4 ♀♀. 2 ♀♀, [**Philippines**], Mindanao, Dapitan, Baker, 13894 (USNM); 1 ♀, Mindanao, Davao, Baker, 13894 (USNM); 1 ♀, [**Philippines**], island of Basilan, Baker (USNM).

One paratype from Dapitan deposited in CNC by permission of USNM.

Condition of holotype. Entire, with mesothorax in flexed position; point-mounted.

Derivation of specific epithet. The latin word "*spinosus*", meaning "thorny"; referring to the spinose mesotibia.

Description. FEMALE. Length = 1.35 cm. HEAD multicolored; frontal aspect brilliant green from just above scrobes to edge of oral cavity, but with interantennal region, clypeus, margins of toruli, and malar sulcus with reddish-yellow luster, and dorsal edge of each scrobal cavity demarked by transverse violaceous-black spot lateral to apex of interantennal region; frontovertex non-metallic black, except for brilliant green spot below median ocellus; occiput greenish-blue over convex dorsal region and narrow smooth region along outer eye margin, but reddish-brown centrally. Head more or less lenticular in lateral view with convex vertex evenly curved into occiput; distinctly transverse in frontal view, with very large eyes; relative measurements, HW = 17.1, HH = 11.9, HL = 7.4. Head below interantennal region finely coriaceous; interantennal region obscurely transverse-strigose; frontal aspect between malar sulcus and dorsal edge of toruli isodiametric-reticulate, cells large and deep (alveolate); small, convexly protuberant region of inner orbits dorsolateral to each torulus finely coriaceous; frontovertex, including dorsal region of scrobes, coriaceous, and with tiny, scattered, setigerous punctures; occiput coriaceous-alutaceous, except smooth along narrow band adjacent to outer eye margin, region distinctly defined by fine ridge-like abrupt edge of sculpture. **Setae** unmodified, whitish and relatively long ventrally, but brownish and shorter over non-metallic frontovertex. **Mouthparts.** Labrum yellow; maxilla and labium brown, except stipes with greenish reflection. Antenna dark brown, except scape with yellowish or greenish luster at some angles; inserted slightly above lower margin of eyes, distance between lower edge of toruli and clypeal edge compared with malar space = 3.1:3.4; scape widened and moderately compressed subapically, with inner edge relatively straight and outer edge sinuate, and apicolaterally carinate and concave for reception of pedicel; relative measurements, scape = 6.9(2.2), pedicel = 2.6(1.2), anellus = 2.2(1.1), funiculars = 4.7(1.1), 4.2(1.1), 4.2(1.1), 3.8(1.1), 3.1(1.1), 2.7(1.1), 2.5(1.2), clava = 4.0(1.7). **Ocelli** with POL = 1.3, LOL = 0.9, OOL = 0.9; median ocellus faced anterodorsally far above scrobal cavities; posterior ocelli faced dorsally on vertex. **Eyes** large-oval, H:W = 9.2(6.5); distance between eyes below = 10.6, above = 5.6. **Scrobes** with lateral margins sinuate dorsolateral to toruli, with small, convexly protuberant lower inner orbits; cavities shallow and obliterate dorsally at about apex of interantennal region, not distinctly coextensive above.

MESOSOMA multicolored; pronotum black dorsally, green laterally; mesoscutum black, except for elongate paramedial green lines dorsally, and narrowly bluish-green along parascutal carina; scutellum greenish laterally, but bluish or violaceous centrally; tegula light brown; prepectus bluish-green; acropleuron varied in color depending on angle of light, green or bluish-green over most of surface but reddish-yellow immediately above acropleural sulcus; mesepisternum greenish with paramedial transepisternal lines reddish-brown; metanotum dark brown dorsally, but metapleuron greenish; propodeum dark brown between spiracles, but with bluish-violaceous luster laterally. Setae unmodified, brown, and relatively even and sparse, but with following glabrous: metanotum, propodeum between spiracles, acropleuron. **Pronotum** coriaceous on sides, transverse-striate to transverse-coriaceous dorsally. **Mesothorax** with mesoscutum isodiametric-reticulate medially over about posterior 0.66, alutaceous to coriaceous behind pronotum and on lateral lobes, but finely rugulose-reticulate near parascutal carina; scutellum reticulate-punctulate, with cells or punctures much smaller than medially on mesoscutum; prepectus isodiametric-coriaceous; sculpture of acropleuron complex, primarily obliquely elongate-coriaceous to striate over about anterior 0.66, except more isodiametric-coriaceous along edges, but with sculpture abruptly altered along slightly carinate line directed posteroventrally from anterior edge of mesopleural wing process, sculpture minute-coriaceous anterior to line medially, and longitudinally coriaceous-striate posterior to line; lower mesepimeron finely coriaceous; mesepisternum finely alutaceous. Scutellar-axillar complex quadrate, length of scutellum (measured from transscutal articulation to transverse posterodorsal edge) compared with width of complex = 6.5:6.5. **Metathorax** with pleuron rugulose-reticulate; dorsellum rectangular, with L:W = 1.4:3.6, very finely and minutely coriaceous and strigulose laterally. **Propodeum** with plical region obliquely strigose on either side of median carina, medial length = 1.2; callar regions very finely coriaceous, minutely so dorsally. **Wings** hyaline, with brownish venation; SMV = 15.3, MV = 17.1, PMV gradually attenuated, apex difficult to distinguish, but approximately = 10.0, STV = 4.0. **Legs** with coxae greenish, otherwise yellow. Profemur ventrally denticle-like protruded subapically.

Middle leg with tibia = 29.1; tarsomeres = 7.3, 2.5, 1.8, 1.3, 2.0.

METASOMA dark brown dorsally, with bluish-green reflection on sides of Mt2-Mt5. Mt1 (petiole) to Mt3 glabrous dorsally, Mt4-Mt7 sparsely setose, and syntergum conspicuously setose, setae brown; sides of all terga setose, with whitish setae anteriorly and brown setae posteriorly. Mt1 with dorsal surface delineated from sides by distinct, anteriorly convergent lateral carina, very finely and minutely coriaceous and sparsely strigulose, length to posterior width = 5.0:2.2; Mt2 isodiametric-coriaceous, cells distinctly larger than those on subsequent terga; Mt3 extended only slightly beyond apex of Mt2, but distinct with transverse-coriaceous sculpture; Mt4 transverse-coriaceous; Mt 5 to syntergum more isodiamteric-coriaceous; syntergum moderately compressed, highly convex and with sides only slightly convergent to apex, 6.8 times as long as basal width; relative measurements = 2.2(m), 15.9(pm), 1.5, 7.0(m), 10.6, 8.3, 10.6, 30.9. **Hypopygium** extended slightly beyond apex of Mt3.

MALE. Length = 0.48 cm. HEAD similar in color to females, except green of lower frontal aspect not as conspicuous and without reddish-yellow areas, and occiput more bluish-violaceous dorsally and laterally, greenish medially; similar in sculpture, setation, and structure to females, with relative measurements, HW = 9.5, HH = 7.2, HL = 4.9; POL = 1.0, LOL = 0.8, OOL = 0.6; eye H:W = 5.4:4.0, distance between eyes below = 6.0, above = 3.8; distance between ventral edge of scrobes and clypeal edge compared with malar space = 2.0:1.9; scape = 3.8(1.0), pedicel = 1.5(0.7), anellus = 1.1(0.5), funiculars = 2.6(0.8), 2.5(0.8), 2.4(0.9), 2.1(0.8) [subsequent flagellomeres missing].

MESOSOMA with mesonotum extirely dark brown, except scutellum with bluish luster medially and violaceous laterally; side of mesosoma with violaceous luster, except mesepisternum with slight greenish reflection. Sculpture, setation, and structure similar to females, except for propodeum; length of scutellum compared with width of scutellar-axillar complex = 4.2:4.0; L:W of dorsellum = 1.3: 2.0; propodeum with plical-region relatively longer and narrower than in females, anterior width to medial length = 1.5:1.4, with sides subparallel. Fore wing with SMV = 9.5, MV = 10.0, PMV gradually attenuated, apex difficult to distinguish, but approximately = 7.0, STV = 2.4. Legs with front coxa greenish and hind coxa violaceous (color of middle coxa obscured by glue); femora brownish, middle femur with white annulus about 0.33 from base; tibiae and tarsi yellowish. Middle leg with tibia = 17.1; tarsomeres = 3.2, 1.4, 0.9, 0.8, 1.3.

METASOMA dark brown. Mt1 (petiole), and Mt2 dorsobasally, glabrous, subsequent terga relatively evenly setose with brown setae similar to those of mesoscutum; Mt1 distinct, with anteriorly convergent lateral carina as for females, but dorsum only very obscurely coriaceous, and relatively much narrower, with length to poster[illegible]h = 1.9:2.0; Mt2 with basomedial convex region, latter distally narrowed and slightly shorter than Mt1, tergum slightly, longitudinally wrinkled lateral to convex region, and isodiametric-coriaceous distal to it; Mt3 as distinct tergum, isodiametric-coriaceous with size of cells distinctly smaller than those on Mt2; Mt4 to syntergum isodiametric-coriaceous, but with size of cells decreased on subsequent terga, with ultimate terga granulate; relative length of terga, 1.9(m), 8.0, 2.7, 3.5, 3.7, 3.6, 3.1, 5.8.

Variation. The female paratypes do not differ significantly from the holotype.

Distribution. Philippine Islands and Papua New Guinea.

5.6 Revision of the genera of Metapelmatinae of the world

5.6.1 Key to genera of Metapelmatinae of the world

1 Antenna 10-articled, with 5 funiculars and 2-articled clava; dorsal axillar surfaces widely separate at basolateral corners of scutellum (Fig. 5.30); scutellum mediall[illegible]ded by longitudinal sulcus (Fig. 5.30); ovipositor exserted only slightly beyond ultimate tergum. .... *Neanastatus* Girault

1' Antenna 13-articled, with 7 funiculars and 3-articled clava; dorsal axillar surfaces contiguous (Figs. 5.25, 5.27); scutellum entire (Figs. 5.25, 5.27); ovipositor exserted by at least 0.5 length of rest of metasoma. 2

2(1) Scrobes Λ-shape convergent above toruli (Fig. 5.15); acropleuron extended to metapleuron, mesepimeron absent (*cf.* Fig. 5.54); dorsal axillar surface with posterolateral angle declined to ventral edge of scutellar-axiliar complex (Fig. 5.27); metanotum transverse and medially concealed beneath apex of scutellum (Figs. 5.27, 5.28). .... *Lambdobregma* n.g.

2' Scrobes as short, vertical depression above each torulus (Fig. 5.14); acropleuron separated from metapleuron by elongate upper mesepimeron and small lower mesepimeron (Fig. 5.53); dorsal axillar surface with posteromedial angle ridge-like extended along side of scutellum (Fig. 5.25); metanotum V-like extended posterior to scutellum (Figs. 5.25, 5.26). .... *Metapelma* Westwood

5.6.2 *Lambdobregma* new genus

(Figs. 5.15, 5.16, 5.27, 5.28, 5.68, 5.85, 5.104)

Type-species. *Lambdobregma schwarzii* (Ashmead), by present designation.

Charitopus schwarzii Ashmead, 1896: 11. Type-despository: USNM.

Zaischnopsis schwarzii; Gahan, 1951: [illegible]2.

Derivation of generic name. Combination of "lambda", eleventh letter [illegible] alphabet, and "bregma", meaning "front part of the head"; referring to Λ -s[illegible] cavities that differentiate individuals of this genus from other members of the subfa[illegible]ender: neuter.

Description. HEAD (Figs. 5.15, 5.16) subrectangular to oval in lateral view, vertex distinct, frons abruptly curved or angled to vertex below median ocellus, with latter faced dorsally; vertex and gena smoothly rounded into occiput; frontovertex minute punctulate-reticulate or rugulose-reticulate, with obscure setigerous punctures. **Scrobes** (Fig. 5.15) separate by distinctly convex, broadly triangular interantennal region; relatively deep ventrally and convergent for at least 0.33 distance to median ocellus; coextensive above in one known species as relatively shallow, broad depression not extended to median ocellus, but in other two known species as vertical channel on frons and more or less horizontal channel on vertex, with combined channels separated and slightly constricted by transverse ridge (Fig. 5.15). **Ocelli** in equilateral to elongate triangle; median ocellus distinctly above scrobal cavity, or within concavity at posterior margin if scrobes extended to ocellus as transversely subdivided channel; posterior ocelli contiguous with eye margin, or separate by about 0.5 ocellar diameter. **Eye** (Figs. 5.15, 5.16) inconspicuously setose to apparently asetose; in lateral view, outer margin straight projected to intersection with malar sulcus (*cf. Metapelma* Westwood and *Neanastatus* Girault) at about 35°-40° angle to posterior margin of head capsule, with width of gena subequal to or greater than malar space (Fig. 5.16) and greater than distance between eyes above. **Antenna** 13-articled, with clava 3-articled by transverse sutures; scape extended to dorsal edge of head; anellus not differentiated from funicular articles, elongate-cylindrical, and subequal in length or only slightly shorter than ful; flagellum with articles subequal in length, or decreased slightly in length distally, but all longer than wide, and increased in width distally; clava 1.5 times or longer than ful.

MESOSOMA. **Mesonotum** (Fig. 5.27) without parapsidal lines or differentiated median mesoscutal lobe; laterally convex or declined, but flattened or slightly concave dorsally; posterior edge articulated with anterior edge of scutellar-axillar complex, with edges contiguous when mesonotum flexed. DAS transverse-subtriangular, or with length and width subequal; basomedial angles contiguous; flat to lowly convex, in same plane as and separate from scutellum by distinct suture or furrow; posterolateral angle evenly declined to ventral edge of scutellar-axillar complex, without ridge-like posteromedial angle extended along side of scutellum (*cf. Metapelma*). Scutellum flat to lowly convex, entire, and acutely angled at transscutal articulation; apex obtusely angled, extended over metanotum and base of propodeum, and ventrally recurved as 'hook', with latter projected into medial depression of dorsellum and basomedial depression of propodeum (*cf.* Figs. 5.27, 5.28). **Prepectus** triangular, varied in size, extended to tegula or separate by about length of tegula when mesonotum in unflexed position. **Mesopleuron** (Fig. 5.68). Acropleuron extended to metapleuron and hind coxa, apex extended almost to apex of mesocoxa; relatively evenly sculptured (*cf. Neanastatus*); acropleural sulcus extended along ventrolateral edge of mesothorax from base of mesocoxa to about apex of procoxa where obliterated, or recurved to base of prepectus as obscure line. Mesepimeron absent. Mesepisternum with distinct transepisternal sulcus on venter of mesothorax, extended between acropleural sulcus and discrimen from middle of mesocoxa to apex of procoxa. Mesotrochantinal plate exposed in ventral view as small, medial, transverse-rectangular region posterior to lower mesepisternum, with trochantinal lobes widely separate at posterolateral corners of plate and partly visible in mesocoxal groove; lower mesepisternum and base of each mesocoxa separated by small, oblique cavity, but without membranous region (Fig. 5.68). Mesotergal-mesotrochanteral depressor (t_1-tr_1) (Fig. 5.104) as small band-like muscle from ventral edge of lateral axillar surface near anterior angle, inserted into strongly sclerotized rod-like pedicel, latter articulated posteriorly with ventral edge of scutellar axillar complex and with tendon-like ligament extended from anterior end to mesotrochanter. **Metathorax.** Metanotum with dorsellum linear and concealed beneath apex of scutellum (*cf.* Figs. 5.27, 5.28); metapleuron separated from mesocoxa by acropleuron. **Legs.** Mesocoxa with basolateral surface convexly rounded and fitted into Λ -shape region between acropleuron and oblique lateral edge of mesotrochantinal plate, without cavity between coxa and latter two structures; mesotibia without dorsobasal carina, nor with setae arranged in distinctly longitudinal rows (*cf. Neanastatus*); mesotibial pegs six or less in number, subequal in length, arranged in straight row, or with ventralmost peg longest, but pegs restricted to ventral half of tibial apex above tibial spur and [illegible]al to insertion of basitarsus; mesotibial spur subequal in length to basitarsus, or basitarsus plus 0.5 subsequent tarsomere; metatibia moderately compressed, but without knife-like dorsal edge as in *Metapelma*; metatarsus with basitarsus compressed-cylindrical, of similar diameter to subsequent tarsomeres. **Wings.** Fore wing setose except for elongate linea calva below parastigma and base of MV; costal cell relatively wide and distinct for entire length; SMV and MV with juncture distinct; SMV longer than MV; MV longer than PMV; PMV longer than STV. Hind wing without basal vein. **Propodeum** (Figs. 5.27, 5.28) with asetose, transverse-rectangular, flat plical region between spiracles, undifferentiated except for basomedial depression for scutellar 'hook'; propodeal foramen very broad.

METASOMA of females 8-segmented; elongate-lanceolate, with ovipositor sheaths exserted for at least 0.66 length rest of metasoma. Mt1 (petiole) wide, but very short to linear; Mt2-Mt5 with posterior margins incised medially; Mt6 with posterior margin entire and transverse; Mt7 posteriorly narrowed, extended over ultimate tergum and base of ovipositor sheaths; Mt8 + Mt9 fused as syntergum, indistinguishably so dorsally, but separate laterally by suture directed posteroventrally from cercus; epiproct only as very small triangular membranous region at apex of syntergum, and inevident in most specimens. **Hypopygium** extended to, or almost to, apex of metasoma excluding ovipositor sheaths.

Male metasoma 8-segmented, with Mt8 and Mt9 fused as syntergum; similar to that of females except only basal one or two terga with posterior margins distinctly incised; syntergum exposed, elongate-triangular with sides convergent to apex, and conspicuously extended beyond apex of ultimate sternum, with genitalia concealed dorsally but visible in large part ventrally.

Distribution. Known only from Nearctic (Florida) and Neotropical (Caribbean islands, Panama, Chile) regions.

Hosts. A single specimen of *L. schwarzii* (Ashmead) [USNM] labelled as "ex cricket egg" [Orthoptera: Grylloidea].

Generic diversity. The type species of the genus is the only described species, but I saw specimens representing an additional two species, *L. schwarzii* is recorded from Florida, Bahama Islands, Jamaica and Panama [USNM, CNC, RNHL]. A closely related species was seen from Trinidad and Panama [MCZ, RNHL]. Striking characters that differentiate this species from *L. schwarzii* are size (smaller), structure (prepectus not extended to tegula when mesonotum in unflexed position, and not as elongate-slender triangular; head more evenly convex, with upper and lower scrobal cavities at obtuse rather than at right-angle, and lower cavity less deeply or distinctly delimited; ovipositor sheaths exserted for less than length of metasoma), and color (hind leg entirely dark brown, except basal 0.33-0.50 of tibia distinctly white). A single male specimen from Chile [MCZ] represents the third species. This specimen is distinguished from those of the two previous species by numerous characters, but is most conspicuous in structure of the head. The scrobal cavity is not extended to the median ocellus as a transversely subdivided channel, but is only obscurely coextensive as a broad and shallow depression distinctly below the median ocellus.

Monophyly and relationships. Monophyly of *Lambdobregma* is indicated by presence of a transepisternal sulcus [Table 5.2, 25(2)], and by structure of the mesotergal-mesotrochanteral (t_2-tr_2) muscle [Table 5.1, 16(4)]. *Lambdobregma* is hypothesized as the sister genus of *Neanastatus*, based on four hypothesized synapomorphies, illustrated in figure 5.2 and described in section 5.7.2.2.

5.6.3 *Metapelma* Westwood

(Figs. 5.14, 5.25, 5.26, 5.53, 5.69, 5.84, 5.101, 5.102, 5.108)

Metapelma Westwood, 1835: 69. **Type species:** *M. spectabile* Westwood. Monotypy. **Type depository:** BMNH.

Metapleura Girault, 1917a: 12. Typographical error.

Description. HEAD (Fig. 5.14) lenticular in lateral view, with frons evenly curved to about level of posterior ocelli, median ocellus faced more or less anteriorly, and vertex short; vertex and gena smoothly rounded to occiput; frontovertex isodiametric- or transverse-coriaceous to transverse rugulose-reticulate, with scattered setigerous punctures. Scrobes (Fig. 5.14) separated by variedly convex interantennal region, latter parallel-sided, with each cavity as short, widely separate vertical depression above each torulus, not coextensive above. Ocelli in equilateral to elongate triangle; median ocellus conspicuously above scrobes; posterior ocelli distinctly separate from eye margin. Eye (Fig. 5.14) setose; in lateral view outer margin not straight projected to malar sulcus, recurved to sulcus just before intersection and at about 10°-20° angle to posterior margin of head capsule, with width of gena (measured where recurved to malar sulcus) subequal to or less than malar space, and distinctly greater than distance between eyes above. **Antenna** 13-articled, with clava 3-articled by transverse sutures; scape relatively short, not extended to dorsal edge of head; anellus varied in length, longer than wide and conspicuously shorter than fu1 in almost all species, but quadrate, or subequal in length to fu1, or both, in a few species; flagellum varied in shape, but widened distally, in most species with fu1 and fu2 elongate-cylindrical and either subequal in length or with fu2 longer, and with subsequent funiculars distinctly shorter, with one or more distal funiculars quadrate or transverse, but few species with fu1 or fu1 and fu2 short, not differentiated from distal funiculars; clava subequal in length or shorter than fu1 in most species.

MESOSOMA. **Mesonotum** (Figs. 5.25, 5.26) with percurrent parapsidal line, as parallel sublateral ridge extended from lateral edge of transscutal articulation to posterior edge of pronotum; convex or declined lateral to each parapsidal line, and flattened or concave dorsally, except for very lowly convex triangular median mesoscutal lobe, latter very short and in most specimens posteriorly attenuated as slightly raised ridge or differentiated line toward transscutal articulation (Fig. 5.26); posterior edge articulated with anterior edge of scutellar-axillar complex, edges contiguous when mesonotum flexed. DAS (Fig. 5.25) transversely triangular, convex and separate from scutellum by distinct furrow, or more or less wedge-like if posteromedial surface flatly declined to scutellum, but with basomedial angles contiguous; posteromedial angle ridge-like extended along side of scutellum. Scutellum convex, or dorsally flattened, but entire and acutely angled at transscutal articulation; apex obtusely angled, but not ventrally recurved as hook nor concealing dorsellum of metanotum (cf. Figs. 5.25, 5.26). **Prepectus** (Fig. 5.26) triangular, extended to, or almost to base of tegula if mesonotum in unflexed position. **Mesopleuron** (Figs. 5.26, 5.53, 5.69). Acropleuron not extended to metapleuron or hind coxa, apex extended only to base of mesocoxa (Fig. 5.69); relatively evenly sculptured, but in most species with small circular region of minute coriaceous sculpture medially below mesopleural wing process; acropleural sulcus straight convergent from anterolateral corner of mesocoxa toward discrimen at apex of procoxa, where abruptly angled to base of prepectus as much finer sulcus (Fig. 5.53) (concealed by procoxa in most specimens). Mesepimeron present, narrow, and divided by transepimeral sulcus into slender upper mesepimeron and much smaller, quadrate to triangular lower mesepimeron (Fig. 5.53). Mesepisternum without transepisternal sulcus or line. **Mesotrochantinal plate** not externally exposed, inflected into body cavity at abrupt angle, with mesepisternum transverse along base of coxa (Fig. 5.69); as triangular plate, with trochantinal lobes widely separate, medially on convergent lateral edges of plate (Fig. 5.84). Mesotergal-mesotrochantinal depressor (t_2-tr_2) two-parted, origin of band-like t_2-tr_2a muscle between lateral axillar surface and ventrally projected, triangular, axillar plate (*cf.* Figs. 5.101a, 5.101b), and tubular t_2-tr_2b muscle from apex of axillar plate (Figs. 5.101b, 5.102), with both inserted into small pedicel, latter free in body cavity and with tendon-like ligament extended from near center to mesotrochanter. **Metathorax.** Metanotum (Figs. 5.25, 5.26) with dorsellum flat, horizontal, and subtriangular, projected over base of propodeum between apex of scutellum and propodeum, with mediolongitudinal ridge in many species (Fig. 5.25); metapleural origin at base of meso- and metacoxa. **Legs.** Mesocoxa basolaterally concave, with distinct cavity between coxa and Λ-shape region formed by acropleuron and oblique lateral edge of mesepisternum (Fig. 5.53); mesotibia without dorsobasal carina, nor with setae in distinctly longitudinal rows; mesotibial pegs more than six in number, subequal in length as more or less straight row (Fig. 5.94), or increased in length medially in form of V-shape row, but extended over both tibial spur and insertion of basitarsus; mesotibial spur extended to apex of basitarsus, or apex of second tarsomere; mesotarsus in very few species with double row of pegs along anterior edge of tarsomeres 1-3; metatibia compressed, dorsal edge at least knife-like, and in most species conspicuously compressed as lamella-like flange, latter wider apically than basally but of varied shapes ~~and widths~~; metatarsus with at least basitarsus compressed, with carinate or knife-like dorsal edge, and in most species tarsus conspicuously decreased in width apically. **Wings.** Fore wing entirely setose, or with variedly developed linea calva below parastigma; costal cell relatively wide and distinct for entire length; SMV longer than MV; MV subequal to or shorter than PMV; PMV longer than STV. Hind wing with short spike-like basal vein. **Propodeum** [illegible] 5.25, 5.26) with plical region subrectangular, but with surface inclined to median, with slight mediolongitudinal ridge, and flattened basally for protuberant dorsellum, also with transverse furrow near edge of propodeal foramen, latter as slender declined region behind furrow (Fig. 5.25).

METASOMA of females 9-segmented; lanceolate with ovipositor sheaths extended for at least 0.5 length of rest of metasoma. Mt1 (petiole) wide but linear, inevident in many specimens; Mt2 with posterior margin medially incised or emarginate; Mt3-Mt6 with posterior margins entire and transverse, or one or more slightly emarginate; Mt7 with posterior edge rounded and extended to base of Mt9 in natural condition; Mt8 and Mt9 independent (Fig. 5.108); Mt8 only visible laterally, extended beneath cercus and Mt9 to apex of Mt9, with dorsal surface transverse and normally concealed by Mt7, but about 0.5 length of Mt9, and longitudinally divided by medial suture or depigmented line; Mt9 relatively short and broad, highly convex in most dried specimens but subquadrate if flattened, sides convergent toward rounded apex, and here with lightly sclerotized or membranous epiproct protruded to apex of ovipositor as elongate, membranous filament (concealed between ovipositor sheaths above terebra in many specimens). Cercus in membrane between Mt8 and Mt9, near basolateral corner of Mt9. **Hypopygium** extended about 0.66-0.75 length of metasoma.

Male metasoma 8-segmented, with Mt8 and Mt9 fused as syntergum, but with oblique suture directed posteroventrally from cercus indicating lateral line of fusion; apex of ultimate tergum and sternum extended approximately same extent, with genitalia equally visible in dorsal and ventral view if protruded.

Synonymy. Z. Bouček informs me (pers. comm.) that he examined the type specimen (male) of *Halidea insignis* Förster, and that it is congeneric with *Anastatus* Motschulsky rather than *Metapelma*. Removal of the name *Halidea* from synonymy with *Metapelma* is based on this information.

Distribution. Known from all biogeographic regions.

Hosts. Xylophagous beetles (Coleoptera) of the families **Bostrichidae**, **Buprestidae**, **Cerambycidae**, and **Curculionidae**.

Figure 3.34. *Gonatocerus* sp., sagittal section of mesosoma, mesofurca and various muscles removed.

Figure 3.35. *Gonatocerus* sp., isolated scutellar-axillar complex.

Figure 3.36. *Palaeomymar* sp., nr. ***anomalum*** (Bl. & Kr.), petiolar segments.

Figure 3.37. *Palaeomymar* sp., nr. ***anomalum*** (Bl. & Kr.), metasoma exclusive of petiolar segments.

Figure 3.38. *Leucospis a. affinis* Say, male genitalia.

a. dorsal view.

b. ventral view.

Figure 3.39. *Palaeomymar* sp., nr. ***anomalum*** (Bl. & Kr.), apex of metasoma.

Scale bar = μm.

Monophyly and relationships. Monophyly of _Metapelma_ is indicated by structure of the parapsidal lines [Table 5.1, 13(3)], structure of the mesotergal-mesotrochantinal (t_2-tr_2) muscle [16(2)], and compressed metatibia and metatarsus [Table 5.2, 35(2)]. _Metapelma_ is hypothesized as the sister taxon of _Lambdobregma_ + _Neanastatus_, as illustrated in Figure 5.2, and discussed in section 5.7.2.2.

Keys. Ferrière 1938 (world); Nikolskaya 1952 (USSR); Erdös 1960 (Hungary).

Catalog of taxa. _M. albisquamulatum_ Enderlin, 1912; ZMHB; E - Sri Lanka [Ceylon].

*_M. angustipes_ Ferrière, 1938; BMNH; E - South Africa.

*_M. atrotegulare_ Gahan, 1925; USNM; O - Philippines. = _M. rufimana_ Westwood, syn. by Ferrière (1938).

M. bachi Girault, 1922; QMB; A - Australia.

M. beenleighi Girault, 1926; QMB; A - Australia. Transferred to _Anastatoidea_ Gahan (Eupelminae) by Ferrière (1938).

*_M. berlandi_ Ferrière, 1938; MNHP; E - Equatorial Guinea [Fernando Po].

M. columbi Girault, 1923; QMB; A - Australia. Transferred to _Anastatoidea_ Gahan (Eupelminae) by Gahan (1927).

*_M. compressipes_ Cameron, 1909; BMNH; O - Borneo.

*_M. cubensis_ Ashmead, 1900; USNM; Nt - USA.

*_M. elegantulum_ Ferrière, 1938; BMNH; E - South Africa.

*_M. feae_ Masi, 1923; MSNG; E - Uganda.

**M. giraulti* Ferrière, 1938; BMNH; A - Australia.

M. gloriosum Westwood, 1874; UMO; O - Philippines.

M. goethei Girault, 1928; QMB; A - Australia.

M. insigne (Förster, 1860); NHMV; P - Germany. As *Halidea* Förster, comb. by Ashmead (1904); transferred to *Anastatus* Motschulsky (Eupelminae), **n. comb.** *vide* Bouček (pers. comm.).

M. ledouxi Risbec, 1953; MNHP; E - Ivory Coast.

M. leucoptera Risbec, 1958; MNHP; E - Zimbabwe [S. Rhodesia].

M. longfellowi Girault, 1923; QMB; A - Australia. Transferred to *Anastatoidea* Gahan (Eupelminae) by Gahan (1927).

**M. madecassa* Ferrière, 1938; MNHP; E - Madagascar.

**M. mesandamana* Mani, 1973; USNM; O - India.

**M. mirabile* Brues, 1906; MPM; E - South Africa.

M. nassaui Girault, 1933; QMB; A - Australia.

M. nobile (Förster, 1860); NHMV; P - Germany. As *Halidea* Förster, comb. by Ashmead (1904).

M. obscuratum Westwood, 1874; UMO; O - India.

M. pacificum Nikolskaya, 1952; ZIL; P - USSR.

M. palauensis Yoshimoto & Ishii, 1965; BPBM; A - Palau Islands.

**M. patrizii* Masi, 1923; MSNG; E - East Africa.

**M.* *ruficauda* Ferrière, 1938; BMNH; E - South Africa.

M. rufimana Westwood, 1874; UMO; O - Borneo.

**M.* *salomonis* Ferrière, 1938; BMNH; E - Solomon Is.

**M.* *schwarzi* (Ashmead, 1890); USNM; N - USA. As *Halidea* Föster, comb. by Ashmead [illegible]904).

M.* *seyrigi* Risbec, 1952; MNHP; E - Madagascar. Transferred to *Tineobius* Ashmead (Eupelminae), **n. comb.

M. sidneyi Girault, 1930; QMB; A - Australia.

**M.* *speciosum* Gahan, 1925; USNM; O - Philippines. = *M. albisquamulatum* Enderlin, syn. by Ferrière (1938).

**M.* *spectabile* Westwood, 1835; BMNH; N - USA.

**M.* *strychnocolum* Mani, 1973; USNM; O - India.

M. superba Dodd, 1917; ?; A - Australia. Transferred to *Anastatoidea* Gahan (Eupelminae) by Gahan (1927).

**M.* *sylvaticum* Risbec, 1953; MNHP; E - Ivory Coast.

M. taprobanae Westwood, 1874; UMO; E - Sri Lanka [Ceylon].

**M.* *tenuicrum* Gahan, 1925; USNM; O - Philippines.

**M.* *turneri* Ferrière, 1938; BMNH; E - South Africa.

M. westwoodi Girault, 1915; QMB; A - Australia.

5.6.4 *Neanastatus* Girault

(Figs. 5.13, 5.29, 5.30, 5.54, 5.70, 5.86, 5.103)

Neanastatus Girault, 1913: 35. **Type species:** *N. cinctiventris* Girault. Monotypy and original designation. **Type depository:** QMB.

Solindenelleus Girault, 1914: 22. **Type species:** *S. pulchricorpus* Girault. Monotypy and original designation. **Type depository:** QMB. Synonymy by Gahan, 1919: 519.

Metaplopoda Masi, 1926: 275. **Type species:** *M. grallaria* Masi. Monotypy. **Type depository:** DEI. Synonymy by Ferrière, 1938: 50.

Description. HEAD (Fig. 5.13) lenticular in lateral view, with frons evenly curved to about level of posterior ocelli, with median ocellus faced more or less anteriorly, and vertex short, only obscurely differentiated from frons; vertex, or vertex and upper gena, carinately angled to occiput; frontovertex isodiametric-reticulate to alveolate-punctate, or alveolate-punctate and punctulate between alveolae. **Scrobes** (Fig. 5.13) not developed, only shallowly impressed immediately above each torulus. **Ocelli** in wide triangle; median ocellus conspicuously above scrobes; posterior ocellus separate from eye margin by one ocellar diameter or more. **Eye** (Fig. 5.13) sparsely and inconspicuously setose, to apparently glabrous; in lateral view outer margin not projected straight to malar sulcus, recurved to sulcus just before intersection and at about 5°-15° angle to posterior margin of head capsule, with width of gena (measured where recurved to malar sulcus) distinctly less than malar space and distance between eyes above. **Antenna** 10-articled, with clava 2-articled by transverse suture; scape short and compact, not extended to median ocellus; anellus differentiated from funicular articles, transverse ring-like and obscure in some specimens; flagellum relatively short in most species, less than or only slightly longer than length of head; funicular articles subequal in length, or decreased in length distally, conspicuously setose in males, with long decumbent white setae; clava longer than ful.

MESOSOMA. **Mesonotum** without parapsidal lines; laterally convex or declined, with dorsum lowly convex, or flattened to shallowly concave if somewhat collapsed in air-dried specimens, and in some specimens with short, obscure, triangular median mesoscutal lobe; posterior edge not articulated along anterior edge of scutellar-axillar complex, with edges separated by membrane when mesonotum flexed. DAS (Fig. 5.30) elongate-subtriangular, small and widely separate at basolateral edge of scutellum; flat, in same plane as, and separate from scutellum by fine suture. Scutellum (Figs. 5.29, 5.30) flat, medially divided by longitudinal sulcus, and transverse along transscutal articulation; apex acutely or right-angled and ventrally recurved as 'hook', latter extended over dorsellum if mesonotum in unflexed condition, but projected over dorsellum into depression of Mt1 (petiole) if mesonotum flexed (*cf.* Figs. 5.29, 5.30). **Prepectus** (Fig. 5.54) massive plate-like quadrate to circular, posterior edge extended to tegula, broad, and slightly incised in most species. **Mesopleuron** (Figs. 5.54, 5.70). Acropleuron extended to metapleuron and hind coxa, apex extended slightly beyond apex of mesocoxa (Fig. 5.70); sculpture abruptly and conspicuously changed along vertical, posteriorly curved medial line, more or less isodiametric-coriaceous or reticulate anterior to line, but elongate-coriaceous with much larger cells posterior to line (Fig. 5.54); acropleural sulci extended along ventrolateral edge of mesothorax as parallel sulci from base of mesocoxa to apex of procoxa, where abruptly angled to prepectus (Figs. 5.54, 5.70). Mesepimeron absent. Mesepisternum without transepisternal sulcus or line. Mesotrochantinal plate not externally exposed, inflected into body cavity at abrupt angle, with mesepisternum transverse along base of coxa (Fig. 5.70); as rectangular plate, with trochantinal lobes widely separate at apicolateral angles of plate (Fig. 5.86). Mesotergal-mesotrochantinal muscle (t_2-tr_2) (Fig. 5.103) two-parted, t_2-tr_2a as short, thin, band-like muscle from DAS, and t_2-tr_2b as short tubular muscle from apex of axillar phragma, both inserted into elongate-slender pedicel, latter posteriorly articulated with ventral edge of scutellar-axillar complex, with tendon-like ligament extended from anterior end to mesotrochanter. **Metathorax.** Metanotum with dorsellum transverse beneath apex of scutellum (Fig. 5.29); metapleuron small and separated from mesocoxa by acropleuron. **Legs.** Mesocoxa basolaterally concave, with distinct cavity between coxa and Λ-shape region formed by acropleuron and oblique lateral edge of mesepisternum (Fig. 5.54); mesotibia with variedly developed arcuate carina, at basal edge and partly extended along anterodorsal edge, and with dorsal setae arranged in distinct longitudinal rows in many species; mesotibial pegs more than six in number, increased in length medially in form of V-shape row, and extended over both tibial spur and insertion of basitarsus; mesotibial spur subequal in length to basal two tarsomeres, to as long as tarsus, and with row of black spines along inner edge in many species; metatibia compressed-cylindrical, but without knife-like dorsal edge; metatarsus with basitarsus subcylindrical and of similar diameter to subsequent tarsomeres. **Wings.** Fore wing setose except for long glabrous band curved from anal area toward anterior margin of wing at about middle of MV; costal cell narrowed from base, with apex indistinct in many specimens; SMV in about same line as MV, with juncture difficult to discern in many specimens; SMV subequal in length to MV; PMV of similar length as MV and much longer than STV. Hind wing without basal vein. **Propodeum** (Figs. 5.29, 5.30) very short medially, linear or as vertical strip, and then apparently divided medially or concealed by overlying scutellar apex in many species.

METASOMA 8-segmented in both sexes; conic-ovate in females, with ovipositor sheaths only slightly exserted beyond apex of syntergum, and cylindrical in males, with apex of syntergum and ultimate sternum extended to same extent, with genitalia equally visible dorsally and ventrally if protruded. Mt1 (petiole) narrow and short, with medial depression for scutellar 'hook'; Mt2-Mt6 with posterior margins entire and transverse, or one or more with margin emarginate medially; Mt7 with posterior edge rounded; Mt8 and Mt9 indistinguishably fused as syntergum; syntergum with sides convergent to rounded apex; epiproct as only small membranous region at apex of syntergum, and inevident in most specimens. **Hypopygium** extended only about 0.33-0.50 length of metasoma.

Distribution. Restricted to the Old World (Palearctic, Ethiopian, Oriental and Australian regions).

Hosts. Parasitic in galls of Cecidomyiidae (Diptera), either as primary parasite, [illegible] secondary parasite of Platygastridae (Hymenoptera: Proctotrupoidea) in galls.

Monophyly and relationships. *Neanastatus* is supported as a monophyletic genus by states of numerous characters [Table 5.1, 2(2), 8(2), 10(3a); Table 5.2, 28-34(2)], and is hypothesized as the sister genus of *Lambdobregma*, as illustrated in figure 5.2 and discussed in section 5.7.2.2.

Keys. Girault 1915 (Australia); Mani 1935 (India and Sri Lanka); Ferrière 1938 (Ethiopian, Oriental); Risbec 1952 (Madagascar); Shafee 1973 (India).

Catalog of taxa. *N. aeschyli* Girault, 1921; QMB; A - Australia.

**N. africanus* Ferrière, 1938; BMNH; E - South Africa.

N. albitarsis* (Girault, 1904); USNM; P - Japan. As *Calosota* Curtis (Calosotinae), **n. comb.

N. ariostoni Girault, 1922; QMB; A - Australia.

N. aurifasciatus Girault, 1915; QMB; A - Australia.

N. aurivertex Girault, 1915; QMB; A - Australia.

N. bilingae Girault, 1923; QMB; A - Australia.

N. cinctiventris Girault, 1913; QMB; A - Australia.

N. darci Girault, 1933; QMB; A - Australia.

N. desertensis Girault, 1915; QMB; A - Australia.

N. divinus Girault, 1922; QMB; A - Australia.

N. flavimesopleurum Girault, 1915; QMB; A - Australia.

N. flavipronotum Girault, 1915; QMB; A - Australia.

**N. gracilipes* Risbec, 1952; MNHP; E - Madagascar.

**N. grallarius* (Masi, 1926); DEI; O - Taiwan [Formosa]. As *Metaplopoda* Masi, comb. by Ferrière (1938).

N. inconspicuus Girault, 1915; QMB; A - Australia.

N. indicus Shafee, 1973; AMUA; O - India.

**N. longitarsis* Ferrière, 1938; BMNH; O - Malaysia.

**N. maiwalei* Ferrière, 1938; BMNH; E - Malawi [Nyasaland].

N. maximicorpus Girault, 1915; QMB; A - Australia.

N. novus Girault, 1920; ?; A - Australia.

**N. obscuratus* Ferrière, 1938; BMNH; E - South Africa.

**N. occidentalis* Ferrière, 1938; MNHP; E - Ivory Coast.

N. orientalis Girault, 1915; USNM; O - Philippines.

**N. oryzae* Ferrière, 1938; BMNH; O - Thailand [Siam].

N. parvus Girault, 1920; ?; A - Australia.

N. philippinensis Girault, 1915; USNM; O - Philippines.

*_N. proximus_ Ferrière, 1938; BMNH; P - Palestine [Israel].

N. pulchricorpus (Girault, 1914); QMB; A - Australia. As _Solindenelleus_ Girault, comb. by Gahan (1919).

N. punctaticeps Girault, 1915; QMB; A - Australia.

N. purpureiscutellum Girault, 1915; QMB; A - Australia.

N. rabalaisi Girault, 1922; QMB; A - Australia.

N. ramakrishnai Mani, 1935; ZSIC; O - India. Transferred to _Anastatus_ Motschulsky (Eupelminae) by Hayat (1975).

N. reymondi Girault, 1915; QMB; A - Australia.

*_N. robustus_ Ferrière, 1938; BMNH; E - South Africa.

*_N. rufatus_ Ferrière, 1938; BMNH; E - South Africa.

*_N. tenuis_ Ferrière, 1938; BMNH; E - South Africa.

*_N. tenuis var. bicolor_ Risbec, 1951; MNHP; E - Senegal.

*_N. tenuis var. platygasteri_ Risbec, 1956; MNHP; E - Cameroons.

N. trinotatus Girault, 1915; QMB; A - Australia.

N. trochantericus Gahan, 1919; USNM; O - India.

*_N. turneri_ Ferrière, 1938; BMNH; E - South Africa.

5.7 Phylogenetic analysis

Distribution of states of 17 characters or character systems is described and analyzed for evidence of monophyly or phylogenetic relationships between Calosotinae, Metapelmatinae, Eupelminae, Tanaostigmatinae (Eupelmidae), Cleonyminae (Pteromalidae), Encyrtidae, and Aphelinidae. Characters considered most important for interpreting relationships between the higher taxa are analyzed first, and characters that indicate patterns are grouped together. Following these, distribution of 8 additional characters is described for members of Calosotinae, and 11 for Metapelmatinae, for evidence of monophyly or relationships between the genera in the two subfamilies. Character states are described in the text, and distribution of the states summarized in tables 5.1 and 5.2. The groundplan state for each higher taxon is also hypothesized in the text, and listed in tables 5.1 and 5.2. An analysis of phylogenetic relationships between the genera of Calosotinae is given in section 5.7.2.1, with alternate hypotheses illustrated in figure 5.1, and an analysis of relationships between the genera of Metapelmatinae is given in section 5.7.2.2, with the hypotheses illustrated in figure 5.2.

5.7.1 Character-state analysis

5.7.1.1 Characters analyzed for evidence of relationships between the higher taxa

1. Sexual dimorphism. Two states are recognized: 1] males and females not dimorphic in the following characters that are analyzed individually below: **(a)** structure of lateral mesopleuron, **(b)** structure of mesotibial spur, **(c)** mesotarsal peg pattern, **(d)** mesopleural-mesocoxal articulation, **(e)**, structure of notauli and correlated mesoscutal structure, **(f)** structure of dorsal axillar surface (DAS), **(g)** presence of mesotibial pegs, and **(h)** structure of mesotergal-mesotrochanteral (t_2-tr_2) muscle; and, 2] males and females are dimorphic in states of the above characters.

Of the taxa included in this analysis, only males and females of Eupelminae are dimorphic in the above-listed characters (Table 5.1). Because members of most of the taxa are not sexually dimorphic, in addition to almost all other chalcidoids, a non-dimorphic structure is hypothesized as plesiomorphic. Consequently, a non-dimorphic ancestor is hypothesized for Eupelminae plus any of the other included taxa, and the autapomorphic dimorphic structure of members of Eupelminae is interpreted as evidence of monophyly of this subfamily.

Character states recognized for each of the eight characters listed above are described in the respective analyses. However, male eupelmines generally exhibit the plesiomorphic state for each character, whereas females exhibit apomorphic states that are either autapomorphic, or are shared with members of one or more of Calosotinae, Metapelmatinae, Tanaostigmatinae, Encyrtidae, and some Aphelinidae (Table 5.1). If Eupelminae and one or more of the above taxa are related, two hypotheses for evolution of sexual dimorphism satisfy the observed pattern of shared states: 1) the non-dimorphic common ancestor had the plesiomorphic states of male eupelmines, which implies that Eupelminae is at most the sister group of the other taxa, and that all the apomorphic states that are shared between female eupelmines and members of the other taxa are independently evolved, or, 2) the non-dimorphic common ancestor had the apomorphic states of female eupelmines, and sexual dimorphism in Eupelminae evolved through secondary loss of all the states in males to plesiomorphic appearing states, *i. e.*, the apparently plesiomorphic states of male eupelmines are actually apomorphic through reversal.

The first hypothesis requires independent and parallel evolution in female eupelmines of all the character states that traditionally have been used to define Eupelmidae, or to infer a sister-group relationship between Eupelminae and Encyrtidae. The latter hypothesis requires secondary loss of all the character states in male eupelmines. I presently interpret the former hypothesis as more likely because the shared apomorphic character states form a functional complex that is correlated with a modified jumping mechanism (see Gibson in press, c). Character states for Eupelminae in the following analyses of characters are polarized based on the hypothesis that sexual dimorphism evolved through secondary modification of females. Furthermore, if the above hypotheses are true, sexual dimorphism indicates that Eupelmidae is a grade-level taxon.

2. Antennal clava. Three states are recognized: 1] clava 1-articled; 2] clava 2-articled; and, 3] clava 3-articled.

A 3-articled clava is hypothesized as the groundplan state for Chalcidoidea, based on 13 articles as the hypothesized groundplan number of antennal articles for the superfamily (Gibson in press, b). A 3-articled clava is also possessed by members of Eupelminae and Tanaostigmatinae, was previously hypothesized as the groundplan state for Encyrtidae (Trjapitzin 1971) and Aphelinidae (Yasnosh 1976), and is here hypothesized as the groundplan state for Metapelmatinae (2-articled clava of individuals of *Neanastatus* [Table 5.1, 2(2)] interpreted as autapomorphic through loss of single article).

Hypotheses of the groundplan state of the clava for Cleonyminae (Pteromalidae) and Calosotinae are uncertain. Of seven cleonymine tribes recognized by Hedqvist (1961), members of five (Cleonymini, Louricini, Lysisini, Thaumasurini, and Leptofoenini), representing 28 of 31 recognized genera, have a 1-articled clava. Individuals of *Oodera*, representing the monotypic tribe Ooderini, and two genera of Heydenini have a 3-articled clava. Members of five genera of Calosotinae have a 1-articled clava, whereas members of the other three recognized genera have a 3-articled clava (Table 5.1). Based on generalized outgroup analysis, the most parsimonious hypothesis is that a 3-articled clava is the groundplan state for Cleonyminae and Calosotinae, and that reductions to a 1-articled clava occurred independently in each taxon. However, the reconstructed phylogeny proposed for Calosotinae (Fig. 5.1) indicates that a 1-articled clava is the more probable groundplan state for the subfamily. The plesiomorphic appearing 3-articled clava of individuals of *Calosota*, *Balcha*, and *Tanythorax* is hypothesized to be synapomorphic for the taxa through a single reversal (Fig. 5.1).

If this hypothesis of polarity is correct, a possible sister-group relationship between Calosotinae and Cleonyminae, or some subgroup of Cleonyminae, is indicated. Furthermore, the 3-articled clava characteristic of members of Eupelminae, Tanaostigmatinae, and Metapelmatinae, could indicate that Eupelmidae is polyphyletic, with these three subfamilies more closely related to some pteromalid group with a 3-articled clava.

3. Structure of lateral mesopleuron. Relative structure of the lateral mesopleuron depends on size of the acropleuron. An increasingly enlarged acropleuron, resulting from enlargement of the pl_2-t_2c muscle (Gibson in press, c), results in a smaller mesepimeron and upper mesepisternum. Consequently, the four states described below are listed in order from "least" to "most" apomorphic.

The four recognized states are: 1] lateral mesopleuron with acropleuron as small subalar region, at most as large as mesepimeron, and latter entire or differentiated into upper and lower mesepimeron, but with upper mesepisternum forming largest part of pleuron (Figs. 5.41, 5.42, 5.58); 2] lateral mesopleuron with acropleuron conspicuous as largest part, but not extended to metapleuron or mesocoxa, mesepimeron interposed between latter two structures and acropleuron (Figs. 5.43, 5.48, 5.53); 3] lateral mesopleuron with acropleuron extended to metapleuron dorsally, but with lower mesepimeron interposed between acropleuron and mesocoxa, either as **(3a)** flat region beneath and below plane of acropleuron (Figs. 5.44, 5.47), or **(3b)** convex region at posteroventral apex of and in same plane as acropleuron (Figs. 5.49-5.51); and, 4] lateral mesopleuron with acropleuron extended to metapleuron and mesocoxa, without exposed mesepimeron (Figs. 5.45, 5.52, 5.54, 5.55, 5.57, 5.59).

An entirely convex mesopleuron (acropleuron) is one of the primary characters that was used in the past to distinguish Eupelmidae and Encyrtidae from other families of

Chalcidoidea, and to infer a relationship between the two families. However, character-state distribution of the lateral mesopleuron in Eupelmidae (Table 5.1) shows both to be invalid. The mesopleuron is unmodified (plesiomorphic) in male eupelmines (Fig. 5.41), and is highly varied in other members of the family (Figs. 5.43-5.45, 5.47-5.55). If sexual dimorphism in Eupelminae (character one) evolved through secondary modification of females, the expanded acropleuron of female eupelmines (Fig. 5.52) is convergent to the similarly expanded acropleura of encyrtids and most other eupelmids. Even if sexual dimorphism in Eupelminae evolved through secondary loss of the apomorphic states in males, if Calosotinae is monophyletic, any common ancestor of the higher taxa must have had a relatively plesiomorphic mesopleuron, with the acropleuron developed no more than in individuals of *Archaeopelma* (Fig. 5.43). A completely expanded acropleuron is a possible synapomorphy only for members of Tanaostigmatinae + Encyrtidae, because this is the hypothesized groundplan state for only these two taxa [Table 5.1, 3(4)].

Structure of the lateral mesopleuron is highly varied in members of Calosotinae. Individuals of *Archaeopelma* have a mesopleuron that is only slightly more apomorphic than that of male eupelmines. Individuals of *Licrooides* have a larger, flatly convex acropleuron that is more conspicuously defined by an acropleural sulcus, but as for individuals of *Archaeopelma*, there is a distinct mesepimeron exposed (Fig. 5.48) [Table 5.1, 3(2)]. Individuals of *Paraeusandalum* have a yet more apomorphic mesopleuron [3(3a)], with the acropleuron distinctly convex and dorsally extended to (or almost to) the metapleuron, but with a large, flat, lower mesepimeron below and in a lower plane than the acropleuron (Fig. 5.44). Individuals of *Eusandalum* have a completely expanded acropleuron [3(4)] (Fig. 5.45), or, like individuals of *Chirolophus*, have only a small, relatively inconspicuous lower mesepimeron below the acropleuron [3(3a)] (Fig. 5.47). Members of *Balcha*, *Tanythorax*, and *Calosota* also have a very large acropleuron, but most individuals have a distinct, convex, subtriangular lower mesepimeron at the posteroventral apex of, and on the same plane as, the acropleuron [3(3b)] (Figs. 5.49-5.51). I consider this latter structure as synapomorphic for the three genera, and the completely expanded acropleuron of some species of *Calosota* as the result of secondary modification. Furthermore, because individuals of *Paraeusandalum* have the lower mesepimeron as a flat sclerite beneath the plane of the acropleuron, I conclude that either *Licrooides* or *Archaeopelma* is the more probable sister group of *Balcha* + *Tanythorax* + *Calosota*.

Individuals of *Metapelma* (Metapelmatinae) have a large convex acropleuron, but with a slender subdivided mesepimeron between the acropleuron and metapleuron (Fig. 5.53) [Table 5.1, 3(2)]. I interpret this as the groundplan state for Metapelmatinae, and a completely enlarged acropleuron as a possible synapomorphy for *Lambdobregma* + *Neanastatus*.

Hayat (1983) recognized 44 genera of Aphelinidae. He stated that the mesopleuron was large and undivided in some species of *Aphytis* Howard and *Centrodora* Förster, was well as in members of *Coccobius* Ratzeburg, *Hirtaphelinus* Hayat, *Marietta* Motschulsky, *Eutrichosomella* Girault, *Samarilola* Hayat, and unnamed genus "A", but did not describe states of the mesopleuron for most of the genera. Of the genera stated by Hayat to have a large and undivided mesopleuron, I saw specimens representing all but genus "A". The mesopleuron of *Hirtaphelinus* is undifferentiated, *i. e.*, without a subalar acropleuron or mesopleural suture, but it is as a flat, high region. This apomorphic structure is probably correlated with brachyptery of individuals, but it is not the same state as in individuals of the other genera. Specimens seen of the other genera had the acropleuron convexly enlarged to varied extents, though only individuals of *Coccobius* (Fig. 5.80) and *Eutrichosomella* had a completely expanded acropleuron [Table 5.1, 3(4)]. Of the aphelinids having a convexly expanded acropleuron, but with the mesepimeron largely exposed, all had the latter as an undifferentiated region, *i. e.*, not divided into an upper and lower mesepimeron, unlike most eupelmids with a similarly exposed mesepimeron. Because of this structural difference, and because only relatively few aphelinids are known to have a convexly enlarged acropleuron, I presently interpret the latter structure as independently derived and convergent to the similarly apomorphic states of encyrtids and many eupelmids.

4. Mesotibial spur. Three relative states are recognized: 1] short and slender; 2] long and slender (Figs. 5.90, 5.91); and, 3] robust (of varied lengths, but thickened) (Figs. 5.92-5.95).

This character is included in the analysis because an "enlarged" (Peck *et al.* 1964, Riek 1970), "thick" (Graham 1969b), "long, thick" (Nikolskaya 1963), or "large and thickened" (Yoshimoto 1984) mesotibial spur is one character state that most authors have used to distinguish or to relate eu[illegible]ds and encyrtids. However, I consider this character to be of little value for phylogenetic inference. Relative length of the mesotibial spur is not significant at the level of analysis attempted because most members of the taxa included, plus members of Signiphoridae and Chalcedectinae (Pteromalidae), have an elongate-slender spur if it is not thickened [Table 5.1, 4(2)]. Furthermore, whether the mesotibial spur is robust or not appears in most instances to be correlated with jumping ability and a convexly enlarged acropleuron. Encyrtids and eupelmids that have an enlarged acropleuron (character 3) also have a robust mesotibial spur. However, male eupelmines, which have a small acropleuron, have only an elongate-slender mesotibial spur, as do individuals (particularly males) of *Archaeopelma*, which have only a moderately enlarged, non-convex acropleuron. Cleonymines and most aphelinids also have a small acropleuron, and an elongate-slender mesotibial spur, except that some aphelinids with the acropleuron convexly enlarged also have a robust spur, of varied lengths.

Individuals of *Oodera* (Cleonyminae) are notable exceptions to the hypothesized correlation between size of the acropleuron and "robustness" of the mesotibial spur. Individuals have a robust spur even though the acropleuron is not enlarged. However, the robust spur is associated with other modifications of the middle legs (presence of mesotarsal pegs [Table 5.1, 5(5)], and an apomorphic mesopleural-mesocoxal articulation [6(2c)]) that indicate individuals of *Oodera* may be strong jumpers. Consequently, I conclude that phylogenetic significance of a robust mesotibial spur probably depends on the number of times increased jumping ability, in most instances through enlargement of the acropleuron, evolved.

5. Mesotarsal peg pattern. Five states are recognized, excluding states exhibited by encyrtids (see below): 1] mesotarsal pegs absent, mesotarsus with row of setae along anteroventral and posteroventral edges (Figs. 5.90, 5.91); 2] mesotarsus with row of pegs along posteroventral edge (Figs. 5.92, 5.95); 3] mesotarsus with row of pegs along anteroventral edge, with one or more pegs extended along anterodistal edge of each tarsomere (Fig. 5.94); 4] mesotarsus with mixed row of setae and pegs along posteroventral edge and with row of pegs along anteroventral edge (Fig. 5.96); and, 5] mesotarsus with row(s) of pegs along anteroventral and posteroventral edges (Figs. 5.93, 5.97, 5.98).

Presence of pegs on the ventral surface of the mesotarsus is one of the primary characters that was used by various authors to distinguish eupelmids and encyrtids from other chalcidoids, and to infer relationships between members of the two families. However, as for the previous character, presence of mesotarsal pegs appears in most instances to be correlated with a convexly enlarged acropleuron, *i. e.*, with increased jumping ability. Except for individuals of *Oodera* (Cleonyminae), individuals of taxa with a relatively small, non-convex acropleuron, lack mesotarsal pegs [Table 5.1, 5(1): Cleonyminae, *Archaeopelma* (Calosotinae), male Eupelminae, and Aphelinidae]. Furthermore, individuals of most taxa with an enlarged acropleuron have mesotarsal pegs. Exceptions to the latter include some Tanaostigmatinae *s. s.*, and most aphelinids with an enlarged acropleuron. The only aphelinids known to have mesotarsal pegs are individuals of *Eutrichosomella*, one of only two genera with members having a completely expanded acropleuron (see character 3). Consequently, I conclude that phylogenetic significance of presence of mesotarsal pegs probably depends on the number of times increased jumping ability, in most instances through enlargement of the acropleuron, evolved.

Absence of mesotarsal pegs from individuals of ***Archaeopelma*** indicates this to be the groundplan state for Calosotinae. If Calosotinae is monophyletic, then this indicates: **a)** the mesotarsal pegs of other calosotines are independently derived from those of most other eupelmids and encyrtids; **b)** that *Paraeusandalum* + *Eusandalum* + *Chirolophus* is a monophyletic assemblage, based on common possession of state two; **c)** that *Licrooides* + *Calosota* + *Balcha* + *Tanythorax* is a monophyletic assemblage, based on common possession of state five; and, **d)** that *Archaeopelma* is the sister group of one, or both of these assemblages.

Monophyly of *Metapelma* + *Neanastatus* + *Lambdobregma* (Metapelmatinae) is also indicated by common possession of state three. Individuals of *Eutrichosomella* (Aphelinidae) have a similar state, but the anteroventral row of pegs is straight (without pegs extended along anterodistal edge of each tarsomere), and similarity is undoubtedly the result of convergence.

Similarity in the mesotarsal peg pattern between metapelmatines and many encyrtids could also be the result of homoplasy. Survey of Encyrtidae was insufficient to adequately categorize the varied states of the mesotarsal pegs, or to attempt to hypothesize the groundplan state of the pegs for this family. However, the most common state seen was similar to that described for metapelmatines (state 3), or with an anterior row of pegs or scattered pegs on the basitarsus and with a Λ-shape arrangement of pegs on the subsequent tarsomeres, but with at least some pegs extended onto the anterior surface of each tarsomere. The possibility of homoplasy for this similarity in mesotarsal structure to that of metapelmatines may be indicated by an apparent correlation between pattern of the mesotarsal pegs, type of mesocoxal articulation, and how the mesotarsi are appressed against the substrate. Individuals of *Cynipencyrtus* (Tanaostigmatinae) have the mesotarsal pegs confined primarily to the anterior edge of the mesotarsus, and those of *Eutrichosomella*, Metapelmatinae, and many Encyrtidae are entirely confined to the anterior edge. These are also the only taxa in which the mesocoxae are unable to rotate anteroventrally out of their fossa (character 6), but which have mesotarsal pegs. Furthermore, the middle legs of metapelmatines and most encyrtids are relatively very long, and each mesotarsus apparently contacts the substrate by its anteroventral surface rather than its ventral surface. Because mesotarsal pegs are hypothesized to reduce slipping and help absorb shock load during jumping (Gibson in press, c), there is undoubtedly a functional advantage, if not a requirement, in having pegs along both the anteroventral edge and anterior surface of the mesotarsus. There is presumably lesser advantage in having a row of pegs along the posteroventral edge of the mesotarsus.

Interpretation of the mesotarsal peg pattern is also uncertain in Tanaostigmatinae *s. l.* Individuals of Tanaostigmatinae *s. s.* either lack mesotarsal pegs [Table 5.1, 5(1)], or have a single row along the posterior edge [5(2)]. This latter state is essentially the opposite of that of individuals of *Cynipencyrtus* [5(4)]. At present, I interpret this distribution to indicate lack of pegs as the groundplan state for Tanaostigmatinae *s. l.*, with two independent origins of pegs in the subfamily, once in *Cynipencyrtus* and once in Tanaostigmatinae (*s. s.*). This hypothesis must be confirmed by an analysis of the relationships between the species in the subfamily.

An hypothesis of the groundplan state of this character for Eupelminae again depends on how sexual dimorphism evolved in the subfamily. The pegs characteristic of female eupelmines [5(5)] are independently derived from those of other eupelmids and encyrtids, unless sexual dimorphism evolved through secondary loss of the apomorphic states in male eupelmines. Though some females lack mesotarsal pegs, or have these reduced in number or size so as to be sparse (Fig. 5.97) or seta-like, these exceptions are undoubtedly the result of secondary modification, and in most instances are correlated with brachyptery.

6. Mesopleural-mesocoxal articulation. Two main states are recognized, with each divided into two or more substates: **1]** mesotrochantinal plate extended internally to metasternum, mesocoxal fossae separate (Figs. 5.80-5.82), and either **(1a)** lower mesepisternum transverse along base of mesocoxae (*cf.* Fig. 5.72), or **(1b)** lower mesepisternum with membranous region anterior to each mesocoxa (Fig. 5.80); and, 2] mesotrochantinal plate not extended to metasternum, mesocoxal fossae partly continuous and connected by intercoxal membrane (Figs. 5.83, 5.84, 5.87), with **(2a)** mesotrochantinal plate extended internally at right-angle to lower mesepisternum, mesotrochantinal lobes projected posteriorly at right-angle to mesotrochantinal plate (Figs. 5.83, 5.84, 5.87), and lower mesepisternum transverse along base of mesocoxae (Figs. 5.69, 5.70, 5:72), or **(2b)** as described for state 2a, but with membranous region anterior to each mesocoxa (Figs. 5.73, 5.74), or **(2c)** mesotrochantinal plate and mesotrochantinal lobes extended more or less posteriorly in same plane as lower mesepisternum, and with membranous region anterior to each mesocoxa (Figs. 5.67, 5.71, 5.75-5.79), or **(2d)** mesotrochantinal plate extended posteriorly (Fig. 5.85), but without membranous region anterior to each mesocoxa (Fig. 5.68).

State 1a is hypothesized as plesiomorphic, based on presence in Cleonyminae (excluding *Oodera*) and other pteromalids and chalcidoids that I have dissected (see also Domenichini 1969). The other described states are hypothesized as apomorphic. A mesotrochantinal plate that is not extended to the metasternum is known only for individuals of *Oodera* (Cleonyminae), Encyrtidae, and Eupelmidae. This includes known encyrtids and eupelmids that lack a membranous region anterior to each mesocoxa [Table 5.1, male eupelmines, metapelmatines, and individuals of *Cynipencyrtus*]. Consequently a mesotrochantinal plate that is only partly extended to the metasternum, with intervening intercoxal membrane, is a possible synapomorphy for *Oodera* + Encyrtidae + Eupelmidae.

Presence of a membranous region anterior to each mesocoxa, which permits the coxa to rotate anteriorly out of its fossa, was first used by Bouček (1967) to distinguish eupelmids from other chalcidoids. LaSalle (1984) hypothesized that this structure was a synapomorphy for Eupelmidae + Tanaostigmatidae (*sensu* LaSalle) + Encyrtidae, but that the regions were subsequently lost in encyrtids. However, Noyes and Hayat (1984, p. 248) stated that most genera of Charitipodini (Encyrtidae: Tetracneminae), "which probably contains some of the most primitive enyrtids known ... have membranous areas surrounding the mid coxa which allow the mid legs to be flexed forwards". Noyes informs me (*in litt.*) that members of at least 20 encyrtid genera (about 60 species) have this structure. I have seen distinct membranous regions in individuals representing the following encyrtid genera: *Lyka* Mercet, *Clausenia* Ishii (Fig. 5.74), *Manicnemius* Hayat (Fig. 5.73), *Mira* Schellenberg, and *Charitopus* Förster.

In addition to some encyrtids and many eupelmids, individuals of *Oodera* (Cleonyminae) and *Coccobius* (Aphelinidae) (Fig. 5.80) also have a membranous region anterior to each mesocoxa. On the other hand, male eupelmines, individuals of *Cynipencyrtus* (Tanaostigmatinae), and members of Metapelmatinae have the lower mesepisternum transverse along the base of the mesocoxae, or at least lack membranous regions [individuals of *Lambdobregma* (Metapelmatinae) (Fig. 5.68)]. Consequently, either membranous regions anterior to the mesocoxae were derived more than once, or they were lost one or more times. Which of the alternatives is correct, or if both are, is uncertain, though I suspect that membranous regions were derived more than once. Independent origin is indicated for at least individuals of *Coccobius*. These have the mesotrochantinal plate extended to the metasternum (Fig. 5.80), which is the hypothesized plesiomorphic structure for this sclerite. Because of this, and because only individuals of *Coccobius* are known to have membranous regions anterior to the mesocoxae, I interpret the latter state as secondarily derived in Aphelinidae and convergent to similar structures in various eupelmids and encyrtids.

Differences in structure of the mesopleural-mesocoxal articulation of other chalcidoids with a membranous region anterior to each mesocoxa may indicate further homoplasy. Encyrtids have a small quadrate mesotrochantinal plate that is projected internally at a right-angle to the lower mesepisternum (Fig. 5.60), whether or not there is a membranous region anterior to each mesocoxa. Consequently, the mesotrochantinal plate is not externally visible (Figs. 5.73, 5.74), and the mesotrochantinal lobes, which project posteriorly at a right-angle to the mesotrochantinal plate, are only partly visible (Fig. 5.73) or are concealed in the base of each mesocoxa (Fig. 5.74). Individuals of *Oodera*, Calosotinae, and female eupelmines have the mesotrochantinal plate extended more or less posteriorly, as are the mesotrochantinal lobes, which are at the posterolateral corners of the mesotrochantinal plate, so that both the plate and lobes are externally visible (Figs. 5.67, 5.75-5.79). Individuals of Tanaostigmatinae *s. s.* also have the mesotrochantinal plate extended more or less posteriorly, but this is largely concealed by a large basomedial lobe of each coxa (Fig. 5.71).

The number of times a membranous region anterior to each mesocoxa was derived is uncertain. However, because I hypothesize that sexual dimorphism in Eupelminae evolved through secondary modification of the females, I conclude that the apomorphic mesopleural-mesocoxal articulation of females (Figs. 5.78, 5.79) evolved independently to those of other chalcidoids with similar structures. Furthermore, based on differences described above in structures of the mesopleural-mesocoxal articulation, I suspect that origin of membranous regions in encyrtids was independent to that of other chalcidoids with similar regions.

Individuals of *Cynipencyrtus* (Tanaostigmatinae), which lack membranous regions anterior to the mesocoxae (Fig. 5.72), otherwise have the mesopleural-mesocoxal articulation (Fig. 5.87) as described for encyrtids. Possible significance of this is discussed further under section 5.7.2.3, "monophyly and relationships of the higher taxa".

7. Notauli and correlated mesoscutal structure. Five general states are recognized: **1]** notauli as percurrent linear sulci that are widely separate at transscutal articulation, with median and lateral mesoscutal lobes relatively evenly convex (Figs. 5.37, 5.39, 5.40); **2]** notauli as V-shape convergent lines or sulci that **(2a)** meet at transscutal articulation (Fig. 5.36), **(2b)** meet anterior to transscutal articulation (Figs. 5.18-5.21), **(2c)** meet anterior to transscutual articulation and extend to articulation as medial line or sulcus, or, **(2d)** are effaced posteriorly, but then slightly (Fig. 5.31) to distinctly (Fig. 5.17) recurved toward transscutal articulation as paramedially parallel sulci or lines, with mesoscutum relatively evenly convex over length notauli extended; 3] notauli as non-percurrent, paramedially parallel lines, with mesoscutum relatively evenly convex over length notauli extended; 4] notauli more or less V-shape, but furrow-like rather than distinctly sulcate, with convex median mesoscutal lobe distinct from flattened or concave posteromedial region (Fig. 5.38); and, 5] notauli absent, with mesoscutum evenly convex (Figs. 5.33, 5.34) or flattened (Figs. 5.25-5.27).

State one is hypothesized as the groundplan state for Cleonyminae and Aphelinidae [Table 5.1, 7(1)], based on common possession. A few cleonymines have the notauli effaced posteriorly, and individuals of *Oodera* have the notauli close together at the transscutal articulation, but I interpret these as secondary modifications. State one is also interpreted as the plesiomorphic state for the taxa analyzed, based on wide distribution of the state throughout Chalcidoidea.

Members of Tanaostigmatinae exhibit all four forms described for state two of the notauli, except for individuals of *Cynipencyrtus*, which lack notauli and have the mesoscutum evenly convex (Fig. 5.33). Most encyrtids have a similar structure of the mesoscutum to that of individuals of *Cynipencyrtus* (Fig. 5.34), but Trjapitzin (1977) stated that complete or well-developed notauli characterize 23 encyrtid genera (of 489 recognized) that belong to diverse tribes. When present, the notauli are of the varied forms described for state two. Because of the similarity between the notauli of encyrtids and tanaostigmatines, LaSalle (1984) hypothesized percurrent, sinuately convergent notauli that meet at the transscutal articulation as a synapomorphy for Tanaostigmatidae (*sensu* LaSalle) and Encyrtidae. Though I agree that the above-described state is the probable groundplan state of the notauli for each taxon, similarity may be the result of symplesiomorphy rather than synapomorphy.

In Calosotinae, individuals of *Calosota*, *Balcha*, and *Tanythorax* have non-percurrent, paramedially parallel notauli (Fig. 5.24), whereas those of *Archaeopelma* (Fig. 5.17), *Paraeusandalum*, *Eusandalum* (Figs. 5.19, 5.20), *Chirolophus* (Fig. 5.21), and *Licrooides* (Fig.

5.18) have V-shape notauli that are confined to the anterior 0.5 of the mesoscutum [some males of *Archaeopelma* with notauli distally recurved and extended to transscutal articulation as obscure, paramedially parallel lines (Fig. 5.17)]. I interpret V-shape notauli as the groundplan state for Calosotinae because of the similar states possessed by various tanaostigmatines and encyrtids, and because the paramedially parallel notauli of individuals of the first three calosotine genera listed above are unique for the taxa included in the analysis.

V-shape, sulcate notauli that meet at or anterior to the transscutal articulation are very uncommon in Chalcidoidea, present in members of the taxa listed above, and in some members of Diparinae (Pteromalidae). Consequently, V-shape, sulcate notauli, is a possible synapomorphy for Calosotinae + Tanaostigmatinae + Encyrtidae. Such notauli presumably evolved through gradual convergence of widely separate notauli (state 1) until they met at the midline of the mesoscutum at the transscutal articulation (state 2a). Because some tanaostigmatines and encyrtids have this form, I conclude that it is the symplesiomorphic form for the three taxa, and other described forms of state two (2b, 2c, 2d), or absence of notauli (state 5), are apomorphic and secondarily derived in each taxon.

V-shape notauli are also possessed by most alate female eupelmines. The notauli are most similar to the V-shape notauli of various calosotines because they meet anterior to the transscutal articulation, but they are more or less furrow-like (Fig. 5.38) rather than sulcate (Figs. 5.17-5.21). Phylogenetic significance of V-shape notauli in female eupelmines is uncertain. Most male eupelmines have state one (Fig. 5.39), the hypothesized plesiomorphic structure of the mesoscutum. Some male eupelmines lack evident notauli, or have the notauli effaced posteriorly, but I interpret these states as the result of secondary reductions. Consequently, either the plesiomorphic-appearing notauli of male eupelmines are apomorphic through reversal, or the V-shape notauli of female eupelmines are convergent to the more or less similar notauli of various calosotines, tanaostigmatines, and encyrtids.

Most individuals of *Metapelma* (Metapelmatinae) have a lowly convex V-shape median mesoscutal lobe that is extended posteriorly as a mediolongitudinal ridge (Fig. 5.26). Thus, the mesoscutum is most similar to that of most alate female eupelmines. However, the region is not delineated by furrow-like notauli and may simply be the result of relatively thin mesoscutal cuticle conforming to the contours of the indirect flight muscles beneath. Individuals of *Lambdobregma* (Fig. 5.27) and *Neanastatus* have the mesoscutum flattened or slightly concave, or at most have only a very obscure median mesoscutal lobe. Consequently, I interpret absence of notauli as the groundplan state for Metapelmatinae, and possible evidence of monophyly of the subfamily.

8. Mesonotal articulatory structure. Two general states are recognized: 1] mesoscutum and scutellar-axillar complex articulated along transscutal articulation, with edges contiguous when mesonotum flexed (Figs. 5.17-5.23); and, 2] mesoscutum and scutellar-axillar complex articulated only laterally, with edges of sclerites separate at least along transscutal articulation when mesonotum flexed (Fig. 5.33), and in most taxa with transverse-depressed region of scutellar-axillar complex (Fig. 5.34), membrane (Fig. 5.30), or both (Fis. 5.32, 5.36) visible between edges.

State one is hypothesized as plesiomorphic based on presence in members of most of the taxa analyzed [Table 5.1, 8(1)], in addition to other known chalcidoids. State two, the hypothesized apomorphic structure, is known only for individuals of *Neanastatus* (Metapelmatinae), and members of Tanaostigmatinae and Encyrtidae.

The mesonotal articulatory structure of individuals of *Neanastatus* (Metapelmatinae) must be convergent to that of members of Tanaostigmatinae (Figs. 5.31, 5.32) and Encyrtidae (Figs. 5.35, 5.36) if Metapelmatinae is monophyletic. However, the similar mesonotal articulatory structures of members of the latter two taxa may indicate a sister-group relationship.

The posterior edge of the mesoscutum was free of the anterior edge of the scutellar-axillar complex in the single specimen of *Cynipencyrtus* (Tanaostigmatinae) that I saw with a flexed mesonotum. However, this was inobvious because no membrane or basally depressed axillar region was evident between the two (Fig. 5.33). This structure is more similar to that of most encyrtids than to other tanaostigmatines. Members of Tanaostigmatinae *s. s.* have the edges of the mesoscutum and scutellar-axillar complex separated by a conspicuous membranous region when the mesonotum is flexed (*cf.* Figs. 5.31, 5.32), whereas encyrtids have only a very slender, often inobvious membranous region or depressed axillar region between the two when the mesonotum is flexed (*cf.* Figs. 5.35, 5.36). I interpret the mesonotal articulatory structure described for *Cynipencyrtus* as more plesiomorphic than that described for members of Tanaostigmatinae *s. s.* because it is more similar to the structure hypothesized as plesiomorphic for Chalcidoidea. Consequently, I interpret a *Cynipencyrtus*-like structure as the groundplan state for Tanaostigmatinae *s. l.*, and the similarity between the mesonotal articulatory structures of *Cynipencyrtus* and encyrtids to be the result of symplesiomorphy.

9. Relative structure of mesoscutal process for pl_2-t_2c and prepectus. The pl_2-t_2c muscle originates from the acropleuron and inserts into the lateral edge of the mesoscutum; different states and functions of this muscle are described for chalcidoids in Gibson (in press, c). Two states are recognized in this analysis for insertion of the muscle, with the second state divided into three substates based on differences in structure of the prepectus. The states and substates recognized are: **1]** pl_2-t_2c inserted directly into lateral edge of mesoscutum, or into small process that does not project anterior to mesothoracic spiracle, with prepectus entire and not projected anterior to mesothoracic spiracle (Figs. 5.41-5.44, 5.47-5.54, 5.58); and, **2]** pl_2-t_2c inserted into elongate process that projects anterior to mesothoracic spiracle (Fig. 5.61), with **(2a)** prepectus extended around process, evenly sclerotized, and externally protuberant anterior to mesothoracic spiracle because pronotum on inner side of mesoscutal process and prepectus (Figs. 5.31, 5.45, 5.46, 5.57, 5.71), or **(2b)** prepectus extended around process and protuberant anterior to mesothoracic spiracle (Fig. 5.56), but latter not externally apparent because pronotum over anterior of mesoscutal process and prepectus (Fig. 5.55), and with internal cuticle much thinner than exposed cuticle (Fig. 5.56), except for ventromesal edge of prepectus, which is thicker and 'strut-like' on inner side of mesoscutal process, or, **(2c)** prepectus not extended around process, but divided into outer prepectal surface lateral to mesoscutal process (Figs. 5.59, 5.60), and "prepectal strut" on inner side of mesoscutal process (Figs. 5.60, 5.61), with structure not externally apparent because pronotum over anterior of mesoscutal process (*cf.* Figs. 5.59, 5.60).

State one is hypothesized as plesiomorphic based on presence in members of most of the taxa analyzed [Table 5.1, 9(1)], in addition to other known chalcidoids. State two, the hypothesized apomorphic structure, is reported for some members of Aphelinidae (Domenichini 1954), and is possessed by individuals of *Eusandalum* (Calosotinae) and members of Tanaostigmatinae and Encyrtidae. Individuals of *Eusandalum* and Tanaostigmatinae *s. s.* have state 2a, whereas individuals of *Cynipencyrtus* (Tanaostigmatinae) have state 2b, and members of Encyrtidae have state 2c [Table 5.1].

Domenichini (1952) originally described the structure detailed above for encyrtids. His "apofisi endoscheletrica costituita dal prolungamento anteriore del processo alare anteriore del mesonoto (br, figs. III.2, VII.1)" (endoskeletal apophysis constituting the anterior prolongation of the anterior wing process of the mesonotum) is what I call the "mesoscutal process for pl_2-t_2c", and his "apofisi pleurosternale di connessione con il prefragma (sp, figs. IV.2 and VII.1)" (pleurosternal apophysis connecting with the prephragma) is what I call the "prepectal strut". He (1954) stated that he found this structure in "a few dozen" encyrtid genera, as well as in *Aphelinus* Dalman and *Paraphelinus* Perkins (Aphelinidae). The latter requires confirmation.

An elongate mesoscutal process for pl_2-t_2c in individuals of *Eusandalum* must be independently derived and convergent to that of members of Tanaostigmatinae and Encyrtidae if Calosotinae is monophyletic. However, the shared state may indicate a sister-group relationship between the latter two taxa. The prepectal state of encyrtids is hypothesized to be the most apomorphic of the three substates described, based on subdivision of the prepectus into two parts. Individuals of *Cynipencyrtus* have what is apparently an intermediate prepectal state (2b: Figs. 5.55, 5.56) between that of tanaostigmatines *s. s.* (2a: Fig. 5.57, 5.71) and that of encyrtids (2c: Figs. 5.59-5.61). However, whether state 2a or 2b is the ancestral state is uncertain. The probable plesiomorphic state of the prepectus depends on whether the mesoscutal process for pl_2-t_2c and prepectus were prolonged beneath the pronotum, and hence *Cynipencyrtus*-like in structure, or were prolonged exterior to the pronotum, and hence similar in structure to the prepectus of members of Tanaostigmatinae *s. s.* If the latter, the most parsimonious transformation series would be 2a → 2b → 2c. This would indicate that *Cynipencyrtus* is more closely related to Encyrtidae than to Tanaostigmatinae *s. s.* However, I presently interpret the former alternative as more likely, based on structure of the pronotum (character 11) and hypothesize that the correct transformation series is 2b → 2a, and 2b → 2c, *i. e.*, two independent transformation series from a *Cynipencyrtus*-like structure.

10. Dorsal axillar surface (DAS). This character is not conducive for dividing into a small number of discrete states because of diversity in structure of the dorsal axillar surface. However, three general states are recognized, somewhat arbitrarily, with the last two states each divided into two substates. The states and substates recognized are: 1] DAS conspicuously declined relative to dorsal surface of scutellum, with basomedial angles widely separate to contiguous, and elongate-subtriangular (*i. e.*, length at least as great as basal width, as opposed to transverse) (Figs. 5.39-5.42); 2] DAS primarily horizontal in relatively flat plane with scutellum, basomedial angles contiguous, and either **(2a)** elongate-subtriangular (Figs. 5.17, 5.25, 5.27, 5.31), or, **(2b)** transverse-subtriangular (Figs. 5.33-5.36); and 3] DAS primarily horizontal in relatively flat plane with scutellum, basomedial angles separate, and either **(3a)** elongate-subtriangular to linear at side of scutellum, with scutoscutellar suture straight (Figs.

5.18, 5.21, 5.22, 5.30, 5.37) to more or less concave (Figs. 5.23), or, (3b) elongate, with scutoscutellar suture convex (outcurved) so scutellum with more or less petiolate base (Figs. 5.19, 5.20).

Individuals of *Oodera* (Cleonyminae) have DAS that are conspicuously advanced anterior to the base of the scutellum and primarily horizontal, forming a relatively flat surface with the scutellum. I consider this structure as secondarily derived in Cleonyminae because only individuals of *Louricia* Ferrière have a similar structure Bouček (1958). Other cleonymines have the DAS not conspicuously advanced anterior to the base of the scutellum, and otherwise as described for state one. Most have the DAS widely separate (Fig. 5.40), but a few have subcontiguous DAS that are very similar in appearance to those of individuals of *Archaeopelma* (Fig. 5.17) and *Paraeudsandalum* (Calosotinae) [Table 5.1, 10(2a)], except that they are conspicuously declined relative to the scutellum.

Somewhat varied forms of state 2a are possessed by at least some members of Calosotinae (Fig. 5.17), Metapelmatinae (Figs. 5.25, 5.27), and Tanaostigmatinae (Fig. 5.31), and is the hypothesized groundplan state for each of these taxa. Furthermore, individuals of *Cynipencyrtus* (Fig. 5.33) and most members of Encyrtidae (Figs. 5.34, 5.35) have what I interpret as an apomorphic form of state 2a, *i. e.*, transverse-subtriangular DAS [10(2b)]. I hypothesize state one as the plesiomorphic structure of the DAS for the taxa analyzed based on presence in most cleonymines, and state 2a as a possible synapomorphic structure that indicates monophyly of Calosotinae + Metapelmatinae + Tanaostigmatinae + Encyrtidae. However, this latter hypothesis is very tenuous until states of this character are more comprehensively surveyed throughout Chalcidoidea. Whether the contiguous DAS of some cleonymines, which are very similar to that hypothesized as the groundplan state for most eupelmids and encyrtids (Fig. 5.17), are the result of convergence, or indicate relationship and the possibility that Cleonyminae is paraphyletic, requires additional study. State 2b is hypothesized as a possible synapomophy for *Cynipencyrtus* (Tanaostigmatinae) + Encyrtidae, *i. e.*, a transformation series in structure of the DAS from 1 → 2a → 2b.

Within Calosotinae, state 2a is shared by individuals of *Archaeopelma* (Fig. 5.17) and *Paraeusandalum*, whe[illegible]ose of *Eusandalum* have state 3b (Figs. 5.19, 5.20), and those of *Chirolophus*, *Licrooides*, *Calosota*, *Balcha*, and *Tanythorax* have various forms of state 3a. Individuals of *Tanythorax* have the DAS reduced to almost a linear strip on each side of the scutellum, as do individuals of many species of *Balcha* and some species of *Calosota* (Fig. 5.23). However, individuals of some species of *Balcha* and many species of *Calosota* have larger, more typical subtriangular DAS (Fig. 5.22). Individuals of *Chirolophus* have DAS of a similar size to the larger DAS found in *Calosota* (*cf.* Figs. 5.21, 5.22), whereas the DAS of *Licrooides* is yet larger (Fig. 5.18). I consider these as intermediate states in a general transformation series of reduction in size of the DAS through gradual separation of the scutoscutellar sutures. Consequently, *Chirolophus* or *Licrooides* is indicated as the sister group of *Calosota* + *Balcha* + *Tanythorax*. Structure of the DAS in *Eusandalum* (Figs. 5.19, 5.20) is apparently autapomorphic, and possibly independently derived from state 2a.

Individuals of *Neanastatus* are unlike other metapelmatines in having small, widely separate, elongate-triangular DAS [10(3a), Fig. 5.30]. I consider this structure as autapomorphic for *Neanastatus* in Metapelmatinae, and convergent to similar structures of the DAS of some other eupelmids.

The groundplan state of the DAS for Eupelminae again depends on whether sexual dimorphism in this subfamily evolved through secondary modification of the females, or secondary loss of the apomorphic states in males. Male eupelmines have the hypothesized plesiomorphic structure of the DAS (Figs. 5.39, 5.41), whereas females have primarily horizontal DAS, with the basomedial angles either contiguous or separate, but with straight scutoscutellar sulci [10(2a, 3a), Fig. 5.38].

Members of Aphelinidae have small, widely separate DAS (Fig. 5.37), and most also have the DAS more or less advanced anterior to the base of the scutellum, unlike eupelmids or encyrtids. Axillar structure of aphelinids has to be compared with other chalcidoids with advanced DAS before relationships can be hypothesized using this character.

11. **Relative structure of pronotum and mesoscutum**. Three general states are recognized, somewhat arbitrarily, with each state divided into two substates. The states and substates recognized are: 1] pronotum campanulate in dorsal view, *i. e.*, sides parallel anterior to mesoscutum before convergent to head, and at least slightly narrower than mesoscutum so side of mesosoma not evenly curved to head, and either **(1a)** wide relative to mesoscutum, with mesoscutal lateral lobes obliquely angled to pronotum (Figs. 5.38, 5.40) so only small or indistinct 'shoulder' on either side of pronotum, or, **(1b)** narrow relative to mesoscutum, with mesoscutal lateral lobes abruptly to right-angled as distinct 'shoulder' on either side of pronotum (Figs. 5.17-5.23); 2] pronotum more or less conical in dorsal view, as wide as mesoscutum posteriorly, with side over base of prepectus, and straight or sinuately convergent to head, and either **(2a)** as long as, or longer than, greatest width (Figs. 5.25, 5.27), or, **(2b)** transverse, but with at least short dorsal surface (Figs. 5.33-5.35, 5.37); and, 3] pronotum vertical, linear at least medially in dorsal view, and narrower than mesoscutum so side not over base of prepectus, which is either **(3a)** anteriorly protuberant on outer side of pronotum (Figs. 5.31, 5.57), or, **(3b)** flat and extended to only posterolateral edge of pronotum (Figs. 5.39, 5.41).

Interpretation of this character is complicated because pronotal shape, which is characteristic for members of the different taxa, is the result of relatively minor changes in dimensions. Furthermore, shape of the pronotum is probably at least partly correlated with body shape. Hypotheses of monophyly or relationships based on analysis of this character are extremely tenuous until more chalcidoid taxa are included in the analysis.

I presently interpret a campanulate pronotum as the plesiomorphic structure based on presence in cleonymines. This basic structure is shared with members of Calosotinae, and females and many males of Eupelminae [Table 5.1, 11(1)]. Cleonymines and eupelmines with a campanulate pronotum have state 1a, whereas calosotines have state 1b, except for individuals of *Tanythorax*, which have state 1a. I interpret state 1a as plesiomorphic because this form is more similar to the pronota of other pteromalids than is state 1b. This latter state is hypothesized as the groundplan state for Calosotinae, based on distribution in the subfamily (Fig. 5.1, character 11), and hence a possible synapomorphy for members of the subfamily. State 1a of individuals of *Tanythorax* is considered as an autapomorphic secondary modification in the subfamily.

Members of Metapelmatinae, Encyrtidae, and *Cynipencyrtus* (Tanaostigmatinae) have a conical pronotum (state 2), which is elongate in metapelmatines [2a], and transverse in *Cynipencyrtus* and encyrtids [2b]. Some encyrtids have an elongate-conical pronotum similar to the pronota of metepelmatines, but Trjapitzin (1977) correlates most such instances with a markedly flattened body and increased prothoracic musculature. He hypothesized a "short" pronotum as the goundplan state for Encyrtidae.

The elongate-conical pronotum is very distinctive of members of Metapelmatinae, and may be an autapomorphic structure that indicates monophyly of the subfamily. However, it is also possible that this state, 2a, represents the ancestral state from which the transverse-conical pronota of tanaostigmatines (*s. l.*) and encyrtids were derived. If so, a conical pronotum might be a synapomorphy for Metapelmatinae + Tanaostigmatinae *s. l.* + Encyrtidae.

I presently interpret the pronotal structure of individuals of *Cynipencyrtus* (Figs. 5.33, 5.55) as the groundplan state for Tanaostigmatinae, and the pronotal structure of members of Tanaostigmatinae *s. s.* (Figs. 5.31, 5.57) as apomorphic, because the latter form of the pronotum is more reduced (vertical without dorsal surface). Consequently, I interpret similarity in structure of the pronotum of individuals of *Cynipencyrtus* and encyrtids (*cf.* Figs.

5.33-5.35) as the result of either symplesiomorphy or homoplasy rather than synapomorphy.

Similarity in structure of the pronotum between tanaostigmatines (*s. s.*) and some male eupelmines (*cf.* Figs. 5.41, 5.57) is interpreted as the result of two independent transformation series from different ancestral states. The pronotum of members of Tanaostigmatinae *s. s.* is hypothesized to be derived from state 2a, whereas that of male eupelmines is hypothesized to be derived from state 1a, each through reduction.

12. Mesotibial apical pegs. Two states are recognzied: **1]** mesotibia with at most robust spines along anteroapical edge (Figs. 5.90-5.93); and, **2]** mesotibia with row or patch of pegs along anteroapical edge (Figs. 5.94, 5.96-5.98).

Absence of mesotibial pegs is hypothesized as plesiomorphic, based on absence from most chalcidoids. Though presence is considered as apomorphic, distribution within the higher taxa [Table 5.1, 12(2)] indicates that the pegs were derived more than once. Presence in some species of *Calosota* (Calosotinae) and in individuals of *Eutrichosomella* (Aphelinidae) is undoubtedly secondary in their respective higher taxon. The mesotibial pegs of most female eupelmines also must be independently evolved from those of other eupelmids and encyrtids if sexual dimorphism in Eupelminae evolved through secondary modification of the females. Furthermore, presence of mesotibial pegs in individuals of *Eutrichosomella*, one of only two aphelinid genera in which members have a completely enlarged acropleuron, plus presence in female eupelmines, but absence of pegs from other aphelinids and from male eupelmines, indicates that presence or absence of pegs is correlated with an enlarged or nonenlarged acropleuron. Consequently, phylogenetic significance of mesotibial pegs may depend on the number of times the acropleuron was enlarged.

Absence of mesotibial pegs from members of Tanaostigmatinae *s. s.*, but presence in individuals of *Cynipencyrtus*, indicates that the pegs were either a groundplan state of the subfamily, which were subsequently lost from members of Tanaostigmatinae *s. s.*, or that the pegs are an apomorphic state of individuals of *Cynipencyrtus*. If the former is true, presence of mesotibial pegs could be a synapomorphy for Metapelmatinae + Tanaostigmatinae + Encyrtidae, but if the latter is true, it could indicate that *Cynipencyrtus* is more closely related to Encyrtidae than to Tanaostigmatinae *s. s.*

13. **Parapsidal lines**. Four states are recognized: 1] absent; 2] as line of minute, differentiated sculpture near anterior edge of mesoscutal lateral lobe adjacent to each notaulus (Fig. 5.24); 3] as percurrent line, which is as line of minute, differentiated sculpture anteriorly, but more ridge-like posteriorly (Figs. 5.25, 5.26); and, 4] as ridge directed anteriorly from transscutal articulation from near middle of, or towards lateral corner of DAS (Fig. 5.38).

Distribution of the above-described states in the higher taxa analyzed is listed in Table 5.1. States 13(2) (Fig. 5.24) and 13(3) (Fig. 5.25) are very unusual forms of the parapsidal lines for Hymenoptera. Most hymenopterans with parapsidal lines have these directed anteriorly from the transscutal articulation, similar to described state 13(4) (Fig. 5.38) (Gibson in press, a). Consequently, parapsidal lines that are anterior on the mesoscutum, adjacent to the notauli [13(2), Fig. 5.24], may represent a synapomorphy for members of Calosotinae. However, confident appraisal of the true level of apomorphy requires a more comprehensive survey of this character in Cleonyminae. Most cleonymines lack parapsidal lines, but individuals of a few taxa have obscure parapsidal lines, and individuals of *Soleneura* Westwood (Lysiscini) and of an undescribed genus of Lysiscini (*sensu* Bouček 1958) have distinct parapsidal lines, like those of calosotines. This similarity may be the result of homoplasy, or indicate that Cleonyminae is paraphyletic.

The parapsidal lines of *Metapelma* (Metapelmatinae) [13(3), Figs. 5.25, 5.26] are interpreted as an autapomorphic state for the genus.

14. **Structure of Mt8 and Mt9 of females**. Two states are recognized, with the first state divided

into two substates: 1] Mt8 and Mt9 independent, and either **(14a)** with Mt8 exposed dorsally as distinct sclerite, or **(14b)** with Mt8 very short dorsally, inobvious or concealed by Mt7 (Figs. 5.108, 5.109); and, 2] Mt8 and Mt9 fused as syntergum, with at most suture beneath cercus indicating line of fusion between two terga (Fig. 5.110).

Distribution of the above-described states in members of the higher taxa analyzed is listed in table 5.1.

In addition to individuals of *Archaeopelma, Eusandalum* (Calosotinae), and *Metapelma* (Metapelmatinae), which have an independent Mt9, some female eupelmines and some encyrtids have structures that superficially look like an independent Mt9, but which are actually secondarily derived structures of the metasoma. Compere and Annecke (1960) originated the term "paratergite" for a linear sclerite that was posterior to each cercus in the membrane between Mt7 (spiracle bearing tergum) and the ultimate tergum in females of some encyrtids (those of the subfamily Tetracneminae *sensu* Trjapitzin 1973). They hypothesized that the ultimate tergum was Mt9, and that the paratergites represent the modified dorsal remnants of Mt8. However, in females of *Grandoriella lamasi* Domenichini, *Moraviella inexspectata* Hoffer, and *Ericydnus* sp., the paratergites were shown to be narrow lateral continuations of the ultimate tergum that are recurved around the anterior edge of each cercus (Trjapitzin 1968). Consequently, independent paratergites are indicated to be secondarily separated posterolateral regions of a syntergum (Mt8 + Mt9).

Some female eupelmines also have a circular sclerite [epiproct *sensu* Domenichini (1953)] that covers the anus at the apex of the metasoma (Figs. 5.111, 5.112). Though this sclerite superficially looks like an independent Mt9, it is apparently a secondarily derived structure. In many females, the tergum surrounding the anal sclerite is traversed by a fine suture immediately anterior to the cerci, with the suture recurved posteriorly below each cercus (Fig. 5.111). I interpret this suture as remnants of the line of fusion between Mt8 and Mt9 because it is in the same position as the line of separation between these two terga in females of

Eusandalum and *Metapelma*.

Trjapitzin (1963) also reported an independent Mt9 from ***Propelma rohdendorfi***, which he described as a new species and genus, based on a female in an inclusion of Baltic amber. However, the structure of the apex of the metasoma that he described and illustrated appears to be the same as that described above for some female eupelmines [*cf.* Fig. 5.111, and fig. 2, Trjapitzin (1963)].

I interpret an independent Mt9 as plesiomorphic because females of Symphyta and females of various apocritans have this state. However, value of this character for phylogenetic analysis is limited because members of most of the taxa surveyed have Mt8 and Mt9 fused. Furthermore, distribution indicates that Mt8 and Mt9 fused independently at least twice in Calosotinae [Fig. 5.1, 14(2)] and once in Metapelmatinae [Fig. 5.2, 14(2)]. Consequently, I do not consider presence of a syntergum as a reliable indicator of relationship. However, independence of Mt8 and Mt9 indicates that Calosotinae and Metapelmatinae are probably very early clades in the evolution of Chalcidoidea. Exact distribution of an independent Mt9 in Chalcidoidea is unknown, but it is at least a rare state. Known cleonymines have Mt8 and Mt9 fused, even though in many there is a conspicuous suture on the syntergum that indicates the line of fusion between the two terga. I interpret presence of a syntergum in Cleonyminae as evidence against possible paraphyly of this subfamily relative to Eupelmidae.

15. Presence of fore wing linea calva. Two states are recognized: 1] fore wing evenly setose, or at most with wide glabrous band adjacent to parastigma; and, 2] fore wing with distinctly delineated elongate-narrow glabrous band directed obliquely toward anal region of fore wing from near marginal vein.

Division of this character into only two states is simplistic. Hennessey (1981) described two structures of the linea calva, a "restraining" type, and a "coupling" type. However, both types were described from Encyrtidae and Aphelinidae, indicating independent origin of at least one of the two types in each family. Distribution of the linea calva listed in Table 5.1 for members of the taxa anlyzed indicates considerable homoplasy, so that the groundplan state for each higher taxon has to be hypothesized before the character can be interpreted. The groundplan state for Cleonyminae, Tanaostigmatinae, Calosotinae, and Eupelminae is undoubtedly absence of a linea calva, with origin of a distinct linea calva in a few taxa of the latter two subfamilies the result of secondary modification. Yasnosh (1976) also hypothesized uniformly setose fore wings as the groundplan state for Aphelinidae. However, Trjapitzin (1968) hypothesized presence of a linea calva as the groundplan state for Encyrtidae, of the type with undifferentiated setae along the glabrous band (restraining type *sensu* Hennessey 1981). I also interpret presence of a linea calva, of the restraining type, as the groundplan state for Metapelmatinae, with absence of a linea calva from the fore wing of some species of *Metapelma* as the result of secondary loss. Metapelmatines with a linea calva have the setae longer and somewhat more robust along the proximal edge than along the distal edge of the glabrous band, but they lack "interlocking setae" *sensu* Hennessey (1981).

16. Mesotergal-mesotrochanteral (t_2-tr_2) muscle. Six states are recognized, with one state divided into two substates: 1] as large tubular muscle, with origin partly from dorsal axillar surface (t_2-tr_2a) and partly from large axillar phragma (t_2-tr_2b), both inserted into golf tee-like pedicel ventrally in body cavity, and pedicel with tendon-like ligament from near center to mesotrochanter (Figs. 5.99, 5.100); 2] as relatively small muscle, with origin partly from between lateral axillar surface and ventrally projected axillar plate (t_2-tr_2a) and from anteroventral apex of axillar plate (t_2-tr_2b), both inserted into small pedicel otherwise similar to that described above (Figs. 5.101, 5.102); 3] as relatively small muscle, with origin partly from dorsal axillar surface (t_2-tr_2a) and partly from small axillar phragma (t_2-tr_2b), both inserted into elongate-narrow pedicel, latter articulated posteriorly with ventral edge of scutellar-axillar complex and with tendon-like ligament extended from either **(3a)** anterior end (Fig. 5.103), or **(3b)** near center (Fig. 5.106) to mesotrochanter; 4] as small, short, band-like muscle, with origin from ventral edge of lateral axillar surface near anterior angle, inserted into strongly sclerotised rod-like pedicel, latter articulated posteriorly with ventral edge of scutellar-axillar complex and with tendon-like ligament extended from anterior end to mesotrochanter (Fig. 5.104); 5] as small, short, band-like muscle within scutellar-axillar complex, origin partly from dorsal axillar surface (t_2-tr_2a) and partly from small axillar phragma (t_2-tr_2b), both convergent ventrally to tendon-like ligament extended to mesotrochanter; and, 6] as tendon-like muscle extended from anteroventral angle of lateral axillar surface to mesotrochanter (Fig. 5.105).

Distribution of the above-described states in members of the higher taxa analyzed is listed in Table 5.1.

State one (Figs. 5.99, 5.100) is hypothesized as plesiomorphic, and the other five states as apomorphic through reduction, as justified in Gibson (in press, b, c). States of this character appear to be of little value for indicating relationships between the higher taxa, but are significant for determining relationships in Metapelmatinae. Structure of the t_2-tr_2 muscle is autapomorphic for individuals of *Metapelma* (Figs. 5.101, 5.102), with the axillar plate apparently representing a ventrally reflected axillar phragma (Gibson in press, c). This structure is so different from those of individuals of *Neanastatus* (Fig. 5.103) and *Lambdobregma* (Fig. 5.104) that two independent transformation series are indicated from a common ancestor that had state one (1 → 2, and 1 → 3a → 4). Consequently, I hypothesize state one as the groundplan state for Metapelmatinae. I also consider the second transformation series hypothesized above as evidence that *Lambdobregma* and *Neanastatus* are sister taxa.

States of the t_2-tr_2 muscle appear to be quite varied in members of Encyrtidae; some have the hypothesized plesiomorphic structure of the muscle, whereas others have the muscle markedly reduced. Because the plesiomorphic structure is possessed by at least some encyrtids, I interpret this as the groundplan state for the family. Consequently, similarity in structure of this muscle between some encyrtids [16(3b), Fig. 5.106] and individuals of *Neanastatus* (Metapelmatinae) [16(3a), Fig. 5.103] is interpreted as convergence.

State one is undoubtedly the groundplan state for Aphelinidae, but survey of the family was insufficient to determine if any members have reduced forms of the t_1-tr_1 muscle. I suspect this to be likely in at least some aphelinids that have an enlarged acropleuron.

An hypothesis of 16(1) (males) (*cf.* Fig. 5.99), or 16(6) (females) (Fig. 5.105) as the groundplan state for the t_1-tr_1 muscle in Eupelminae again depends on how sexual dimorphism evolved in the family. Lack of known intermediate states prevents development of an hypothesis of how the tendon-like muscle of females evolved from the large tubular muscle hypothesized as plesiomorphic.

17. Protibial apical spines. Two states are recognized: 1] dorsoapical edge of protibia with 1 or more short, stout, curved spines (Figs. 5.88, 5.89); and, 2] dorsoapical edge of protibia without spines.

Distribution of the two states descibed above for members of the higher taxa analyzed is listed in Table 5.1.

I consider this character to be unreliable for phylogenetic interpretation because presence of dorsoapical spines on the protibia is correlated with parasitism of wood-boring insects. Chalcidoids of a number of different families that are parasitoids of wood-borers have dorsoapical protibial spines, as do numerous other apocritans with such hosts. Consequently, presence in Cleonyminae, Calosotinae, and Metapelmatinae could be the result of homoplasy, because most members of these taxa are known parasitoids of wood-borers, or are suspected as such.

The host range and microhabitat location of hosts for Eupelminae is very diverse, though relatively very few eupelmines are known to be parasitoids of wood-borers. However, because both sexes of Eupelminae have dorsoapical protibial spines, presence is indicated as a groundplan state of this subfamily, and apparently a relictual state from an ancestor that was a parasitoid of wood-borers. Though very indirect evidence, this could indicate that Eupelminae is closely related to one of the three taxa listed above with dorsoapical protibial spines.

Absence of dorsoapical protibial spines from tanaostigmatines and encyrtids must be the result of secondary loss if these two taxa form a monophyletic assemblage with the above taxa, and then absence is a possible synapomorphy for the two.

5.7.1.2 Characters analyzed for intergeneric relationships of Calosotinae

18. Structure of acropleural sulcus. Two states are recognized: 1] acropleural sulcus as distinct sulcus posteriorly, or posteriorly and ventrally, but abruptly reflexed anterodorsally as straight (Figs. 5.43, 5.44) to posteriorly recurved (Figs. 5.47, 5.67) finer sulcus or line; and, 2] acropleural sulcus more or less evenly curved from above mesocoxa toward anterodorsal or anteroventral edge of mesopleuron as distinct or gradually attenuate sulcus (Figs. 5.48-5.51).

Distribution of the above-described states for members of genera of Calosotinae is listed in Table 5.2. I interpret state one as plesiomorphic because this state is possessed by individuals of *Archaeopelma*, which have the least developed acropleuron of known calosotines (Fig. 5.43). Consequently, I interpret state two as a possible synapomorphy for *Licrooides* + *Calosota* + *Balcha* + *Tanythorax*.

19. Protibial dorsal spicules. Two states are recognized: 1] protibia with one or more denticle-like spicules along dorsal surface (Fig. 5.88); and, 2] protibia without denticle-like spicules along dorsal surface.

Distribution of protibial dorsal spicules for members of genera of Calosotinae is listed in Table 5.2. Individuals of all the other higher taxa examined for this study lacked protibial spicules, except for one female that represents an undescribed genus of Cleonyminae from Malaysia (HTC).

Protibial dorsal spicules is certainly apomorphic, and could be a synapomorphy for *Archaeopelma* + *Paraeusandalum* + *Eusandalum* + *Chirolophus* (absence in some species of *Eusandalum* is undoubtedly secondarily derived in the genus). However, presence of spicules in members of at least one cleonymine genus indicates that presence could be the groundplan state for Calosotinae. If so, secondary loss of the spicules could be a synapomorphy supporting monophyly of *Licrooides* + *Calosota* + *Balcha* + *Tanythorax*. The former hypothesis is perhaps more probable based on present knowledge, but a more comprehensive survey is required to substantiate distribution of protibial spicules.

20. Scutoscutellar suture. Two states are recognized: 1] scutoscutellar suture extended from transscutal articulation to apex of DAS, with side of scutellum rounded or angled distal to DAS (Figs. 5.17-21); and, 2] scutoscutellar suture extended from transscutal articulation to near apex of scutellum, with latter carinate distal to DAS (Figs. 5.22, 5.23, 5.65, 5.66).

Distribution of the above-described states for members of genera of Calosotinae is listed in Table 5.2.

State one is hypothesized as plesiomorphic based on presence in members of all of the other higher taxa included in this analysis. Consequently, state two is hypothesized as a synapomorphy for *Calosota* + *Balcha* + *Tanythorax*.

21. Antennal funicular structure of males. Two major states are recognized: 1] antennal funicle filiform; and, 2] antennal funicle pectinate.

Males of *Archaeopelma*, *Calosota*, *Balcha*, and *Tanythorax* have filiform antennae, as do males of most species of *Eusandalum*. Males of some species of *Eusandalum* (mostly from Australian and Oriental regions) have pectinate antennae, as do males of *Chirolophus* and *Licrooides* [Table 5.2]. However, there is considerable variation in structure of the pectinate antennae. Males of *Licrooides* have the proximal five or six funicular articles with a compressed asetose ramus, and with these all short and about the same length, each extended at most two funicular articles in length. Males of at least one species of *Eusandalum* have cylindrical, elongate, setose rami, but males of most species of *Eusandalum* with pectinate antennae have the rami as described for males of *Licrooides*, or relatively longer, with all rami extend to about the same point near the apex of the antenna. Males of *Chirolophus* have the last-described state, all apparently with the proximal five funiculars having rami.

Filiform antennae are hypothesized as plesiomorphic based on this state being the most common for males of the other higher taxa included in the analysis. Hypotheses of the level of apomorphy represented by pectinate antennae shared by various calosotines are made in section 5.7.2.1, "monophyly and intergeneric relationships of Calosotinae".

22. Prepectal size. Two states are recognized: 1] prepectus relatively large, apex extended to base of tegula (Figs. 5.43-5.45, 5.49, 5.50), or almost so; and, 2] prepectus relatively small, apex distinctly separate from base of tegula by about width or length of tegula (Figs. 5.47, 5.48, 5.51).

Individuals of the type species of *Archaeopelma* are somewhat varied in this character. The prepectus either extends to the base of the tegula (Fig. 5.43), or is slightly separate from it. Individuals of *Paraeusandalum* and *Calosota*, and individuals of most species of *Eusandalum* also have the prepectus extended to the tegula. Individuals of some species of *Eusandalum* have a small prepectus, as do individuals of *Chirolophus*, *Licrooides*, *Balcha*, and *Tanythorax* (Table 5.2). I hypothesize state one as the groundplan state for Calosotinae because this state is shared with members of Cleonyminae and other eupelmids. Further hypotheses of possible transformation series and apparent homoplasy in this character are given in section 5.7.2.1, "monophyly and intergeneric relationships of Calosotinae".

23. Mesoscutal pattern of color and sculpture. Three states are recognized: **1]** mesoscutum relatively evenly reticulate to coriaceous (Figs. 5.17-5.24), and black or of relatively dull metallic colors, but without distinct regions of correlated sculpture and color as described for state three; 2] mesoscutum black, with relatively coarse punctures toward transscutal articulation and laterally on mesoscutal lateral lobes, but with distinctly finer sculpture between notauli; and, 3] mesoscutum of various bright metallic colors and coarsely punctate or umbilicate at least laterally along mesoscutal lateral lobes (Fig. 5.51), but black and much more finely sculptured between notauli and along parapsidal lines.

This character is analyzed primarily for relationships between *Calosota*, *Balcha*, and *Tanythorax*. Individuals of a very few species of *Eusandalum* have a mesoscutum similar to that described as state three, but this is undoubtedly secondarily derived in the genus. State three is otherwise possessed only by individuals of *Balcha*. State one is shared by other calosotines, including individuals of *Tanythorax* and those of almost all species of *Calosota*. However, individuals of a few species of *Calosota*, including *C. stenogastra* Masi, *C. ferrieri* Hedqvist, and *C. testaceipes* Hedqvist have state two.

I consider state one as plesiomorphic for Calosotinae, and state three as apomorphic and evidence for monophyly of *Balcha*. However, state two appears to be an intermediate state between states one and three. If state two is not an independent transformation series in *Calosota* from state one, then species of *Balcha* are indicated to be more closely related to *C. stenogastra*, *C. ferrieri*, and *C. testaceipes*, than to other species of *Calosota*, *i. e.*, *Calosota* is paraphyletic.

24. Relative length of first funicular article (ful) of females. Two states are recognized: 1] ful distinctly longer than clava; and, 2] ful subequal in length or shorter than clava.

Individuals of *Archaeopelma*, *Eusandalum*, *Chirolophus*, *Paraeusandalum* (length of clava unknown, but ful long), *Balcha*, and *Tanythorax* have state one, whereas individuals of *Licrooides* and *Calosota* have state two (Table 5.2).

State one is hypothesized as plesiomorphic based on wide distribution in the subfamily. Further hypotheses of transformation series and possible homoplasy in this character are delayed until section 5.7.2.1, "monophyly and intergeneric relationships of Calosotinae".

25. Transepisternal sulcus. Two states are recognized: 1] lower mesepisternum without transepisternal sulcus, at most with longitudinal line of differentiated sculpture or color (Fig. 5.67); and, 2] lower mesepisternum with distinct longitudinal sulcus between acropleural sulcus and discrimen (Fig. 5.48).

Only individuals of *Licrooides* have a transepisternal sulc[illegible] in Calosotinae [Table 5.2, 25(2)]. Furthermore, of the taxa included in this analysis, only individuals of *Lambdobregma* (Metapelmatinae) are known to have a similar sulcus (Fig. 5.68). I interpret this similarity as convergent, and interpret presence of a transepisternal sulcus as autapomorphic for *Licrooides* in Calosotinae, and for *Lambdobregma* in Metapelmatinae.

5.7.1.3 Characters analyzed for intergeneric relationships of Metapelmatinae

25. Transepisternal sulcus. See above.

26. Relative structure of scutellum and metanotum. Two states are recognized: 1] apex of scutellum simple and projected slightly over base of metanotum (Fig. 5.26), latter extended as flattened triangular dorsellum posterior to scutellum, visible in dorsal view (Fig. 5.25); and, 2] apex of scutellum ventrally recurved as hook (Figs. 5.28, 5.29), with dorsellum of metanotum as transverse region beneath scutellar apex, concealed in dorsal view (Fig. 5.27).

Individuals of *Metapelma* have state one (Figs. 5.25, 5.26) whereas those of *Neanastatus* (Figs. 5.29) and *Lambdobregma* (Figs. 5.27, 5.28) have state two. Interpretation of this character is uncertain because the groundplan state of the subfamily can not be confidently hypothesized. It is unknown whether states one and two are independent transformation series from a more plesiomorphic groundplan state, or represent a single transformation series. However, I presently interpret state two as apomorphic, and a possible synapomorphy for *Neanastatus* + *Lambdobregma* because in most eupelmids the apex of the scutellum is simple and the dorsellum is visible in dorsal view, though not extended as in individuals of *Metapelma*.

27. Head structure. Two states are recognized: 1] head more or less quadrate or oval in lateral view (Fig. 5.16), with Λ -shape scrobal cavities above toruli (Fig. 5.15); and, 2] head more or less lenticular in lateral view, with scrobes as short, vertical furrow above each torulus (Figs. 5.13, 5.14).

Individuals of *Lambdobregma* have state one, whereas those of *Metapelma* and *Neanastatus* have state two. State one is hypothesized as plesiomorphic, based on similarity in structure to other eupelmids. Consequently, state two is a possible synapomorphy for *Metapelma* + *Neanastatus*.

28. Ovipositor length. Two states are recognized: 1] ovipositor exserted by at least 0.5 length of metasoma; and, 2] ovipositor only slightly exserted beyond apex of metasoma.

Females of *Metapelma* and *Lambdobregma* have a long ovipositor, whereas those of *Neanastatus* have a very short ovipositor. I presently interpret a long ovipositor as plesiomorphic because a long ovipositor is possessed by many parasitoids of wood-boring beetles (Coleoptera), and I hypothesize these as the original hosts of members of Metapelmatinae. Wood-boring beetles are indicated as the original hosts because metapelmatines, including individuals of *Neanastatus*, have protibial dorsoapical spines (character 17). Furthermore, the hosts of species of *Metapelma* are wood-boring beetles, whereas those of *Neanastatus* are cecidomyiids (Diptera: Cecidomyiidae) or platygastrids (Hymenoptera: Platygastridae) in cecidomyiid galls. This latter host niche is very unusual for eupelmids, and is most likely secondarily derived.

29. **Occiput**. Two states are recognized: 1] vertex and temples smoothly rounded into occiput (Figs. 5.14, 5.16); and, 2] vertex and temples carinately angled to occiput (Fig. 5.13).

Individuals of *Metapelma* and *Lambdobregma* have state one, whereas those of *Neanastatus* have state two [Table 5.2]. State one is hypothesized as plesiomorphic based on presence of this state in members of the other higher taxa analyzed. Consequently, state two is interpreted as an autapomorphy for *Neanastatus*.

30. **Number of antennal funicular articles**. Two states are recognized: 1] funicle with 7 articles; and, 2] funicle with 5 articles.

Distribution of states and interpretation of polarity as given for character 29.

31. **Structure of scutellum**. Two states are recognized: 1] scutellum entire; and, 2] scutellum divided mediolongitudinally (Figs. 5.29, 5.30).

Distribution of states and interpretation of polarity as given for character 29.

32. **Prepectus**. Two states are recognized: 1] prepectus subtriangular (Fig. 5.26); and, 2] prepectus subrectangular to subcircular (Fig. 5.54).

Distribution of states and interpretation of polarity as given for character 29.

33. Propodeum. Two states are recognized: 1] propodeum rectangular in dorsal view, with apex of scutellum distant from base of metasoma (Figs. 5.25, 5.27); and, 2] propodeum medially linear, apex of scutellum extended to base of metasoma (Fig. 5.29).

Distribution of states and interpretation of polarity as given for character 29.

34. Mesotibia. Two states are recognized: 1] mesotibia without carinae; and, 2] mesotibia with proximal arcuate carina that is extended along anterodorsal edge.

Distribution of states and interpretation of polarity as given for character 29.

35. Metatibia and metatarsus. Two states are recognized: 1] metatibia and metatarsus cylindrical or moderately compressed, but with rounded dorsal edge; and, 2] metatibia and at least basi-metatarsus compressed, with dorsal edge carinate.

Individuals of *Neanastatus* and *Lambdobregma* have state one, whereas individuals of *Metapelma* have state two. State one is hypothesized as plesiomorphic based on presence of this state in most members of the other higher taxa analyzed. Consequently, state two is interpreted as an autapomorphy for *Metapelma* in Metapelmatinae.

Table 5.1. Matrix of characters analyzed for evidence of monophyly and relationships between the higher taxa.
[Character states defined in text]

		Pteromalidae (Cleonyminae)		Calosotinae									Eupelminae			Metapelmatinae				Tanaostigmatinae			Encyrtidae		Aphelinidae	
No.	Character	GPS		GPS	Arc	Par	Eus	Chi	Lic	Cal	Bal	Tan	GPS	♀¹	♂	GPS	Met	Nea	Lam	GPS	Tno	Cyn	GPS		GPS	
1	Sexual dimorphism	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1
2	Antennal clava	1?	1, 3	1	1	1	1	1	1	3	3	3	3	3	3	3	3	2	3	3	3	3	3	1, 2, 3	3	1, 2, 3
3	Lateral mesopleuron	1	1	2	2	3a	3a,4	3a	2	3b,4	3b	3b	1	4	1	2	2	4	4	4	4	4	4	4	1	$1,2,3,4^{3,4}$
4	Mesotibial spur	2	$1, 2, 3^2$	2	2	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	3	3	2	1, 2, 3
5	Mesotarsal pegs	1	$1, 5^2$	1	1	2	2	2	5	5	5	5	1	5	1	3	3	3	3	1?	1,2	4	?	–	1	$1, 3^3$
6	Mesocoxal articulation	1a	$1a, 2c^2$	2c	2c	2c	2c	2c	2c	2c	2c	2c	2a	2c	2a	2a?	2a	2a	2d	?	2c	2a	2b	2a, 2b	1a	$1a, 1b^4$
7	Notauli	1	1	2	2	2	2	2	2	3	3	3	1	4	1	5	5	5	5	2	2	5	2	2, 5	1	1
8	Mesonotal articulation	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	2	2	2	2	1	1
9	Pl_2-t_2c + prepectus	1	1	1	1	1	2a	1	1	1	1	1	1	1	1	1	1	1	1	2b	2a	2b	2c	2c	1	1, 2c?
10	DAS	1	1	2a	2a	2a	3b	3a	3a	3a	3a	3a	1	2a,3a	1	2a	2a	3a	2a	2a	2a	2b	2b	2b	3a	3a
11	Pronotal structure	1a	1a	1b	1b	1b	1b	1b	1b	1b	1b	1a	1a	1a	1a,3b	2a	2a	2a	2a	2b	3a	2b	2b	2a,2b	2b	2b
12	Mesotibial pegs	1	1	1	1	1	1	1	1	1,2	1	1	1	1,2	1	2	2	2	2	2?	1	2	2	2	1	$1, 2^3$
13	Parapsidal lines	1	1, 2	2	2	2	2	2	2	2	2	2	1	1,4	1	1	3	1	1	1	1	1	1	1	1	1
14	Mt8 + Mt9	2	2	1a	1a	2?	1b	2	2	2	2	2	2	2	2	1b	1b	2	2	2	2	2	2	2	2	2
15	Linea calva	1	1	1	1	1	1	1	1	1,2	1	1	1	1,2	1	2	1,2	2	2	1	1	1	2	1,2	1	1,2
16	t_1-tr_1	1	1	1	1	1	1	1	1	1	1	1	1	6	1	1	2	3a	4	1	1	1	1	1,3b,5	1	1
17	Protibial apical spines	2	1, 2	2	2	2	1,2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	?	1	1	1	1

GPS= Groundplan state
1 = alates only
2 = Oodera Westwood
3 = Eutrichosomella Girault
4 = Coccobius Ratzeburg

Arc = Archaeopelma n. gen.
Par = Paraeusandalum n. gen.
Eus = Eusandalum Ratzeburg
Chi = Chirolophus Haliday

Lic = Licrooides n. gen.
Cal = Calosota Curtis
Bal = Balcha Walker
Tan = Tanythorax n. gen.

Met = Metapelma Westwood
Nea = Neanastatus Girault
Lam = Lambdobregma n. gen.

Tno = Tanaostigmatinae s.s.
Cyn = Cynipencyrtus Ishii

Table 5.2 Matrix of characters analyzed for evidence of monophyly and intergeneric relationships in Calosotinae and in Metapelmatinae. [Character states defined in text]

		Calosotinae									Metapelmatinae			
No.	Character	GPS	Arc	Par	Eus	Chi	Lic	Cal	Bal	Tan	GPS	Met	Neo	Lam
18	Acropleural sulcus	1	1	1	1	1	2	2	2	2				
19	Protibial spicules	?	1	1	1, 2	1	2	2	2	2				
20	Scutoscutellar suture	1	1	1	1	1	1	2	2	2				
21	Male antenna	1	1	?	1, 2	2	2	1	1	1				
22	Propectal size	1	1	1	1, 2	2	2	1	2	2				
23	Mesoscutum	1	1	1	1	1	1	1, 2	3	1				
24	Female fu1	1	1	1?	1	1	2	2	1	1				
25	Transepisternal sulcus	1	1	1	1	1	2	1	1	1	1	1	1	2
26	Scutellum + metanotum										1	1	2	2
27	Head shape										1	2	2	1
28	Ovipositor length										1	1	2	1
29	Occiput										1	1	2	1
30	Funicle										1	1	2	1
31	Scutellum										1	1	2	1
32	Propectal shape										1	1	2	1
33	Propodeum										1	1	2	1
34	Mesotibial carina										1	1	2	1
35	Metatibia + metatarsus										1	2	1	1

Abbreviations of taxa as given in table 5.1

5.7.2 Analyses of phyletic relationships

5.7.2.1 Monophyly and intergeneric relationships of Calosotinae

The following analysis does not fully resolve phylogenetic relationships between the eight genera included in Calosotinae [*Archaeopelma, Paraeusandalum, Eusandalum, Chirolophus, Licrooides, Calosota, Balcha,* and *Tanythorax*]. Uncertainty about polarity of some character states, and apparent homoplasy in chararacter states in members of some genera, precludes any single hypothesis of character-state evolution, and consequently any single hypothesis of relationships. Alternate hypotheses of character-state evolution that are advanced below are illustrated in figures 5.1a, 5.1b, and 5.1c.

This analysis assumes monophyly of Calosotinae even though evidence for this is extremely tenuous. Of the characters previously analyzed for evidence of relationships between the hig[illegible]axa, only two states indicate possible monophyly of Calosotinae. The first is form of the parapsidal lines (Fig. 5.24) [Table 5.1, 13(2)]. However, rather than synapomorphic for members [Fig. 5.1a, 13(2)], this state could be symplesiomorphic [Fig. 5.1b, 13(2)] because it is shared with individuals of at least two genera of Cleonyminae (Pteromalidae). The second state is relative structure of the pronotum and mesoscutum, with the mesoscutal lateral lobes abruptly angled and distinctly 'shoulder-like' on either side of the relatively narrow pronotum (Figs. 5.17-5.23) [Table 5.1, 11(1b); Figs. 5.1a, 5.1b, 11(1b)]. This latter hypothesis of synapomorphy for members of Calosotinae assumes an autapomorphic reversal in relative pronotal-mesoscutal structure of individuals of *Tanythorax*, to a plesiomorphic-like state [Figs.

5.1a, 5.1b, 11(1a)]. Furthermore, reliable transformation series cannot be hypothesized for this character, and it is possible that state 11(1b) is ancestral to one or more other states described for members of other higher taxa.

Indirect evidence against monophyly of Calosotinae is that the groundplan state hypothesized for most of the characters analyzed is equally or more plesiomorphic for calosotines than the groundplan states hypothesized for Eupelminae (excluding males), Metapelmatinae, Tanaostigmatinae, and Encyrtidae. Furthermore, hypothesized transformation series of many of the characters in Calosotinae include apomorphic states that are shared with members of one or more of the four higher taxa listed above. However, whether Calosotinae is paraphyletic to one or more of the other recognized higher taxa, or not, probably does not affect relationships between the included genera. If paraphyletic, exclusion of some taxa probably only affects the immediate sister group of a genus, and not the relationships between the included genera.

Two major clades are hypothesized in Calosotinae based on mesotarsal peg pattern: *Paraeusandalum* + *Eusandalum* + *Chirolophus* [Figs. 5.1a, 5.1b, 5(2)], and *Licrooides* + *Calosota* + *Balcha* + *Tanythorax* [Figs. 5.1a, 5.1b, 5(5)] (for brevity I will call the first clade the *Eusandalum*-clade and the second clade the *Licrooides*-clade). Monophyly of the *Eusandalum*-clade is supported by only this single character, but monophyly of the *Licrooides*-clade is additionally supported by form of the acropleural sulcus [Figs. 5.1a, 5.1b, 18(2)].

This hypothesis of two major clades depends on accuracy of the hypothesis that states two and five of the mesotarsal peg pattern are independent transformation series from state one, *i. e.*, that the three states do not represent a single transformation series from state one (row of setae along posterior and anterior ventral edges of mesotarsus) → state two (row of pegs along posterior edge and row of setae along anterior edge) → state five (row of pegs along posterior and anterior edges). Both rows of mesotarsal pegs are equally developed in members of the *Licrooides*-clade, with the "pegs" little more than robust spines in individuals of *Licrooides* (Fig. 5.93), so that structure of the pegs is relatively very plesiomorphic in members of this genus. Consequently, structural evidence of the pegs is lacking for the latter hypothesis of a single transformation series.

Archaeopelma is indicated as a lineage that is basal to both the *Eusandalum*-clade and the *Licrooides*-clade, based on possession of state one of the mesotarsal peg pattern. However, it is uncertain whether *Archaeopelma* is the sister group of the *Eusandalum*-clade + *Licrooides*-clade together [Fig. 5.1a], or whether *Archaeopelma* is the sister group of the *Eusandalum*-clade, and these two lineages together are the sister group of the *Licrooides*-clade [Fig. 5.1b]. The latter hypothesis is supported by a single possible synapomorphy, presence of protibial dorsal spicules [Fig. 5.1b, 19(1)]. If true, this is additional evidence for monophyly of the *Eusandalum*-clade, and therefore further supports the previous hypothesis of two major clades in Calosotinae. However, individuals of at least one cleonymine genus are known to have protibial dorsal spicules. If presence of the spicules [Fig. 5.1a, 19(1)] is a symplesiomorphic state for Calosotinae, then secondary loss of the spicules [19(2)] is a third apomorphy indicating monophyly of the *Licrooides*-clade. The first hypothesis that *Archaeopelma* is the sister group of both the *Eusandalum*-clade + *Licrooides*-clade is indicated by members of the latter two clades sharing somewhat more apomorphic states of the mesopleuron [Fig. 5.1a, 3] and mesocoxal articulation [6(2c)] than possessed by individuals of *Archaeopelma*. Members of the two major clades have a convexly expanded acropleuron that is larger than the flat to slightly concave acropleuron of individuals of *Archaeopelma* (Fig. 5.43). Furthermore, individuals of *Archaeopelma* have the mesotrochantinal lobes very widely separate, with only an oblique membranous region anterior to each mesocoxa (Fig. 5.75), whereas the mesotrochantinal lobes are closer together and the membranous regions are larger to varied extents in members of the *Eusandalum*- and *Licrooides*-clades. For both of the above characters, individuals of *Licrooides* have the next most plesiomorphic states in Calosotinae to those of *Archaeopelma*.

Relationships between the genera of the *Eusandalum*-clade remain unresolved. *Paraeusandalum* + *Chirolophus* might represent the sister group of *Eusandalum* based on a single possible synapomorphy, fusion of Mt8 and Mt9 as a syntergum in females [Fig. 5.1b, 14(2)]. However, this suspected structure for females of *Paraeusandalum* still has to be confirmed by dissections. Furthermore, independent fusion of Mt8 and Mt9 has to be hypothesized for the *Licrooides*-clade, as well as in Metapelmatinae [Fig. 5.2, 14(2)], and in the common ancestor(s) of the other higher taxa analyzed (Table 5.1). Consequently, I do not consider this character state as reliable evidence of relationships. I presently hypothesize that *Paraeusandalum* is the sister taxon of *Eusandalum* + *Chirolophus* [Fig. 5.1a]. Individuals of the latter two genera have the acropleuron more completely expanded (Figs. 5.45, 5.47) than do individuals of *Paraeusandalum* (Fig. 5.44). Furthermore, they have the posterior row of mesotarsal pegs as distinct pegs (Fig. 5.92), whereas females of *Paraeusandalum* have the posterior row of pegs as only more robust spines compared with the anterior row (*cf.* Fig. 5.95). It is also possible that separate DAS [Fig. 5.1a, 10(3)] indicates monophyly of *Eusandalum* + *Chirolophus*. However, separation of the DAS also has to be hypothesized for the *Licrooides*-clade (Figs. 5.1a, 5.1b), and the two different states of the DAS in individuals of *Eusandalum* [10(3b), Figs. 5.19, 5.20] and *Chirolophus* [10(3a), Fig. 5.21] may indicate two independent reductions from a *Paraeusandalum*-like structure of the DAS (*cf.* Fig. 5.17).

The above hypotheses of relationships in the *Eusandalum*-clade are based on a hypothesis that both *Eusandalum* and *Chirolophus* are monophyletic. This is very likely for *Chirolophus*, with known individuals possessing the following combination of apomorphic states: **(1)** Mt8 and Mt9 fused in females [14(2)], **(2)** prepectus distinctly separate from base of tegula [22(2)], **(3)** males with pectinate antennae, the proximal five funiculars each with a compressed basal ramus extended to about the same point near the apex of the antenna [21(2)], **(4)** males with glabrous or sparsely setose wings, and **(5)** individuals with short to punctiform, subequal PMV and STV (latter two characters not included in character analysis).

Monophyly of *Eusandalum* is supported by two hypothesized apomorphic states: **(1)** unique form of the DAS [10(3b)], and **(2)** slightly protuberant prepectus, which is projected as a small, acutely angled lobe beneath the mesothoracic spiracle [9(2a)]. However, development of this latter state is varied in members of *Eusandalum*, and a comprehensive survey is required to hypothesize the groundplan state for the genus. Monophyly of *Eusandalum* is questionable because individuals of various species, primarily from the Oriental and Australian regions, share with individuals of *Chirolophus* one to all of the last four apomorphic states described for *Chirolophus*. These apomorphic states would have to be the result of independent origin and convergence if *Eusandalum* is monophyletic.

I hypothesize *Licrooides* as the sister taxon [illegible]*ota* + *Balcha* + *Tanythorax* in the *Licrooides*-clade [Figs. 5.1a, 5.1b]. Monophyly of the final three genera is supported by four hypothesized apomorphic states, all of which are autapomorphic in Calosotinae. Two of the character states are also autapomorphic for the higher taxa analyzed: **(1)** scutoscutellar suture extended along side of the scutellum so that this appears carinate to apex [20(2)], and **(2)** notauli as paramedially parallel lines of differentiated sculpture on dorsum of mesoscutum [7(3)]. A 3-articled antennal clava is shared with members of most of the other higher taxa included in the analysis [2(3)], but is hypothesized as an apomorphic state in Calosotinae. The fourth character state that indicates monophyly of *Calosota* + *Balcha* + *Tanythorax*, is the convex, subtriangular lower mesepimeron at the apex of the acropleuron of individuals [3(3b)] (absence from some species of *Calosota* interpreted as secondary through complete expansion of the acropleuron).

Though monophyly of *Calosota* + *Balcha* + *Tanythorax* appears to be reliably supported, relationships between the three genera remain uncertain. Of the four genera included in the *Licrooides*-clade, individuals of *Licrooides*, *Balcha*, and *Tanythorax* have a small prepectus [22(2)], which is hypothesized as apomorphic in Calosotinae. Either the small prepectus was derived in the common ancestor of the *Licrooides*-clade [Fig. 5.1b, 22(2)], and the large prepectus [22(1)] characteristic of individuals of *Calosota* is the result of a reversal, and an apomorphic state that supports monophyly of this genus, or, a small prepectus was independently derived in *Licrooides* and in the common ancestor of *Balcha* + *Tanythorax* [Fig. 5.1a, 22(2)]. Interpretation of distribution of states of the first antennal funicular article of females is equally uncertain. A first funicular article that is distinctly longer than the clava [24(1)] is hypothesized as plesiomorphic for Calosotinae, with individuals of *Balcha* and *Tanythorax* sharing this state. Individuals of *Licrooides* and *Calosota* have the hypothesized apomorphic state of fu1, *i. e.*, subequal in length or shorter than the clava [24(2)]. Consequently, either there were two independent reductions of fu1 in *Licrooides* and *Calosota*, supporting monophyly of each genus [Fig. 5.1a, 24(2)], or, there was a single reduction in relative length of fu1 in the common ancestor of the *Licrooides*-clade [Fig. 5.1b, 24(2)], and a secondary reversal in this character in the common ancestor of *Balcha* + *Tanythorax* [24(1)].

In addition to the above-described uncertainty about character-state evolution in the *Licrooides*-clade, monophyly of *Calosota* is questionable. *Licrooides* is indicated as a monophyletic taxon based on presence of a transepisternal sulcus [Figs. 5.1a, 5.1b, 25(2)], and pectinate antennae of males [21(2)]. *Tanythorax* is also indicated as a monophyletic genus based on relative structure of the pronotum and mesoscutum [Figs. 5.1a, 5.1b, 11(1a)], the elongate mesothorax, and presence of spines on the mesotibia (latter two characters not included in analysis or in Fig. 5.1). Finally, monophyly of *Balcha* is indicated by the distinctive mesoscutal color and sculptural pattern of individuals [Figs. 5.1a, 5.1b, 5.1c, 23(3)]. However, individuals of a few species of *Calosota*, known from the Oriental and Ethiopian regions, have what appear to be intermediate states of the mesoscutal sculpture [23(2)] between the apomorphic sculpture of individuals of *Balcha* [23(3)], and the hypothesized plesiomorphic state shared by individuals of *Tanythorax* and most species of *Calosota* [23(1)]. Either states 23(2) and 23(3) are independent transformation series from 23(1), and similarity is the result of convergence, or they form a single transformation series from 23(1) [23(1) → 23(2) → 23(3)], and *Calosota* is paraphyletic relative to *Balcha* [Fig. 5.1c].

Individuals of some species of *Calosota* also have the DAS relatively large-triangular, separated by little more than the basal width of one (Fig. 5.22), whereas others have the DAS more reduced, in some to only a linear strip along each edge of the scutellum (Fig. 5.23). This latter, more apomorphic state, is shared with individuals of *Tanythorax*, and though there is some variation, the DAS are separated by at least 2.5 times the basal width of one in species of *Balcha*. Both of the above characters indicate that *Calosota* is possibly paraphyletic relative to *Balcha*. However, if this is so, it necessitates a large prepectus [22(1)] as the plesiomorphic state of the prepectus, and consequently an hypothesis of independent reductions of the prepectus in *Balcha* and *Tanythorax* [Fig. 5.1c, 22(2)]. At present, uncertainty about polarity and correct groundplan states of the genera is such that I prefer not to hypothesize about the correct relationships between *Calosota*, *Balcha*, and *Tanythorax*.

Relationships between the eight genera assigned to Calosotinae are not fully resolved. Further resolution, and testing of the hypotheses presented, can be accomplished by two main methods other than analysis of more characters. The most practical is revision of the species of each genus and analysis of the relationships between the species. Groundplan states for each genus can be more reliably hypothesized by this method, and these then used to construct more reliable hypotheses of monophyly and intergeneric relationships. Furthermore, when geographic distribution of the species is overlaid on the reconstructed phylogeny of species for each genus, regional patterns of structure, sculpture, or color (see for example, Mason 1964) may become apparent. This would help differentiate similarity due to homoplasy from similarity due to synapomorphy. The second method is to discover specimens representing new taxa that have combinations of character states that either clarify polarity of the character states, or their level of apomorphy.

5.7.2.2 Monophyly and intergeneric relationships of Metapelmatinae

Monophyly of Metapelmatinae is indicated by a combination of five or six character states shared between members. These states, listed in decreased order of hypothesized reliability are: **(1)** structure of mesoscutum (dorsally flattened without notauli, Figs. 5.25, 5.27) [Table 5.1, Fig. 5.2, 7(5)]; **(2)** pattern of mesotarsal pegs (single anterior row, Fig. 5.94) [5(3)]; **(3)** structure of pronotum (elongate-conical, Figs. 5.25, 5.27) [11(2a)]; **(4)** presence of fore wing linea calva [15(2)]; and, **(5)** presence of mesotibial apical pegs (Fig. 5.94) [12(2)].

Mesoscutal structure is interpreted as the most reliable indicator of monophyly of Metapelmatinae because presence of notauli is hypothesized as the groundplan state for each of the other higher taxa analyzed (Table 5.1). I also consider pattern of the mesotarsal pegs as a reliable indicator of monophyly, even though the same, or a similar pattern of pegs is shared with many encyrtids. I interpret this similarity as the result of convergence, most likely because of a functionally similar type of mesocoxal articulation (see under character 6), because I hypothesize Tanaostigmatinae *s. l.* as the sister group of Encyrtidae, and absence of mesotarsal pegs as the ancestral state for Tanaostigmatinae + Encyrtidae (see section 5.7.2.3, "monophyly and relationships of the higher taxa"). Reliability of the very distinctive pronotal structure of metapelmatines is lessened as an indicator of monophyly because this structure [11(2a), Figs. 5.25, 5.27] could be ancestral to what is hypothesized as the groundplan state of the pronotum for Tanaostigmatinae + Encyrtidae. Presence of a linea calva and mesotibial apical pegs are also not considered reliable indicators of monophyly because the former state is shared with encyrtids, and the latter state is shared with encyrtids and is the hypothesized groundplan state for tanaostigmatines [Table 5.1].

A sixth possible indicator of monophyly of the subfamily is absence of the specialized mesocoxal articulation that permits the mesocoxae to rotate anteriorly out of their fossae (character 6). Absence of the specialized mesocoxal articulation from members of Metapelmatinae is synapomorphic if absence is the result of secondary loss.

Of the three included genera, a possible sister-group relationship between *Metapelma* and *Neanastatus* is indicated by a similar, apomorphic head structure. Individuals of these two genera have the head more or less lenticular in lateral view, with the scrobes reduced to short, vertical furrows above each torulus (Figs. 5.13, 5.14). I presently consider this similarity to be the result of convergence [Fig. 5.2, 27(2)] because I hypothesize that *Metapelma* is the sister group of *Lambdobregma* + *Neanastatus*. The latter hypothesis is based on four shared character states that I interpret as synapomorphies for members of these two genera: **(1)** a completely expanded acropleuron [Fig. 5.2, 3(4)]; **(2)** Mt8 and Mt9 fused as syntergum [14(2)]; **(3)** relative structure of the scutellum and metanotum [26(2)]; and, **(4)** structure of the t_2-tr_2 muscle [16(3a, 4)].

I consider structure of the t_2-tr_2 muscle as the most reliable evidence of monophyly of *Neanastatus* + *Lambdobregma*. I interpret the characteristic structures of this muscle for individuals of *Neanastatus* [16(3a), Fig. 5.103] and *Lambdobregma* [16(4), Fig. 5.104] as two states in a single transformation series from structure of the muscle hypothesized as plesiomorphic for the higher taxa [16(1), Figs. 5.99, 5.100]. I further consider the structure of t_2-tr_2 in individuals of *Neanastatus* as intermediate between the hypothesized plesiomorphic structure and the most apomorphic structure, which is possessed by individuals of *Lambdobregma*, *i. e.*, 16(1) → 16(3a) → 16(4). Consequently, I interpret state of t_2-tr_2 in individuals of *Lambdobregma* as autapomorphic and indicative of monophyly of the genus. I also interpret the structure of t_2-tr_2 in individuals of *Metapelma* [16(2), Figs. 5.101, 5.102] as autapomorphic, representing a second, independent transformation series from the plesiomorphic structure of the muscle.

Monophyly of *Metapelma* is supported by states of three characters studied [Fig. 5.2: 13(3), 16(2), 35(2)], *Neanastatus* by ten states [2(2), 8(2), 10(3a), 28-34(2)], and *Lambdobregma* by two or three states [6(2d)?, 16(4), 25(2)].

I am uncertain about the correct polarity of character six, articulation of the mesocoxae. Individuals of *Neanastatus* and *Metapelma* have the mesotrochantinal plate reflected internally, with the lower mesepisternum transverse along the base of the mesocoxae [6(2a), Figs. 5.69, 5.70], whereas individuals of *Lambdobregma* have the mesotrochantinal plate extended somewhat posteriorly and partly visible in ventral view, with an oblique cavity between the base of each mesocoxa and the lower mesepisternum [6(2d), Fig. 5.68]. If *Lambdobregma* and *Neanastatus* are sister groups, as hypothesized above, then the structure characteristic of individuals of *Lambdobregma* is indicated as a secondarily derived, autapomorphic state. However, if the structure represents an intermediate state in the loss of the apomorphic mesocoxal articulation, it would support a possible sister-group relationship between *Metapelma* and *Neanastatus*.

5.7.2.3 Monophyly and relationships of the higher taxa

Previously, if Eupelmidae *s. l.* (Calosotinae + Eupelminae + Metapelmatinae + Tanaostigmatinae) and Encyrtidae were considered as a monophyletic group, the hypothesis was based on three character states that members were supposed to share: **(1)** a convexly expanded mesopleuron (acropleuron), **(2)** a robust mesotarsus with pegs on the ventral surface, and **(3)** a robust mesotibial spur. However, character-state distribution was based primarily on comparisons of the highly apomorphic structures of encyrtids and female eupelmines. Tanaostigmatinae was recognized as a distinct taxon, but Eupelmidae *s. s.* was otherwise considered to be a relatively cohesive taxon, the concept of which was essentially the same as the present concept of Eupelminae. It was not realized that Eupelmidae *s. s.* is composed of three discrete assemblages, which may or may not represent monophyletic clades. Furthermore, phylogenetic significance of sexual dimorphism in Eupelminae was not appreciated.

Male eupelmines are basically pteromalid-like in structure, lacking the apomorphic features that characterize females of the subfamily. The apomorphic states of females that males lack are: **(1)** a convexly expanded acropleuron [character 3, *cf.* Figs. 5.52, 5.41], **(2)** robust mesotibial spur [character 4, *cf.* Figs. 5.98, 5.90], **(3)** robust mesotarsus with ventral pegs [character 5, *cf.* Figs. 5.98, 5.90], **(4)** mesopleural-mesocoxal articulation that permits anterior rotation of mesocoxa [character 6, *cf.* Figs. 5.78, 5.83], **(5)** V-shape, furrow-like notauli that are not extended to transscutal articulation [character 7, *cf.* Figs. 5.38, 5.39], **(6)** relatively flat DAS in horizontal plane with scutellum [character 10], **(7)** mesotibial apical pegs [character 12, *cf.* Figs. 5.98, 5.90], and **(8)** tendon-like mesotergal-mesotrochantinal (t_2-tr_2) muscle [character 16, *cf.* Figs. 5.105, 5.99].

As justified under character one (sexual dimorphism), a non-dimorphic common ancestor must be hypothesized for Eupelminae plus any of Calosotinae, Metapelmatinae, Tanaostigmatinae, and Encyrtidae. Consequently, I interpret sexual dimorphism as an autapomorphic state that indicates monophyly of Eupelminae. Furthermore, because most of the eight apomorphic states listed above for female eupelmines are shared with both sexes of some or all of the other four higher taxa, either: **1)** Eupelminae is at most the sister group of the other four higher taxa, and all the apomorphic states of female eupelmines are independently and convergently evolved, or **2)** structure of male eupelmines is the result of secondary reversal of the apomorphic states of females to plesiomorphic-appearing states.

Neither of the above two hypotheses for evolution of sexual dimorphism in Eupelminae appears reasonable because of the number of states that either have to be independently derived, or secondarily lost. However, an hypothesis of convergence in structure of female eupelmines to that of other "eupelmids" and encyrtids, *i. e.*, that Eupelmidae may represent a grade of structure, is perhaps indicated by character-state distribution in members of the other taxa. Within Calosotinae, individuals of *Archaeopelma* have only a moderately enlarged, non-convex acropleuron (Fig. 5.43), a non-robust mesotibial spur, and a non-robust mesotarsus that lacks pegs (Fig. 5.91). Consequently, the apomorphic structures of these characters, which most calosotines possess, must be convergently evolved to similar states of metapelmatines, tanaostigmatines, encyrtids, and female eupelmines, unless Calosotinae is paraphyletic. Furthermore, the different patterns of mesotarsal pegs indicate that these are not the result of a single derivation of "pegs", but the result of separate transformation series from a plesiomorphic state of two ventral rows of setae (character 5).

The apomorphic states that are traditionally used to define Eupelmidae, or to relate eupelmids and encyrtids, are not independent of each other, but form a functional complex. All the apomorphic states appear to be correlated with modifications for improved jumping ability. This is important for the hypothesis that Eupelmidae could represent a grade of structure, resulting from parallel evolution of similar suites of character states.

The plesiomorphic mechanism of jumping in Chalcidoidea is contraction of large mesotergal-mesotrochanteral (t_2-tr_2) muscles acting directly on the middle legs. The convexly expanded mesopleuron of encyrtids and most eupelmids is the result of massive enlargement of a pleuro-tergal muscle, the pl_2-t_2c muscle. These enlarged muscles apparently either supplement the power produced for jumping by the large t_2-tr_2 muscles (calosotines, tanaostigmatines, and some encyrtids), or in yet more apomorphic jumping mechanisms replace the t_2-tr_2 muscles as the primary muscles for jumping (metapelmatines, some encyrtids, and female eupelmines). The modifications of the middle legs (robust mesotibial spur, mesotibial pegs, robust mesotarsus with pegs, and specialized mesopleural-mesocoxal articulation) are all hypothesized to protect the middle legs from the greater forces transmitted through them during jumping, or to protect the body when landing (Gibson in press, c). Consequently, independent enlargements of the pl_2-tr_2 muscle, reflected in a convexly enlarged acropleuron, might well result in similar, independently derived modifications of the middle legs.

Structural diversity of the mesothorax of aphelinids supports this hypothesis. Most aphelinids have the hypothesized plesiomorphic structure of the lateral mesopleuron [Table 5.1, 3(1), Fig. 5.58], though some have a convexly enlarged acropleuron, and members of two genera, *Eutrichosomella* Girault and *Coccobius* Ratzeburg, have a completely enlarged acropleuron [3(4)] similar to encyrtids and many eupelmids. Most aphelinids also have an elongate, if not a robust mesotibial spur. Because of these two character states some authors have either classified aphelinids as a subfamily of Encyrtidae (*e. g.*, Gordh 1979, Riek 1970), or considered aphelinids as a family that is closely related to Encyrtidae (*e. g.*, Mercet 1929, Compere and Annecke 1961). However, signiphorids and some pteromalids (*e. g.*, chalcedectines and some cleonymines) also have an elongate mesotibial spur, so that this state is not necessarily evidence of a close relationship of aphelinids with encyrtids or eupelmids. Furthermore, based on restricted distribution, I interpret the enlarged acropleuron of some aphelinids as the result of secondary modification, and convergent to similar states of encyrtids and many eupelmids. Significantly, only individuals of *Eutrichosomella* in Aphelinidae are known to have mesotibial pegs [Table 5.1, 12(2)] and mesotarsal pegs [5(3)], and only individuals of *Coccobius* are known to have a membranous region anterior to each mesocoxa [6(1b)]. I interpret this as evidence that one or more of the apomorphic character states of the middle legs are likely to evolve if the acropleuron is greatly enlarged, and thus indirect evidence that Eupelmidae could represent a grade-level taxon, at least if Eupelminae is included.

Possible monophyly of Calosotinae + Eupelminae + Metapelmatinae + Tanaostigmatinae + Encyrtidae is indicated by state of a single character studied in this analysis. Members do not have the mesotrochantinal plate extended to the metasternum, hence, the mesocoxal fossae are at least partly continuous, connected by intercoxal membrane [Table 5.1, 6(2)]. This includes male eupelmines, metapelmatines, individuals of *Cynipencyrtus* (Tanaostigmatinae), and various encyrtids, which have the lower mesepisternum transverse along the base of the mesocoxae so that there is no membranous region anterior to each mesocoxa [6(2a)]. Except for individuals of *Oodera* (Pteromalidae: Cleonyminae), other chalcidoids for which states of this character are known have the mesotrochantinal plate extended to the metasternum, including individuals of *Coccobius* (Aphelinidae), which have a membranous region anterior to each mesocoxa (Fig. 5.80).

Individuals of *Oodera* have a middle leg structure that is very perplexing; the mesopleural-mesocoxal articulation is similar to that of calosotines and female eupelmines, *i. e.*, with the mesotrochantinal plate extended more or less posteriorly, rather than internally, so there is both intercoxal membrane and a membranous region anterior to each mesocoxa [Table 5.1, 6(2c), *cf.* Fig. 5.76]. Furthermore, individuals have a robust mesotibial spur [4(3)] and a row of robust spines or pegs along both the ventral edges of the mesotarsus [5(5)]. Because of these similarities in structure, some authors (*e. g.*, Bouček 1958, Graham 1969b) have hypothesized that *Oodera* is a "link" between Cleonyminae and Eupelmidae. If so, two hypotheses explain distribution of states of the mesocoxal articultion in Eupelmidae: **1)** the relatively more plesiomorphic mesocoxal articulations of male eupelmines, metapelmatines, and individuals of *Cynipencyrtus* are the result of separate reversals, or, **2)** the apomorphic mesocoxal articulation is synapomorphic for only *Oodera* + Calosotinae, and the similarly apomorphic articulations of female eupelmines and tanaostigmatines (*s. s.*) are independently derived, *i. e.*, Eupelmidae is polyphyletic. A third hypothesis is that the apomorphic character states of the middle legs of individuals of *Oodera* are independently derived and convergent to those of many eupelmids and encyrtids. I presently interpret this as the most likely hypothesis because in Calosotinae the apomorphic leg structures are indicated to have evolved concomitant with, or after partial enlargement of the acropleuron. Individuals of *Oodera* do not have the acropleuron enlarged, but the middle leg modifications are relatively more apomorphic than those of individuals of *Archaeopelma* (Calosotinae).

Function of the calosotine-like and female eupelmine-like middle legs of individuals of *Oodera* is unknown, but if the apomorphic states are independently evolved to those of eupelmids and encyrtids, this lessens state of the mesotrochantinal plate [6(2)] as a reliable synapomorphy for Eupelmidae + Encyrtidae.

Structure of the mesotrochantinal plate is tenuous evidence that Eupelmidae + Encyrtidae represent a monophyletic taxon, whereas sexual dimorphism in Eupelminae indicates that Eupelmidae is a grade-level, possibly polyphyletic taxon. Eupelmidae is indicated to be at least a paraphyletic taxon because Tanaostigmatinae and Encyrtidae are supported as sister taxa by states of at least three characters.

Monophyly of Tanaostigmatinae + Encyrtidae is supported by states of two structural characters of adults: **(1)** mesoscutal process for attachment of pl_2-t_2c elongated as distinct "arm" anterior to mesothoracic spiracle [Table 5.1, 9(2)], and **(2)** posterior edge of mesoscutum and anterior edge of scutellar-axillar complex free of each other except laterally, not joined along transscutal articulation [8(2)]. Individuals of *Eusandalum* (Calosotinae) have the mesoscutal process for pl_2-t_2c also extended anteriorly, but not nearly so conspicuously as in tanaostigmatines and encyrtids, and individuals of *Neanastatus* (Metapelmatinae) have a similar mesonotal articulatory structure to those of tanaostigmatines and encyrtids. However, I interpret these similarities as the result of independent origin of the respective states in *Eusandalum* and *Neanastatus*.

A third possible synapomorphy that indicates monophyly of Tanaostigmatinae + Encyrtidae is egg structure (not included in the character analysis). LaSalle and LeBeck (1983) hypothesized this after reporting the ovarian eggs of females of two tanaostigmatine species, representing two genera, as "encyrtiform", *i. e.*, composed of two bladders connected by an elongate-narrow tube. They stated that encyrtiform eggs "occur throughout, and are typical of, Encyrtidae", but are "unknown from Eupelmidae which have stalked eggs". However, egg structure described for Eupelmidae is based on eggs of various species of Eupelminae, and egg structure is unknown for females of Calosotinae and Metapelmatinae.

Absence of protibial apical spines from members of Tanaostigmatinae and Encyrtidae [17(1)] could be a fourth synapomorphy, if absence is the result of secondary loss. However, because monophyly of Tanaostigmatinae + Encyrtidae + Eupelmidae *s. s.* is not supported by reliable synapomorphies, absence could be the result of symplesiomorphy. Presence of a completely expanded acropleuron [3(4)] is also not considered as a reliable indication of monophyly because of apparent homoplasy in this character [Table 5.1].

Though I hypothesize Tanaostigmatinae *s. l.* as the sister group of Encyrtidae, I am uncertain about correct relationships of *Cynipencyrtus* to Tanaostigmatinae *s. s.* and Encyrtidae. *Cynipencyrtus* was originally described in Encyrtidae by Ishii (1928), but was recently transferred to Tanaostigmatidae (*sensu* LaSalle and Noyes) by LaSalle and Noyes (1985). They classified *Cynipencyrtus* in Tanaostigmatidae because individuals possess the single apomorphy that they used to distinguish the family, "a large prepectus which is distinctly swollen anteriorly", and because individuals lack "several apomorphic character states which are found in encyrtids" (LaSalle and Noyes 1985, p. 1261). However, absence of the apomorphic states only indicates *Cynipencyrtus* is at most the sister group of Encyrtidae, not that it is more closely related to Tanaostigmatinae *s. s.* Furthermore, I interpret an anteriorly protuberant prepectus as symplesiomorphic for *Cynipencyrtus* and Tanaostigmatinae *s. s.*, based on hypothesized transformation of the prepectus with elongation of the mesoscutal process for pl_2-$\mathrm{t}_2\mathrm{c}$ (character 9).

I found no structural character states shared between adults of *Cynipencyrtus* and Tanaostigmatinae *s. s.* that I interpret as apomorphic. However, states of two characters may indicate that *Cynipencyrtus* and Encyrtidae are sister taxa: **(1)** transverse, subtriangular dorsal axillar surfaces (DAS) [Table 5.1, 10(2b), Figs. 5.33-5.36], and **(2)** presence of mesotibial apical pegs [12(2), Fig. 5.96]. I do not consider the latter state as reliable evidence of relationship because absence of pegs from individuals of Tanaostigmatinae *s. s.* could be the result of secondary loss. Furthermore, presence of pegs appears to be correlated with an enlarged acropleuron, *i. e.*, probably prone to homoplasy (see character 12). Structure of the pronotum is a third character in which individuals of *Cynipencyrtus* and encyrtids are similar [11(2b), Figs. 5.33-5.35, 5.55, 5.59], and dissimilar to tanaostigmatines (*s. s.*) [11(3a), Figs.

5.31, 5.57). I interpret the pronotal structure of tanaostigmatines (*s. s.*) as apomorphic and evidence for monophyly of Tanaostigmatinae *s. s.*, hence I interpret the similar pronotal structure of members of the former two taxa as the result of symplesiomorphy.

A possible sister-group relationship between *Cynipencyrtus* and Tanaostigmatinae *s. s.* is indicated by a single life-history character. Encyrtids and eupelmids (*s. s.*) are parasitoids of the immature stages of various insects and arachnids. Individuals of *Cynipencyrtus* are also parasitoids, of larvae of several species of Cynipidae (Cynipoidea) that form galls on *Quercus serrata* (Fagaceae) (Ishii 1928; Tachikawa 1973, 1978b), whereas tanaostigmatines (*s. s.*) are phytophagous, the majority being gall-formers on hosts in Fagaceae (LaSalle 1984). Some eupelmids, but very few encyrtids, are known parasitoids in cynipid or cecidomyiid (Diptera: Cecidomyiidae) galls (Tachikawa 1978a, Narendran 1984). I interpret phytophagy as apomorphic, and a synapomorphy for members of Tanaostigmatinae *s. s.*, but the gall-niche may also be a synapomorphy for *Cynipencyrtus* + Tanaostigmatinae *s. s.* The similarly transverse DAS of individuals of *Cynipencyrtus* and encyrtids must be the result of convergence if this latter-hypothesized relationship is true, and absence of mesotibial pegs from individuals of Tanaostigmatinae *s. s.* then indicated to be the result of secondary loss.

Correct relationships of *Cynipencyrtus* to Tanaostigmatinae *s. s.* and Encyrtidae remain uncertain. Interpretation of states of the mesopleural-mesocoxal articulation of individuals of the three taxa is also uncertain. Individuals of *Cynipencyrtus* have a relatively plesiomorphic-appearing mesopleural-mesocoxal articulation [Table 5.1, 6(2a), Figs. 5.72, 5.87] compared with those of tanaostigmatines (*s. s.*) [6(2c), Fig. 5.71] and encyrtids [6(2b), Figs. 5.60, 5.73, 5.74]. I do not consider presence of a membranous region anterior to each mesocoxa in tanaostigmatines (*s. s.*) and some encyrtids as synapomorphic; rather, either symplesiomorphic or the result of independent origin from a *Cynipencyrtus*-like structure of the articulation. I suspect the latter is true because of differences in structure of the articulation described for states 2c (tanaostigmatines *s. s.*) and 2b (encyrtids) under character six.

If Tanaostigmatinae + Encyrtidae are sister taxa, relationships between this assemblage and Eupelmidae *s. s.* remain unresolved. Monophyly of Eupelmidae *s. s.* is not supported by states of any characters studied, though possible monophyly of Calosotinae + Metapelmatinae + Tanaostigmatinae + Encyrtidae is supported by distribution of states of two characters. The groundplan state of the dorsal axillar surfaces (DAS) hypothesized for each of the above higher taxa is contiguous, subtriangular DAS that are in a relatively flat plane with the scutellum (character 10). This structure of the DAS could be synapomorphic for members of the four taxa. However, female eupelmines have a very similar DAS structure, which lessens state of the DAS as a reliable indicator of monophyly, because similarity between DAS structure of female eupelmines and other eupelmids and encyrtids is interpreted as the result of convergence. Male eupelmines have a plesiomorphic structure of the DAS, which is the hypothesized groundplan state for Eupelminae. Furthermore, hypotheses of relationship based on structure of the DAS are not reliable until structure of the DAS is more comprehensively studied throughout Chalcidoidea.

The second character that may indicate monophyly of at least Calosotinae + Tanaostigmatinae + Encyrtidae is structure of the notauli (character 7). At least some members of these three taxa have V-shape notauli that meet at, or anterior to the transscutal articulation [Table 5.1, 7(2), Figs. 5.17-5.21, 5.31, 5.36]. Such V-shape notauli are otherwise known for only some Diparinae (Pteromalidae), and consequently could be a synapomorphy for Calosotinae + Tanaostigmatinae + Encyrtidae. However, this is not reliable evidence of relationship between only these three taxa, because absence of notauli from members of Metapelmatinae is undoubtedly secondary. Consequently, metapelmatines can not be excluded from any monophyletic group hypothesized on basis of structure of the notauli. Furthermore, female eupelmines have what appear to be a modified (furrow-like) form of the V-shape notauli [7(4), Fig. 5.38], though I presently interpret this similarity as the result of convergence because I hypothesize state of the notauli in male eupelmines [7(1), Fig. 5.39] as the groundplan state for the subfamily.

Relationships between Eupelmidae *s. s.* and Tanaostigmatinae + Encyrtidae remain unresolved. Relationships between Calosotinae + Metapelmatinae + Eupelminae (Eupelmidae *s. s.*) also remain unresolved. This is possibly because the taxa represent a grade-level, polyphyletic assemblage. Whether this is true, or not, present analysis is insufficient to confidently hypothesize relationships between the taxa.

5.7.2.4 Classification of eupelmids in Chalcidoidea

Higher classification of eupelmids ultimately should reflect the evolutionary history and phyletic relationships of eupelmids with other chalcidoids. However, results of the present analysis are so inconclusive that several equally tenable hypotheses of relationships, and hence classifications, of the included taxa are possible based on available evidence. Though results are not sufficient to fully clarify higher classification of eupelmids, they can be used to test previous classifications, and to propose alternate classifications that can be tested in the future.

Riek (1970, p. 914) proposed a novel classification of Chalcidoidea, with "primary divisions ... based on the manner in which the antennae are cleaned and on the ability to jump". He assigned to the family Encyrtidae all chalcidoids "in which the mid leg is modified for jumping: the tibial spur is enlarged, and the tarsal segments have rows or patches of modified setae on the ventral (plantar) surface except in the most primitive species" (Riek 1970, p. 923). Five subfamilies of Encyrtidae were recognized by him, Encyrtinae, Eupelminae, Tanaostigmatinae (Tanostigmodinae *sensu* Riek), Aphelininae, and Signiphorinae (Thysaninae *sensu* Riek). The present analysis indicates that this classification probably reflects a grade of structure, *i. e.*, is phenetic, rather than phyletic relationships. Members share only a single derived character state, an elongate mesotibial spur, but this is also shared with members of

Chalcedectinae and some members of Cleonyminae (Pteromalidae). In order to falsify common ancestry as the reason for common possession of the elongate mesotibial spur, it is necessary to demonstrate that members of one or more of the taxa included in Encyrtidae by Riek are more closely related to some taxon whose members have a plesiomorphic, short spur. This analysis is not comprehensive enough to do so. However, absence of additional, congruent apomorphies indicates that common possession of an elongate mesotibial spur is probably at least partly the result of homoplasy. Character-state distribution of such other apomorphies as mesotibial and mesotarsal pegs, an enlarged acropleuron, and membranous regions anterior to the mesocoxae, indicates that common possession by some Eupelmidae *s. l.*, Encyrtidae, and Aphelinidae, is partly the result of homoplasy. Hence, this study does not support the familial classification of Encyrtidae proposed by Riek (1970).

Gordh (1979), following Burks (1979), also classified signiphorids and aphelinids as subfamilies of Encyrtidae, but recognized Eupelmidae (Calosotinae, Eupelminae, and Tanaostigmatinae) as a separate family. Representatives of Signiphoridae were not included in the present analysis, hence relationships can not be hypothesized. However, Domenichini (1954) concluded after a detailed study of adult structure that members of Signiphoridae (Thysanidae *sensu* Domenichini) and Encyrtidae "have little in common and that if the former show an affinity with any group, it is with the Aphelinidae" (Domenichini 1954, p. 107). Otherwise, the present analysis does not support the classifications of Gordh (1979) and Burks (1979). No autapomorphies are known to support monophyly of Eupelmidae *sensu* Burks (1979) or Encyrtidae *sensu* Gordh (1979). Rather, inclusion of aphelinids in Encyrtidae probably makes this latter taxon polyphyletic because encyrtids are indicated to be more closely related to some, or all eupelmids (*s. l.*), than to aphelinids. Furthermore, encyrtids are indicated to be more closely related to tanaostigmatines. Hence, inclusion of tanaostigmatines in Eupelmidae makes this latter taxon paraphyletic.

LaSalle (1984) classified the above-discussed taxa in five families: Si[illegible]idae, Aphelinidae, Encyrtidae, Tanaostigmatidae, and Eupelmidae (Calosotina[illegible]pelminae). Signiphorids and aphelinids were excluded from Encyrtidae because the last three families were proposed as a monophyletic clade based on three hypothesized synapomorphies: 1) mesopleuron large, convex, longer than high, and without groove or furrow for reception of mesocoxa; 2) mesoscutum and scutellum joined by flexible membrane and articulating along transscutal articulation (scutoscutellar suture *sensu* LaSalle); and 3) middle leg with combination of large tibial spur and one or two rows of strong, peg-like spines on ventral surface of basitarsus. Encyrtids and tanaostigmatines were each accorded familial status because each was hypothesized as a monophyletic clade, and more closely related to each other than to the rest of the assemblage, which was assigned to Eupelmidae. Synapomorphies were not proposed for this latter family. Present analysis indicates that of the three synapomorphies proposed for Eupelmidae + Tanaostigmatidae + Encyrtidae, common possession of character two results from symplesiomorphy, and characters one and three at least partly from homoplasy. Analysis does support monophyly of Encyrtidae and of Tanaostigmatinae *s. s.* (excluding *Cynipencyrtus* Ishii), and supports a sister-group relationship between the two. Monophyly of each of Eupelminae, Calosotinae, and Metapelmatinae is also supported. However, there is no evidence that this latter assemblage, *i. e.*, Eupelmidae *s. s.*, constitutes a monophyletic taxon. Sexual dimorphism in Eupelminae indicates that Eupelmidae *s. s.* is a grade-level taxon, but the analysis is insufficient to determine whether it is polyphyletic, paraphyletic, or monophyletic, or to determine correct phyletic relationships with Tanaostigmatinae + Encyrtidae.

Proper higher classification of "eupelmids" and "encyrtids" must await clarification of the relationships between the subfamilies of Eupelmidae *s. s.*, and between these and Tanaostigmatinae + Encyrtidae. However, if tanaostigmatines and encyrtids are each accorded familial status solely on the basis of being monophyletic taxa, *i. e.*, the classification of LaSalle (984), then familial status should also be accorded to calosotines, metapelmatines, and eupelmines. This philosophy would result in a proliferation of chalcidoid families. Present knowledge indicates that tanaostigmatinae is better classified as a subfamily of Encyrtidae, the family minimally composed of two subfamilies, Tanaostigmatinae and Encyrtinae. In this classification, members of Encyrtidae are distinguished from other chalcidoids by an elongate process for pl_2-t_2c in combination with an apomorphic structure of the transscutal articulation (posterior ~~edge of mesoscutum free~~ from anterior edge of scutellar-axillar complex). Resolution of encyrtid infrafamilial classification requires clarification of the relationships of *Cynipencyrtus* to Tanaostigmatinae *s. s.* and "encyrtines". If *Cynipencyrtus* is demonstrated as the sister group of "encyrtines", it is probably better to recognize three subfamilies, Tanaostigmatinae, Cynipencyrtinae, and Encyrtinae.

At present, no one classification of "eupelmids" is better than any other. Calosotinae, Metapelmatinae, and Eupelminae could be classified as separate subfamilies of Pteromalidae. This family is acknowledged as a "repository for monophyletic groups not readily placed in other families and not considered to warrant separate family status" (Heraty and Darling, 1984, p. 309). Furthermore, at least Calosotinae appears to be closely related to Cleonyminae (Pteromalidae~~). This classification~~ reflects ignorance of true relationships and does not convey a false impression that Calosotinae, Metapelmatinae, and Eupelminae constitute a demonstrably monophyletic clade. However, relationships between these three taxa are so uncertain that it is perhaps better to assign them to the family Eupelmidae, and retain this traditional higher taxon for present stability of higher classification of Chalcidoidea.

Analysis of character states and their distribution in this study was restricted to representatives of Cleonyminae (Pteromalidae), Eupelmidae *s. l.*, Aphelinidae, and Encyrtidae. Only these taxa were selected for study because of an initial hypothesis, based on previous classifications and statements about relationships, that they, with the possible exception of Aphelinidae, constitute a monophyletic clade in Chalcidoidea. Results of the study dispute this initial hypothesis. Most of the apomorphic character states that members of these taxa share

are correlated with an apomorphic method of generating energy for jumping, *i. e.*, are a functional complex. Distribution of states in members of the taxa indicate that the apomorphic method of powering jumping and suite of correlated states were probably derived more than once, and hence are at least partly homoplasous. However, some evidence indicates that at least part of the assemblage studied does represent a monophyletic clade. To further clarify relationships it will be necessary to expand the present study, both to include more chalcidoid taxa, and more characters, particularly those that are not correlated with jumping.

Figure 5.1. Hypotheses of character-state evolution and cladistic relationships among genera of Calosotinae.

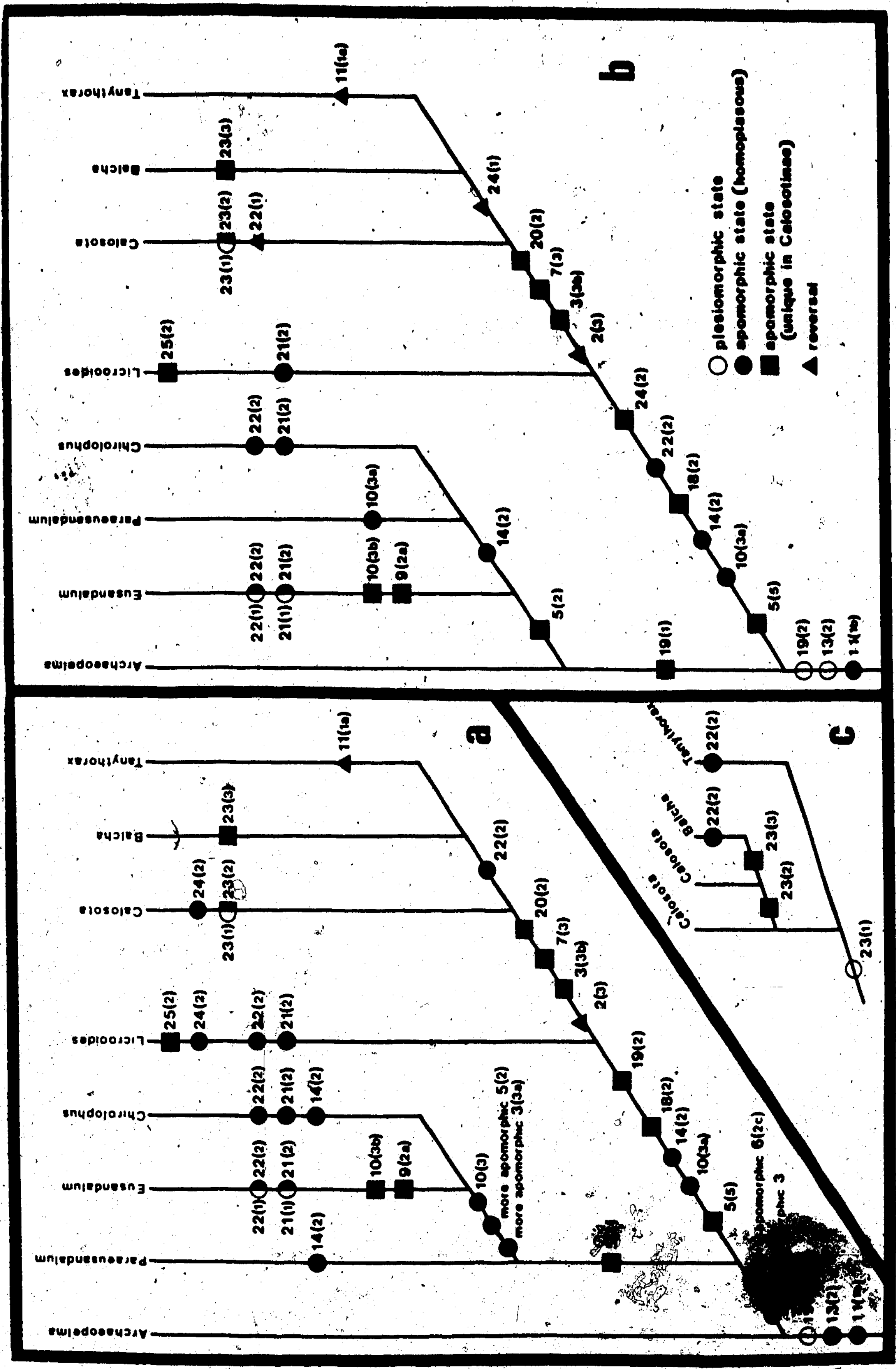
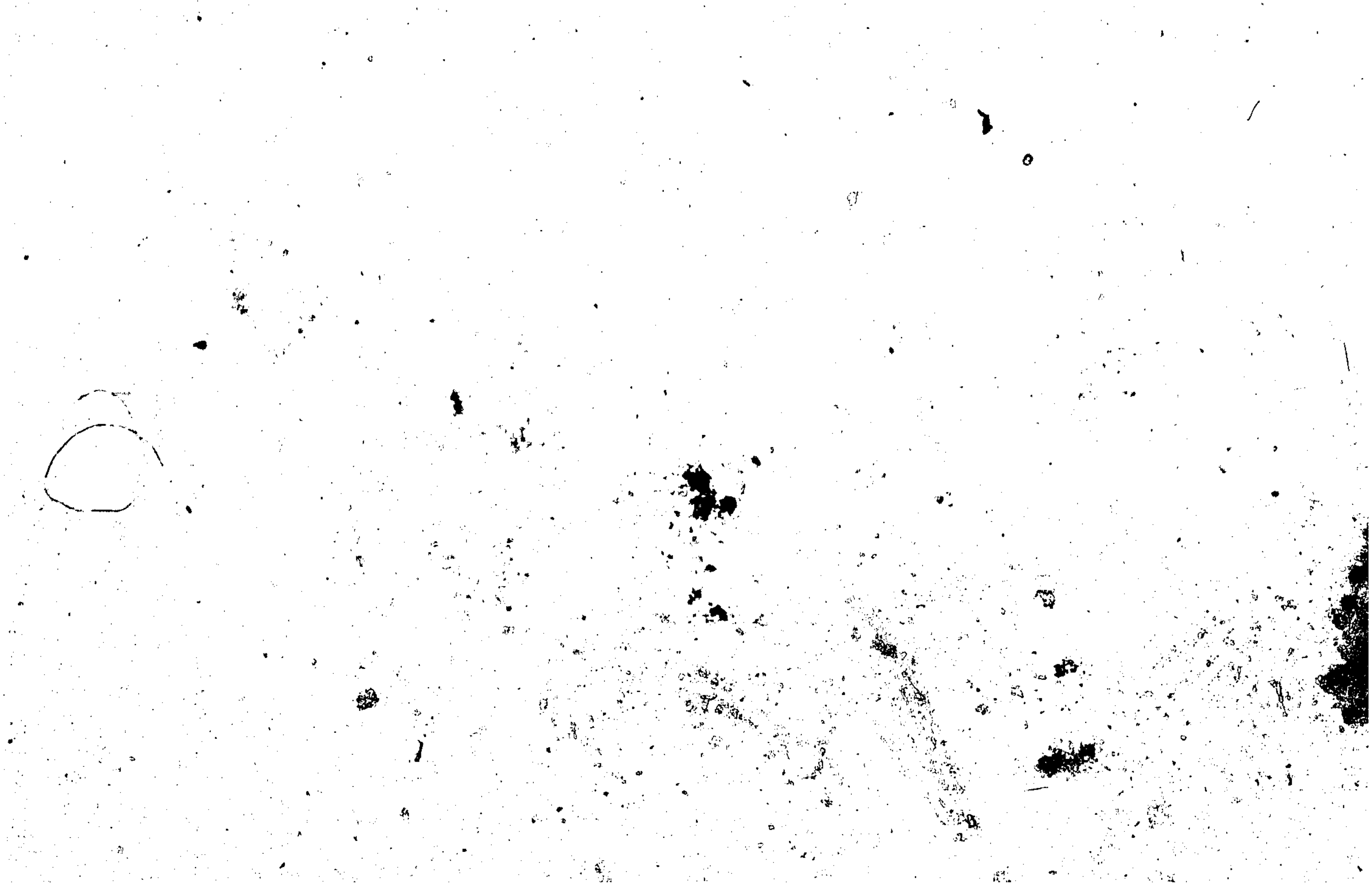

a
b
c
Archaeopelma
Paraeusandalum
Eusandalum
Chirolophus
Licrooides
Calosota
Balcha
Tanythorax
pleiomorphic state
apomorphic state (homoplasious)
apomorphic state (unique in Calosotinae)
reversal
more apomorphic 5(2)
more apomorphic 3(3a)
apomorphic 6(2c)
11(1a)
23(3)
23(2)
23(1)
22(1)
24(1)
20(2)
7(3)
3(3b)
2(3)
24(2)
22(2)
21(2)
25(2)
18(2)
14(2)
10(3a)
10(3b)
9(2a)
5(2)
5(5)
19(1)
19(2)
13(2)
21(1)
10(3)

Figure 5.2. Hypothesized cladistic relationships among genera of Metapelmatinae.



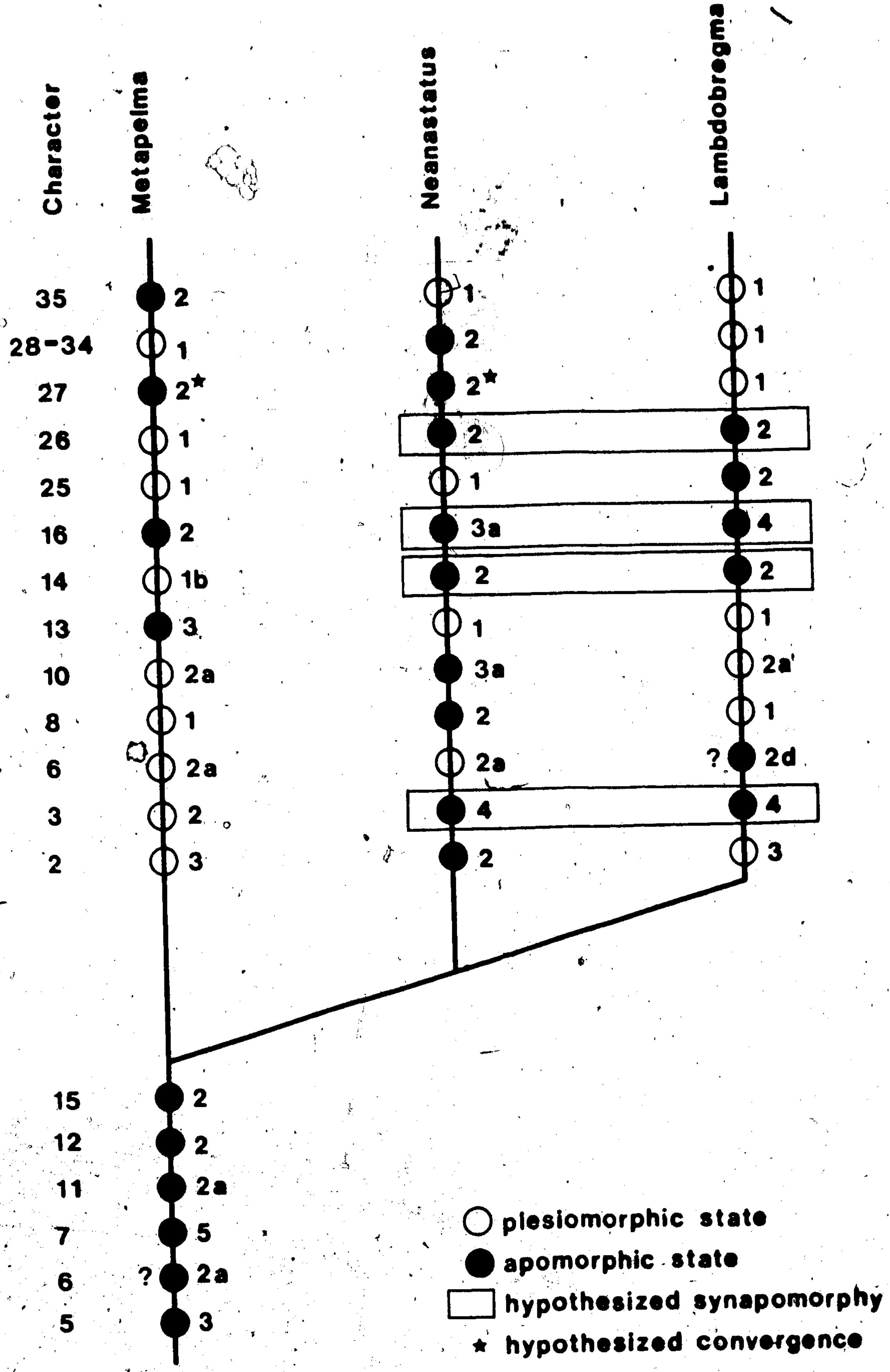

Character
Metapelma
Neanastatus
Lambdobregma
35
28-34
27
26
25
16
14
13
10
8
6
3
2
2
1
2*
1
1
2
1b
3
2a
1
2a
2
3
1
2
2*
2
1
3a
2
1
3a
2
2a
4
2
1
1
1
2
2
4
2
1
2a'
1
?
2d
4
3
15
12
11
7
6
5
2
2
2a
5
?
2a
3
○ plesiomorphic state
● apomorphic state
hypothesized synapomorphy
* hypothesized convergence

Figure 5.3. *Archaeopelma tropeotergum*, n. gen., n. sp. (♂), frontal view of head.

Figure 5.4. *Archaeopelma tropeotergum*, n. gen., n. sp. (♂), dorsal view of head.

Figure 5.5. *Eusandalum* sp. (♀), frontal view of head.

Figure 5.6. *Eusandalum* sp. (♀), lateral view of head.

Figure 5.7. *Eusandalum cyaneum* (Ashmead) (♂), frontolateral view of head.

Figure 5.8. *Licrooides umbilicatus*, n. gen., n. sp. (♂), frontolateral view of head.

Figure 5.9. *Licrooides umbilicatus*, n. gen., n. sp. (♂), dorsal view of head.

Figure 5.10. *Balcha cylindrica* Walker (♀), frontal view of head.

Scale bar = x100 μm. Illustrated measurements defined in section 5.3.2.1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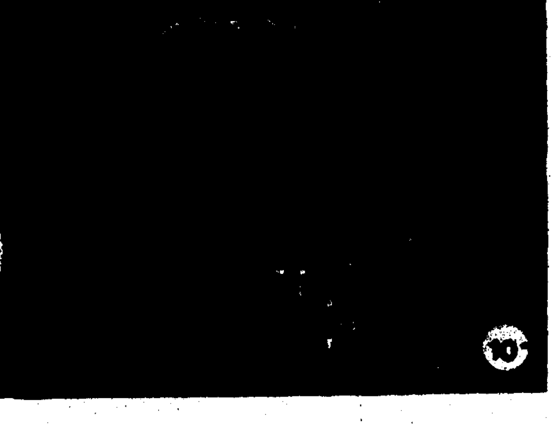
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Figure 5.11. *Calosota metallica* Gahan (♀), frontolateral view of head.

Figure 5.12. *Calosota* sp. (♀), frontolateral view of head.

Figure 5.13. *Neanastatus* sp. (♀), frontolateral view of head.

Figure 5.14. *Metapelma spectabile* Westwood (♀), frontolateral view of head.

Figure 5.15. *Lambdobregma schwarzii* (Ashmead) (♀), frontal view of head.

Figure 5.16. *Lambdobregma schwarzii* (Ashmead) (♀), lateral view of head.

Figure 5.17. *Archaeopelma tropeotergum*, n. gen., n. sp. (♂), dorsal view of mesosoma.

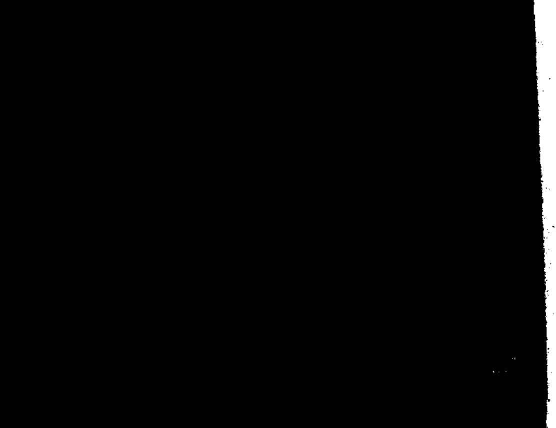
Figure 5.18. *Licrooides umbilicatus*, n. gen., n. sp. (♂), dorsal view of mesosoma.

Scale bar = x100 μm. not = notaulus.

11

carina
1
13

1
14



17

Figure 5.19. *Eusandalum* sp. (♀), dorsal view of mesosoma.

Figure 5.20. *Eusandalum cyaneum* (♂), dorsal view of mesosoma.

Figure 5.21. *Chirolophus eques* Haliday (♀), dorsal view of mesosoma.

Figure 5.22. *Calosota acron* (Walker) (♀), dorsal view of mesosoma.

Figure 5.23. *Calosota* sp. (♀), dorsal view of mesosoma.

Figure 5.24. *Calosota* sp. (♀), dorsal view of anterior of mesoscutum.

Figure 5.25. *Metapelma spectabile* Westwood (♀), dorsal view of mesosoma.

Figure 5.26. *Metapelma spectabile* Westwood (♀), dorsolateral view of mesosoma.

Scale bar = x100 μm. Illustrated measurements defined in section 5.3.2.1. **axc** = axillar carina, **das** = dorsal axillar surface, **no**$_3$ = metanotum, **not** = notaulus, **pl** = parapsidal line, **pro** = propodeum, **scl** = scutellum, **sss** = scutoscutellar suture.

Figure 5.27. *Lambdobregma schwarzii* (Ashmead) (♀), dorsal view of mesosoma.

Figure 5.28. *Lambdobregma schwarzii* (Ashmead) ([illegible]), dorsolateral view of scutellum-propodeum.

Figure 5.29. *Neanastatus* sp. (♀), dorsolateral view of scutellum-propodeum.

Figure 5.30. *Neanastatus* sp. (♀), posterior view of scutellum-propodeum (mesonotum flexed).

Figure 5.31. *Tanaostigmoides howardii* Ashmead (♀), dorsal view of mesosoma (mesonotum unflexed).

Figure 5.32. *Tanaostigm[illegible]s howardii* Ashmead (♀), dorsal view of mesosoma (mesonotum flexed).

Figure 5.33. *Cynipencyrtus flavus* Ishii (♀), dorsal view of mesosoma (mesonotum flexed).

Figure 5.34. *Manicnemius indicus* (Mani & Saraswat) (♀), dorsal view of mesosoma (mesonotum flexed).

Scale bar = x100 μm. **das** = dorsal axillar surface, **dr** = depressed ridge of scutellar-axillar complex, **mb** = membrane, **no_1** = pronotum, **no_3** = metanotum, **not** = notaulus, **pre** = prepectus, **pro** = propodeum, **scl** = scutellum.

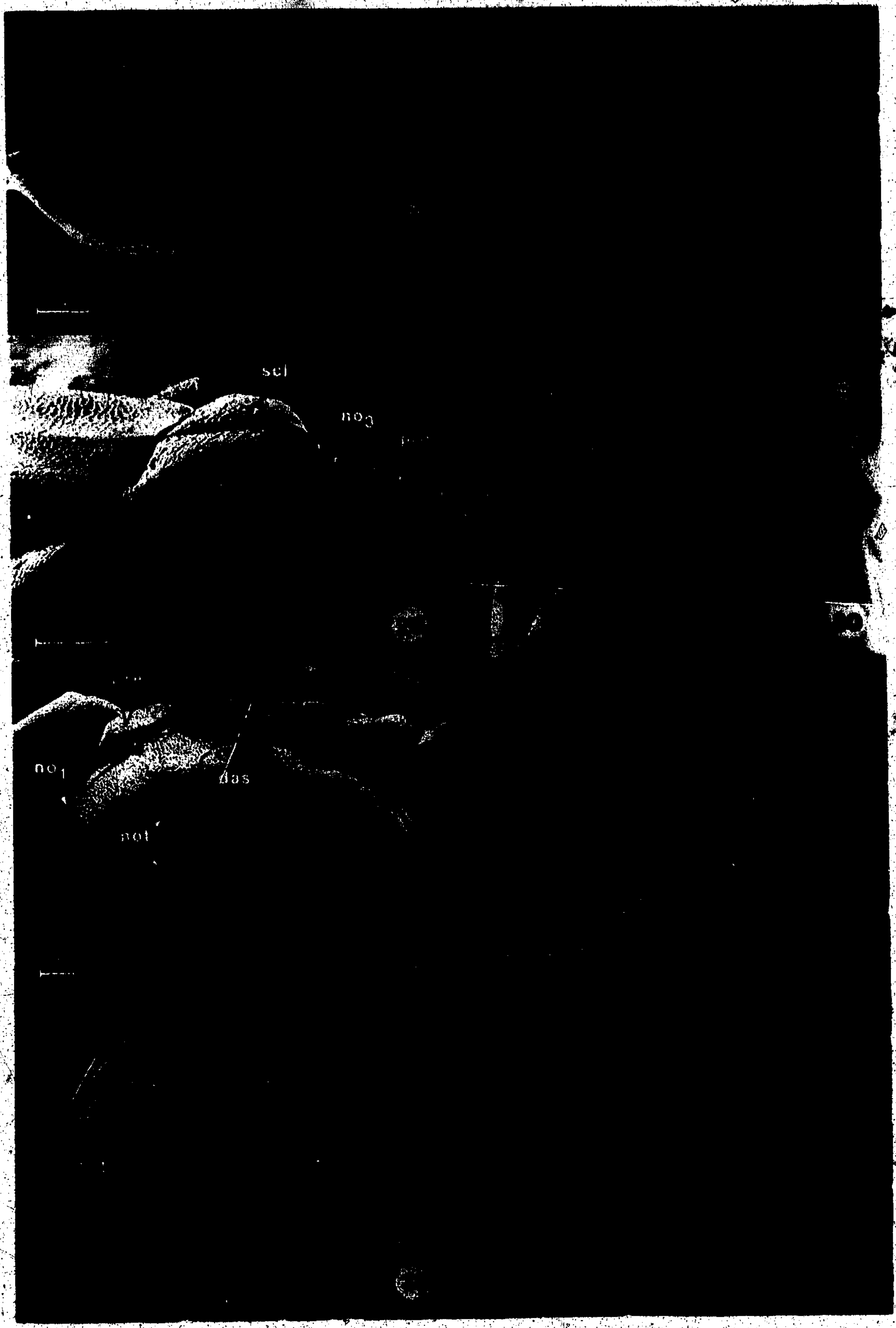

scl
no_3
no_1
das
not

Figure 5.35. *Charitopus* sp. (♀), dorsal view of mesosoma (mesonotum unflexed).

Figure 5.36. *Charitopus* sp. (♀), dorsal view of mesosoma (mesonotum flexed).

Figure 5.37. *Coccobius* sp. (♀), dorsal view of mesosoma (mesonotum flexed).

Figure 5.38. *Arachnophaga picea* (Howard) (♀), dorsal view of mesosoma (mesonotum unflexed).

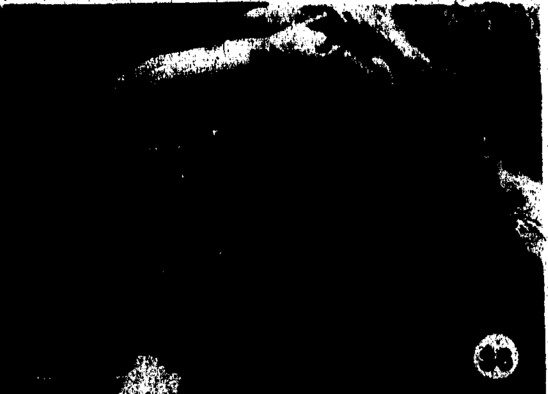
Figure 5.39. *Brasema* sp. (♂), dorsal view of mesosoma.

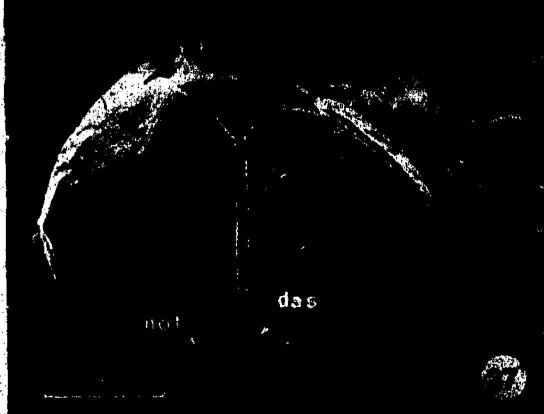
Figure 5.40. *Lysisca* sp. (♀), dorsal view of mesosoma.

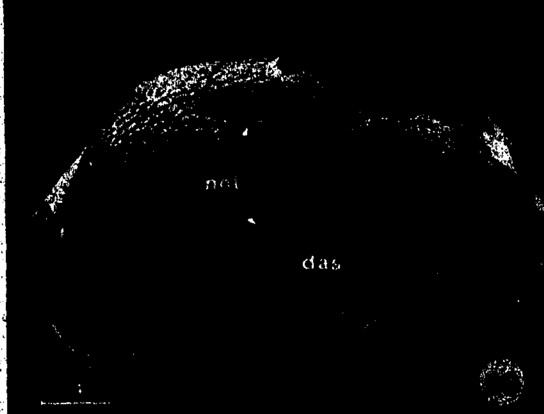
Figure 5.41. *Brasema* sp. (♂), lateral view of mesosoma.

Figure 5.42. *Lysisca* sp. (♀[illegible]ral view of mesosoma.

Scale bar = x100 μm. **ac** = acropleuron, **acs** = acropleural sulcus, **das** = dorsal axillar surface, **dr** = depressed ridge of scutellar-axillar complex, **epm$_2$** = mesepimeron, **eps$_2$** = mesepisternum, **lepm$_2$** = lower mesepimeron, **mb** = membrane, **not** = notaulus, **pl** = parapsidal line, **pls$_2$** = mesopleural suture, **tps** = transepimeral sulcus, **uepm$_2$** = upper mesepimeron.




das
not


not
das

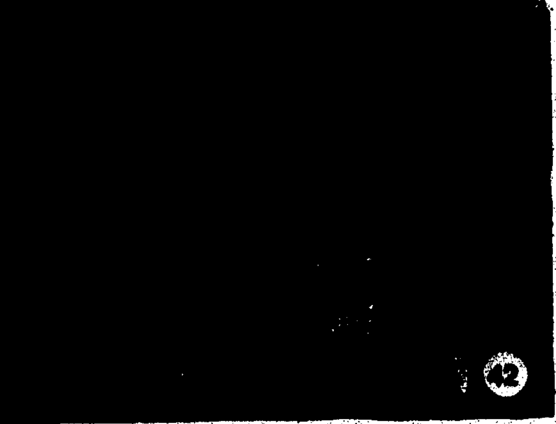

42

Figure 5.43. *Archaeopelma tropeotergum* n. gen., n. sp. (♂), lateral view of mesosoma.

Figure 5.44. *E[illegible]usandalum chiliensis* n. gen., n. sp. (♀), lateral view of mesosoma (uncoated paratype).

Figure 5.45. *Eusandalum* sp. (♀), lateral view of mesosoma.

Figure 5.46. *Eusandalum* sp. (♀), dorsal view of anterior of mesoscutum (left mesothoracic spiracle removed).

Figure 5.47. *Chirolophus eques* Haliday (♀), lateral view of mesosoma.

Figure 5.48. *Licrooides umbilicatus* n. gen., n. sp. (♂), ventrolateral view of mesosoma.

Figure 5.49. *Calosota acron* (Walker) (♀), lateral view of mesosoma.

Figure 5.50. *Calosota* sp. (♀), lateral view of mesosoma.

Scale bar = x100 μm. **acs** = acropleural sulcus, **epm$_2$** = mesepimeron, **lepm$_2$** =lower mesepimeron, **pls$_2$** = mesopleural suture, **pre** = prepectus, **sp$_2$** = mesothoracic spiracle, **tps** = transepimeral sulcus, **tss** = transepisternal sulcus, **uepm$_2$** = upper mesepimeron.

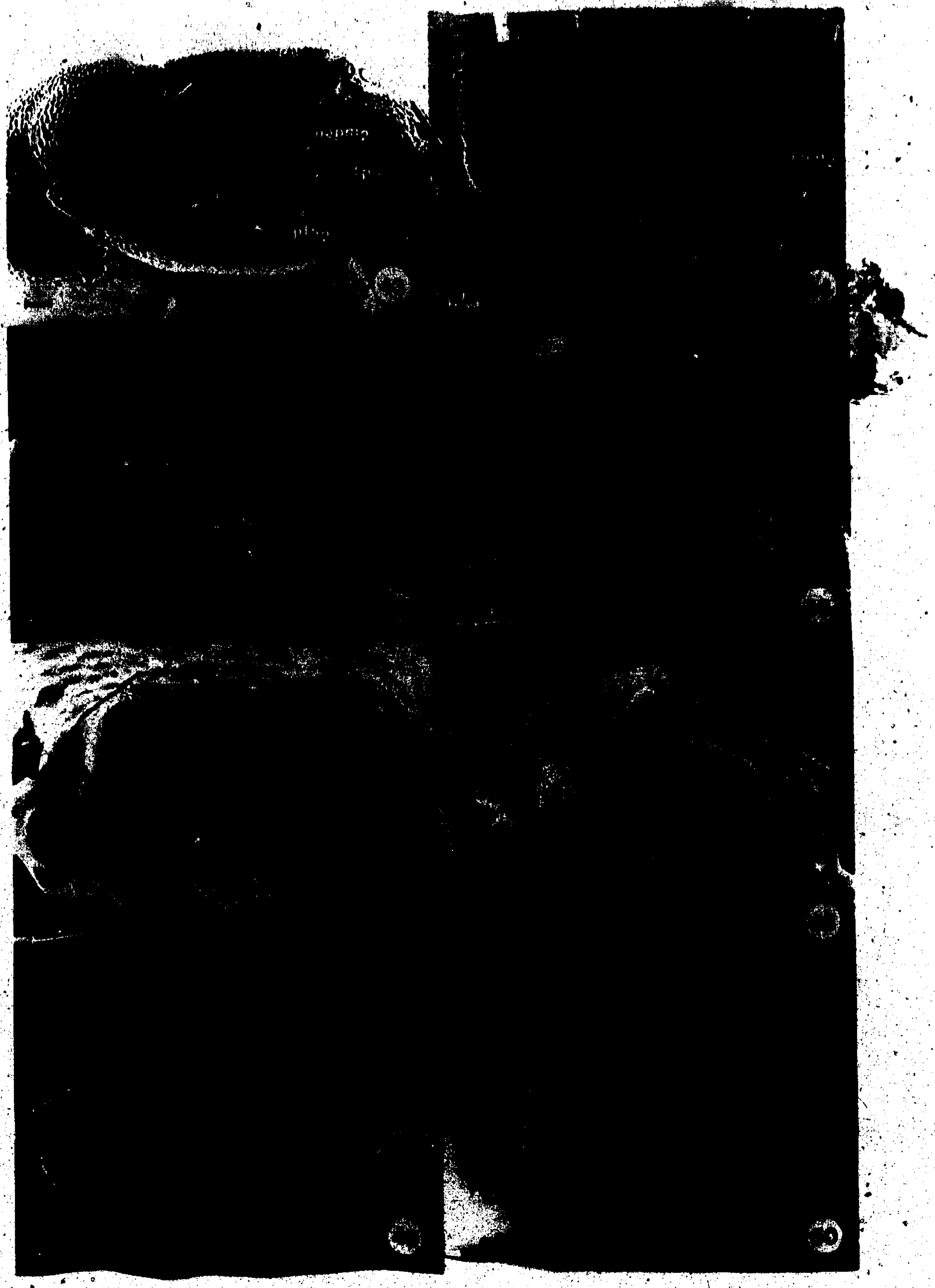


Figure 5.51. *Balcha cylindrica* Walker (♀), lateral view of mesosoma.

Figure 5.52. *Brasema* sp. (♀), lateral view of mesosoma.

Figure 5.53. *Metapelma spectabile* Westwood (♀), ventrolateral view of mesosoma.

Figure 5.54. *Neanastatus* sp. (♂), ventrolateral view of mesosoma.

Figure 5.55. *Cynipencyrtus flavus* Ishii (♀), ventrolateral view of mesosoma.

Figure 5.56. *Cynipencyrtus flavus* Ishii (♀), prepectus (pronotum removed).

Figure 5.57. *Tanaostigmodes howardii* Ashmead (♀), lateral view of mesosoma.

Figure 5.58. *Coccophagus* sp. (♀), lateral view of mesosoma.

Scale bar = x100 µm. ac = acropleuron, acs = acropleural sulcus, epm$_2$ = mesepimeron, eps$_2$ = mesepisternum, lepm$_2$ = lower mesepimeron, pre = prepectus, sp$_2$ = mesothoracic spiracle, uepm$_2$ = upper mesepimeron.

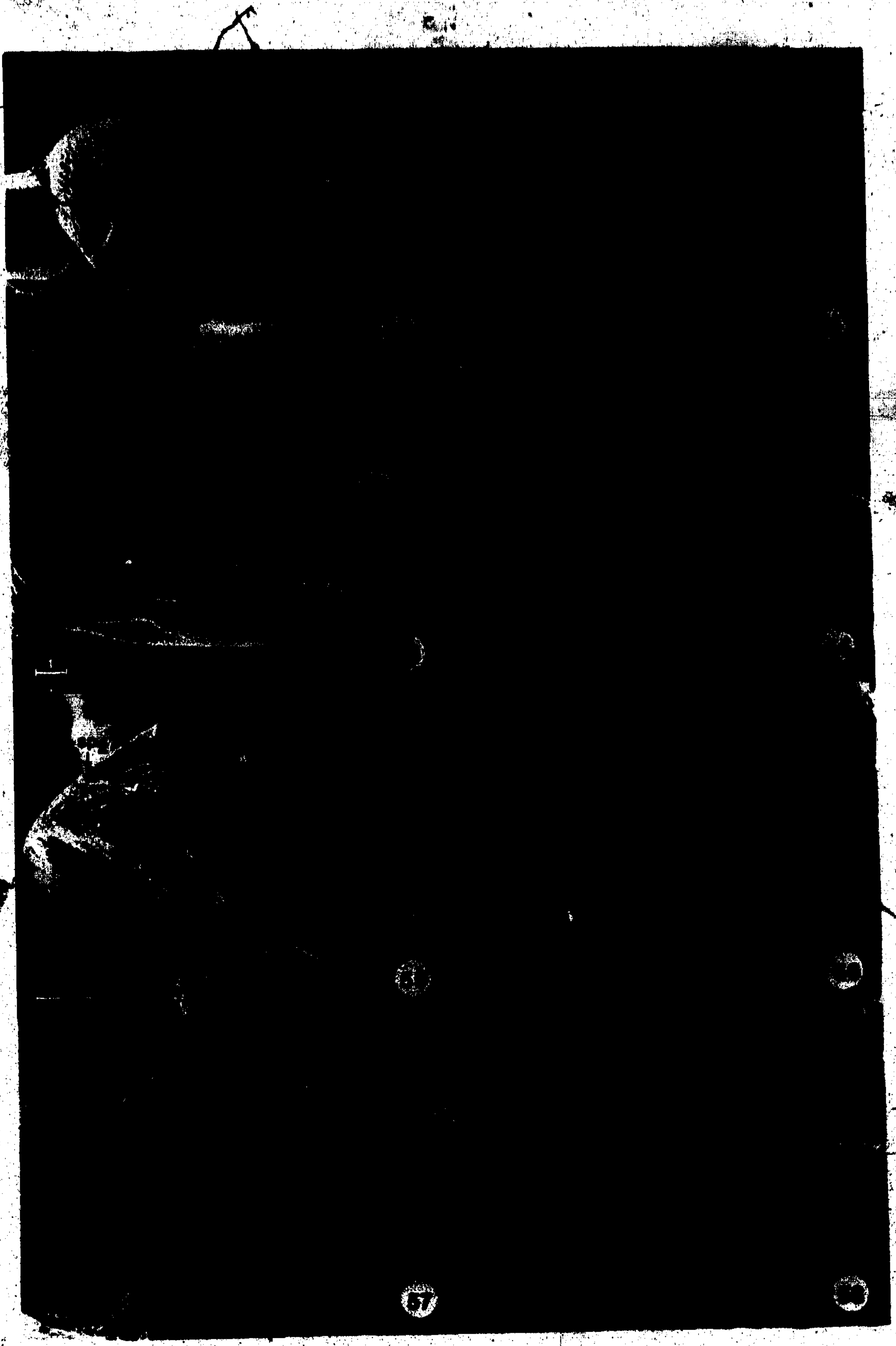


Figure 5.59. *Clausenia purpurea* Ishii (♀), lateral view of mesosoma.

Figure 5.60. *Encyrtus fuscus* (Howard) (♀), ventral view of mesosoma (prothorax, right lateral prepectal surface, and meso- and metacoxae removed).

Figure 5.61. *Encyrtus fuscus* (Howard) (♀), anterolateral view of anterior of mesoscutum (prothorax, and right prepectus and pl_2-t_2c removed).

Figure 5.62. *Licrooides umbilicatus* n. gen., n. sp. (♂), dorsal view of apex of scutellum-propodeum.

Figure 5.63. *Eusandalum* sp. (♀), dorsal view of apex of scutellum-propodeum.

Figure 5.64. *Chirolophus eques* Haliday (♀), dorsal view of apex of scutellum-propodeum.

Figure 5.65. *Calosota* sp. (♀), dorsal view of apex of scutellum-propodeum.

Figure 5.66. *Balcha cylindrica* Walker (♀), dorsal view of apex of scutellum-propodeum.

Scale bar = x100 μm. **ac** = acropleuron, **cx_2** = mesocoxa, **icm** = intercoxal membrane, **msp** = mesoscutal process for pl_2-t_2 muscle, **mtp** = mesotrochantinal plate, **pre** = prepectus, **prs** = prepectal strut, **rsp** = resilin pad of pl_2-t_2 muscle, **sp_2** = mesothoracic spiracle.

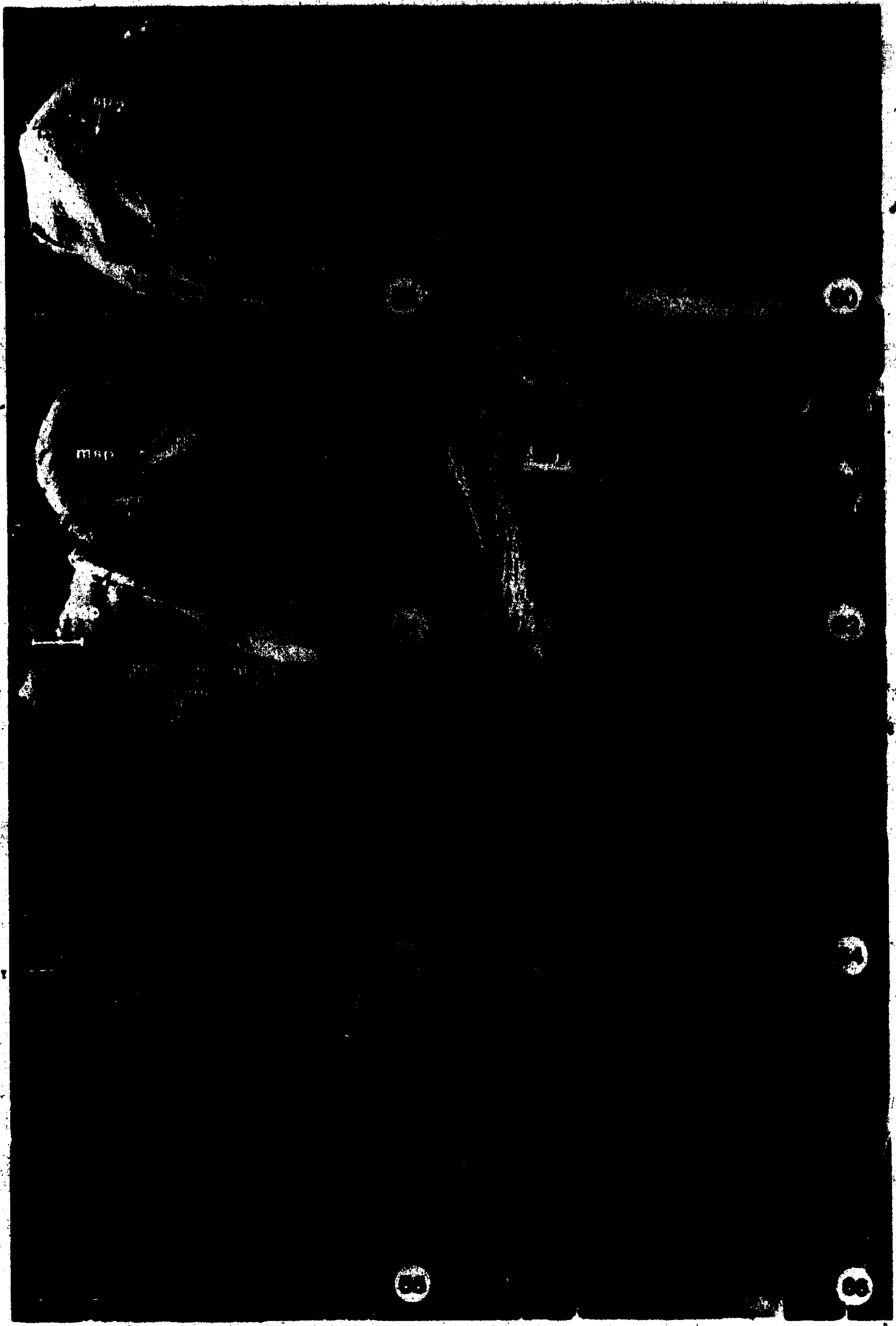

msp

Figure 5.67. *Eusandalum* sp. (♀), ventral view of mesosoma.

Figure 5.68. *Lambdobregma schwarzii* (Ashmead) (♀), ventral view of mesoso[illegible]

Figure 5.69. *Metapelma spectabile* Westwood (♀), ventral view of mesosoma.

Figure 5.70. *Neanastatus* sp. (♂), ventral view of mesosoma.

Figure 5.71. *Tanaostigmodes albiclavus* Girault (♀), ventral view of mesosoma.

Figure 5.72. *Cynipencyrtus flavus* Ishii (♀), ventral view of mesosoma.

Figure 5.73. *Manicnemius indicus* (Mani & Saraswat) (♀), ventral view of mesosoma.

Figure 5.74. *Clausenia purpurea* Ishii (♀), ventral view of mesosoma.

Scale bar = x100 μm. acs = acropleural sulcus, no$_1$ = pronotum, pre = prepectus, tss = transepisternal sulcus.

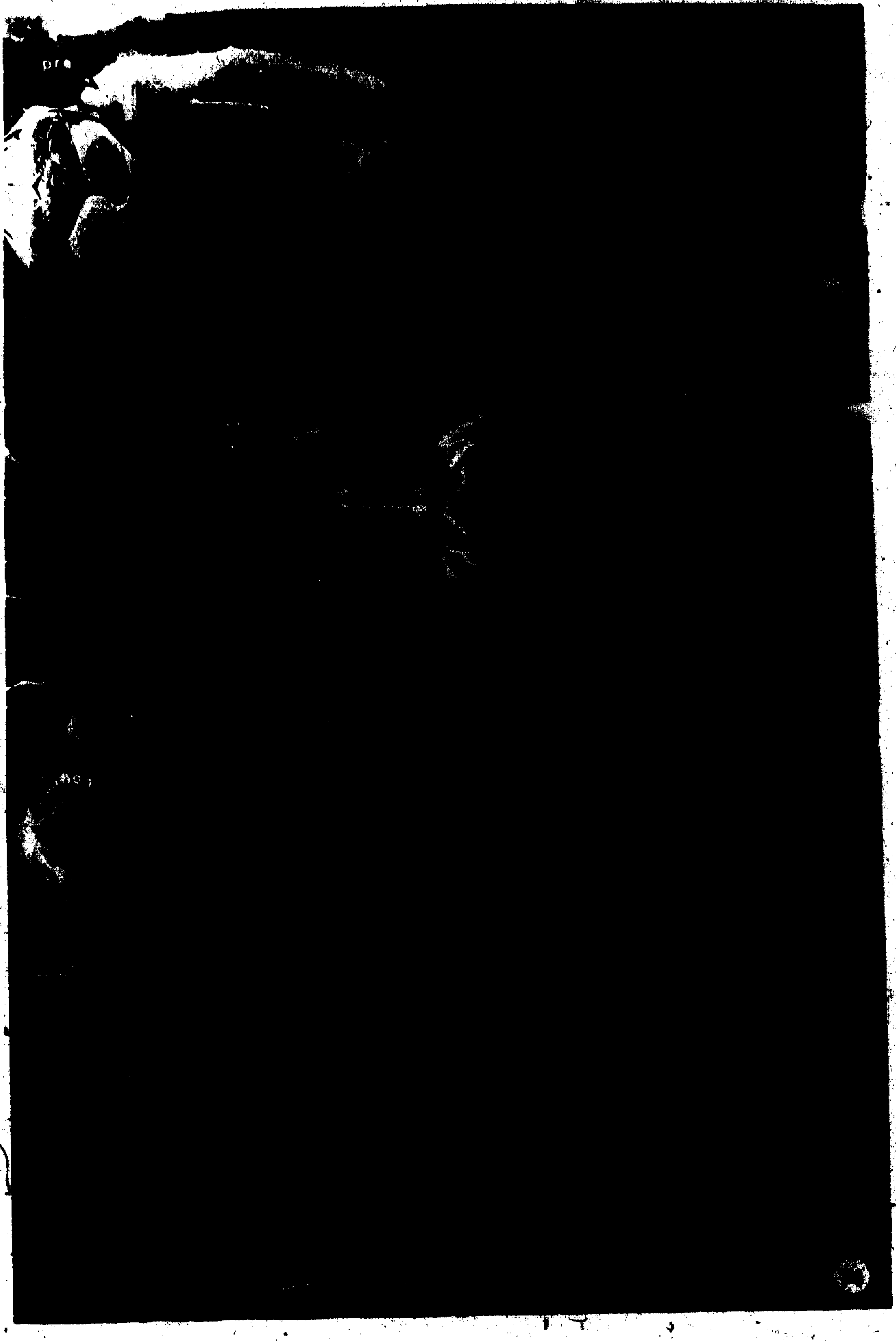

pre
no

Figure 5.75. *Archaeopelma tropeotergum* n. gen., n. sp. (♂), ventral view of mesosopleural-mesocoxal articulation.

Figure 5.76. *Licrooides umbilicatus* n. gen., n. sp. (♂), ventral view of mesosopleural-mesocoxal articulation.

Figure 5.77. *Calosota metallica* Gahan (♀), ventral view of mesosopleural-mesocoxal articulation.

Figure 5.78. *Eupelmus* sp. (♀), ventral view of mesosopleural-mesocoxal articulation.

Figure 5.79. *Brasema* sp. (♀), ventral view of mesosopleural-mesocoxal articulation.

Figure 5.80. *Coccobius* sp. (♀), ventral view of mesosopleural-mesocoxal articulation.

Figure 5.81. *Epistenia* sp. (♀), posteroventral view of mesotrochantinal plate.

Figure 5.82. *Heydenia unica* Cook & Davis (♀), posteroventral view of mesotrochantinal plate.

Scale bar = x100 μm. cx_2 = mesocoxa, icm = intercoxal membrane, mb = membrane, mtl = mesotrochantinal lobe, mtp = mesotrochantinal plate, st_3 = metasternum.

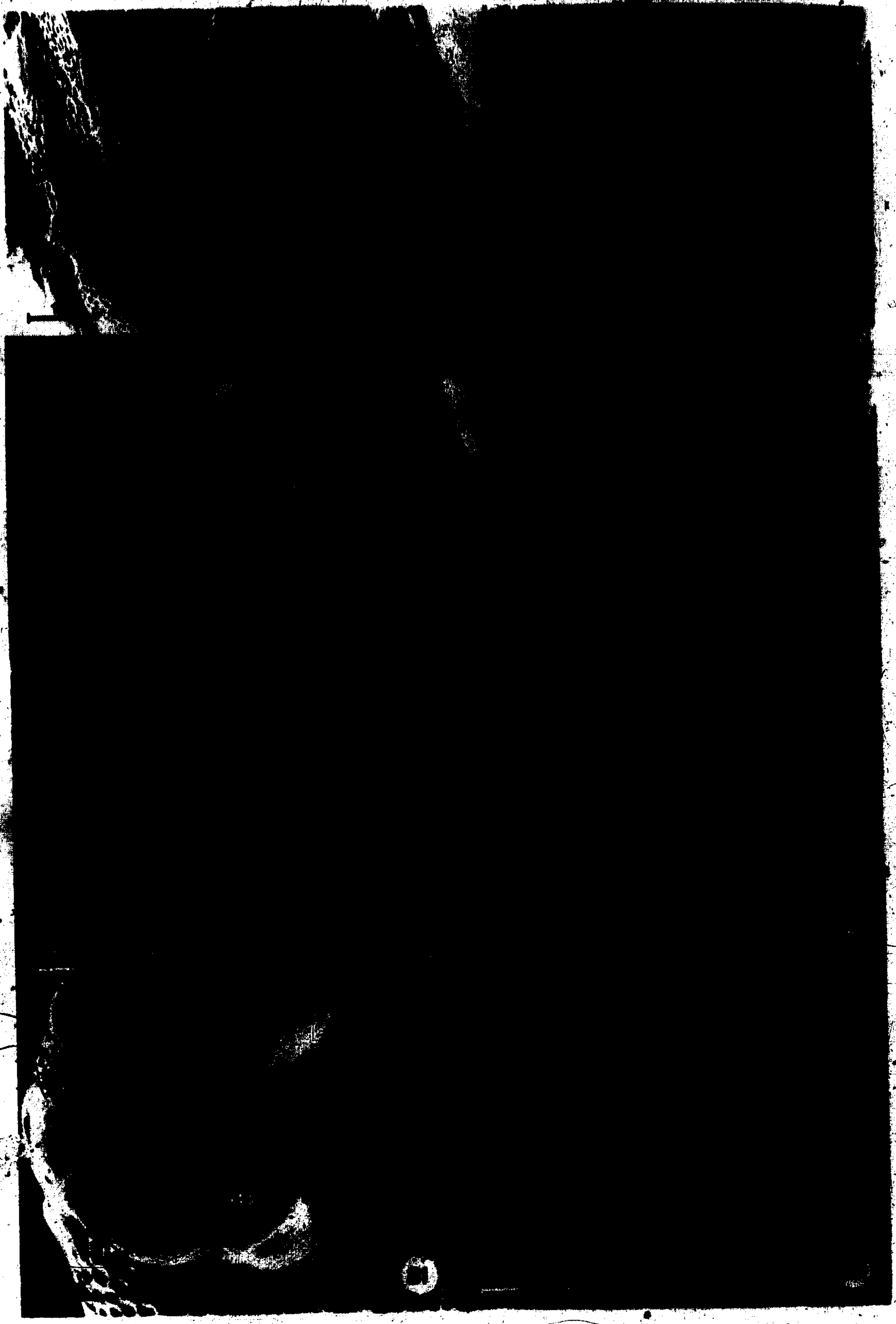


Figure 5.83. *Brasema* sp. (♂), posteroventral view of mesotrochantinal plate.

Figure 5.84. *Metapelma spectabile* Westwood (♀), posteroventral view of mesotrochantinal plate.

Figure 5.85. *Lambdobregma schwarzii* (Ashmead) (♀), ventral view of mesotrochantinal plate.

Figure 5.86. *Neanastatus* sp. (♀), ventral view of mesotrochantinal plate.

Figure 5.87. *Cynipencyrtus flavus* Ishii (♀), posteroventral view of mesotrochantinal plate.

Figure 5.88. *Archaeopelma tropeotergum* n. gen., n. sp. (♂), protibia.

Figure 5.89. *Eusandalum* sp. (♀), apex of protibia.

Figure 5.90. *Brasema* sp. (♂), anteroventral view of mesotarsus.

Scale bar = x100 μm. **ac** = acropleuron, **icm** = intercoxal membrane, **mtp** = mesotrochantinal plate, **pap** = protibial apical pegs, **pdp** = protibial dorsal pegs, **st$_3$** = metasternum.

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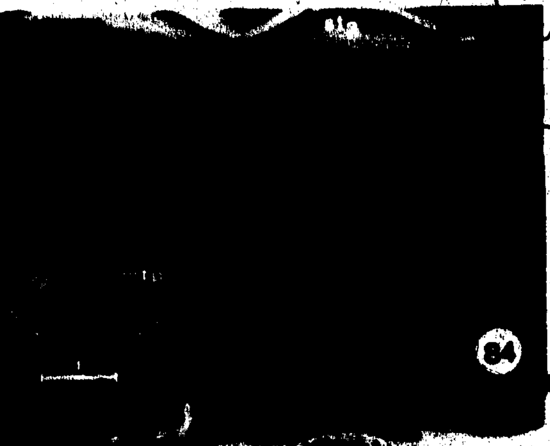

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Figure 5.91. *Archaeopelma tropeotergum* n. gen., n. sp. (♂), anteroventral view of mesotarsus.

Figure 5.92. *Eusandalum* sp. (♀), anterolateral view of mesotarsus.

Figure 5.93. *Licrooides umbilicatus* n. gen., n. sp. (♂), anteroventral view of mesotarsus.

Figure 5.94. *Metapelma spectabile* Westwood (♀), anteroventral view of mesotarsus.

Figure 5.95. *Tanaostigmodes albiclavus* Girault (♀), posteroventral view of mesotarsus.

Figure 5.96. *Cynipencyrtus flavus* Ishii (♀), anteroventral view of mesotarsus.

Figure 5.97. *Macroneura vesicularis* (Retzius) (♀), anteroventral view of mesotarsus.

Figure 5.98. *Eupelmus* sp. (♀), anteroventral view of mesotarsus.

Scale bar = x100 μm. [Arrow-heads indicate location of pegs along posterior edge of mesotarsus in Fig. 5.96.]

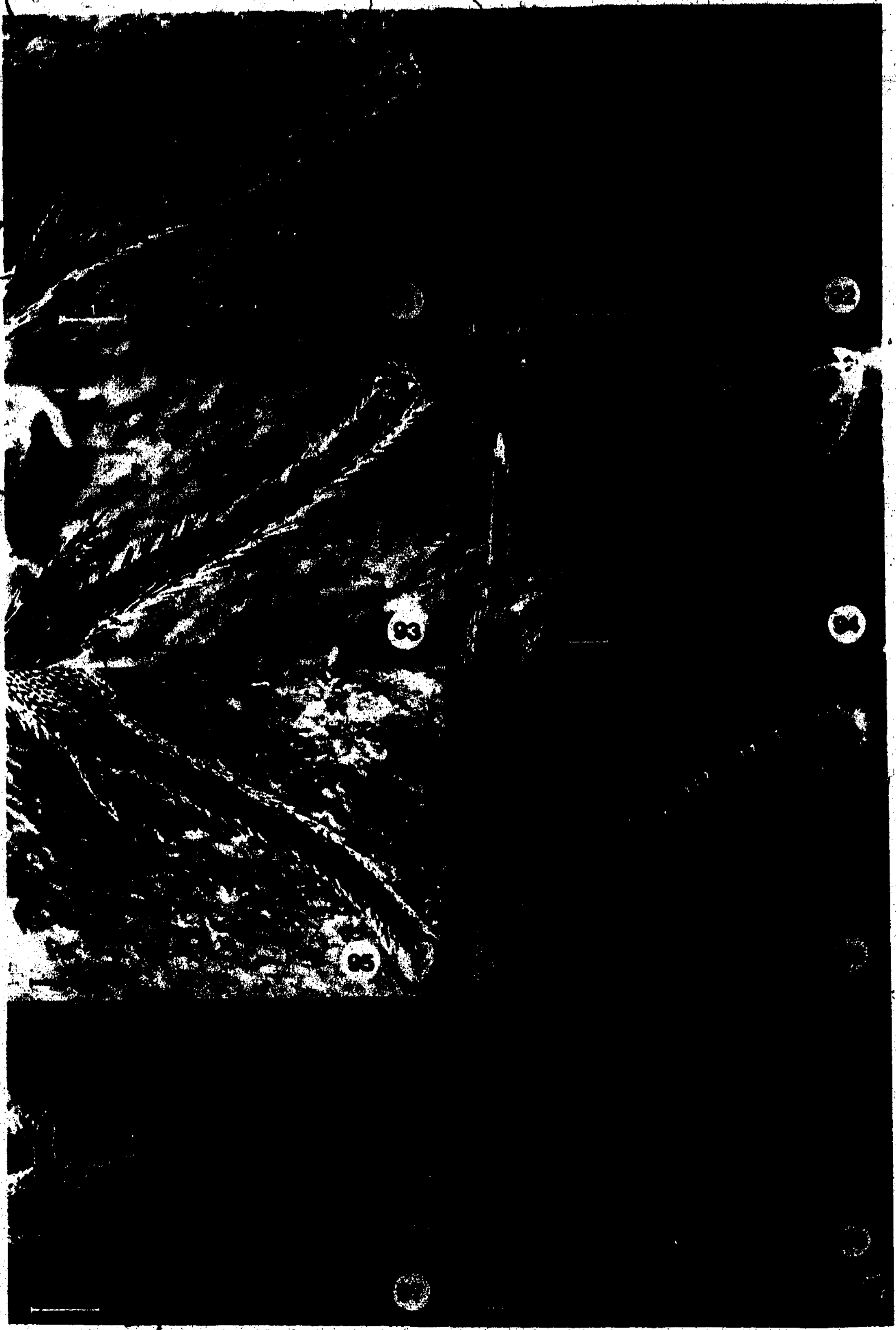

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Figure 5.99. *Epistenia* sp. (♀), sagittal section of mesosoma showing t_2-tr_2.

Figure 5.100. *Eusandalum* sp. (♀), sagittal section of mesosoma showing t_2-tr_2.

Figure 5.101. *Metapelma spectabile* Westwood (♀).

a. outer view of t_2-tr_2.

b. outer view of axillar plate.

Figure 5.102. *Metapelma spectabile* Westwood (♀), inner (sagittal) view of axillar plate and t_2-tr_2.

Figure 5.103. *Neanastatus* sp. (♀), inner (sagittal) view of t_2-tr_2.

Figure 5.104. *Lambdobregma schwarzii* (Ashmead) (♀), inner (sagittal) view of t_2-tr_2.

Figure 5.105. *Eupelmus* sp. (♀), sagittal section of mesosoma showing t_2-tr_2.

Figure 5.106. *Encyrtus fuscus* (Howard) (♀), sagittal section of mesosoma showing t_2-tr_2.

Scale bar = x100 μm. **axp** = axillar phragma, **axpl** = axillar plate, **cx_2** = mesocoxa, **las** = lateral axillar surface, **pdl** = pedicel of mesotergal-mesotrochantinal muscle, **prs** = prepectal strut, **t_2-tr_2** = mesotergal-mesotrochantinal muscle: **a** - from dorsal axillar surface, **b** - from axillar phragma.

Figure 5.107. *Tanaostigmodes howardii* Ashmead (♀), dorsolateral view of apex of metasoma.

Figure 5.108. *Metapelma spectabile* Westwood (♀), lateral view of apex of metasoma.

Figure 5.109. *Eusandalum* sp. (♀), lateral view of apex of metasoma.

Figure 5.110. *Chirolophus eques* Haliday (♀), lateral view of apex of metasoma.

Figure 5.111. *Eupelmus* sp. (♀), posterolateral view of apex of metasoma (Mt6 distended).

Figure 5.112. *Eupelmus* sp. (♀), posterolateral view of apex of metasoma.

Scale bar = x100 μm. Illustrated measurements defined in section 5.3.2.1. cer = cercus, Mt = metasomal tergum, sp = metasomal spiracle, syn = syntergum.

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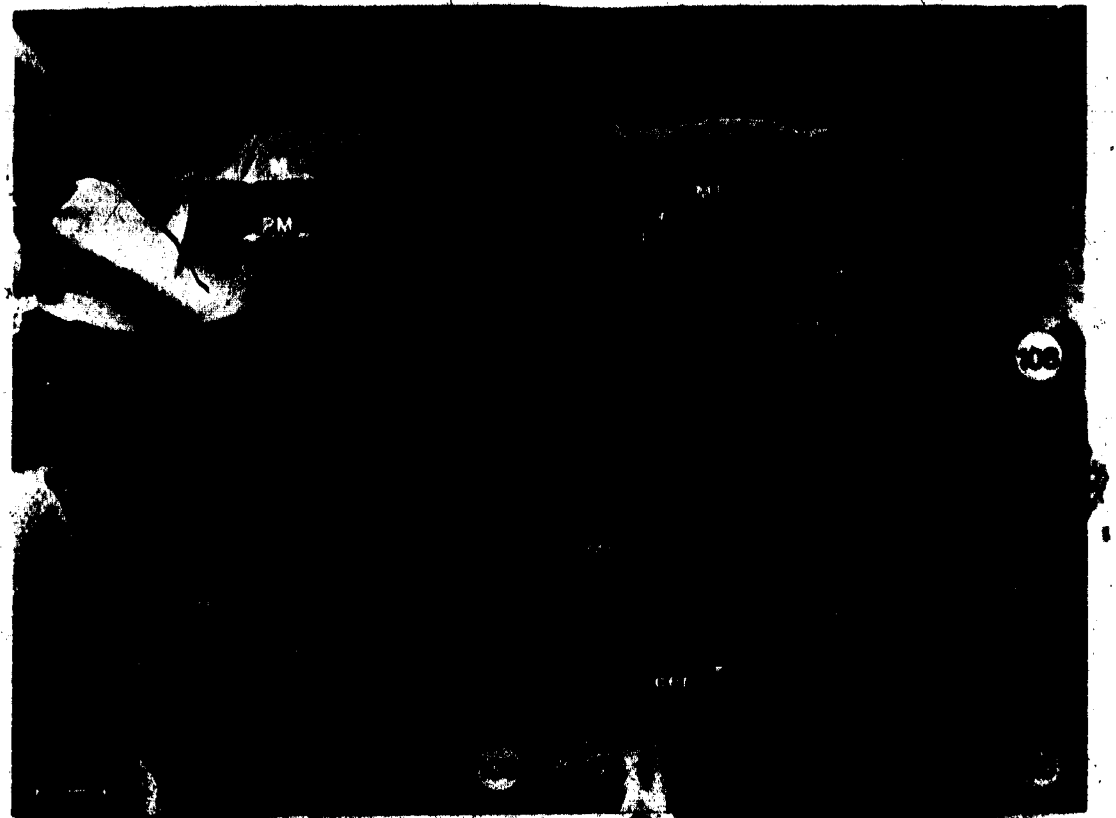

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6. CONCLUSION

Snodgrass (1928, p 2) noted that "it is regrettable that we must arrive at understanding of things by way of the human mind ... we can only hold opinions or build theories as to the course of events that have preceded us upon the earth. Knowledge advances by what biologists call the method of trial and error, but the mind can not rest without conclusions. Most conclusions, therefore, are premature and consequently either wrong or partly wrong, and once in every generation, or sometimes twice, reason back tracks and takes a new start at a different angle, which eventually leads to a new error. By a zigzag course, however, progress is slowly achieved. Error, then, is a byproduct of mental growth. It is not a misdemeanor in scientific research unless the erring [is of clinging] to his position when he should see its weakness".

I have attempted to investigate phylogenetics of eupelmids by "back tracking", and hopefully am not too guilty of "erring". Unfortunately, present knowledge of systematics of Chalcidoidea, and Hymenoptera, often is sufficent to recognize "weaknesses" in higher classification, but not to indicate better solutions. Classifications are the foundation for storage and retrieval of information, hence they must be relatively stable for effective communication. Since writing the four chapters of this thesis, a new family of Hymenoptera, Peradeniidae (Aprocrita: Proctotrupoidea *s. l.*), has been described from Australia (Naumann and Masner 1985); I have received three males from Nepal that represent a fourth genus of Metapelmatinae; and I have correspondence from John Noyes [British Museum (Nat. Hist.)] stating that he has specimens from Zimbabwe that represent an undescribed genus "which seems to be intermediate between *Cynipencyrtus* and tanaostigmatines proper". These illustrate that none of the studies presented are complete or "final" works. Many character systems are yet to be studied and many taxa are yet to be discovered that will modify present hypotheses of the evolutionary history of Chalcidoidea and Hymenoptera. Our aim should be ultimate accuracy, and hence stability of classification of Hymenoptera based on documented hypotheses of relationships, not the presentation of new classifications with each new analysis. This philosophy may be construed as "clinging" to traditional concepts, but it is necessary if taxonomy is to function as a science.

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