SYSTEMATICS OF LITTLE KNOWN PARASITIC WASPS OF THE FAMILY RHOPALOSOMATIDAE (HYMENOPTERA: VESPOIDEA)

by

Antonia Elena Guidotti

A thesis submitted in conformity with the requirements
for the degree of Master of Science
Graduate Department of Zoology
University of Toronto

©Copyright by Antonia Elena Guidotti 1999

National Library of Canada

Acquisitions and Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada

Acquisitions et services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-46189-0

Canada

SYSTEMATICS OF LITTLE KNOWN PARASITIC WASPS OF THE FAMILY RHOPALOSOMATIDAE (HYMENOPTERA: VESPOIDEA)

Antonia Elena Guidotti, Master of Science Degree, 1999

Department of Zoology, University of Toronto

ABSTRACT

Three new species of *Paniscomima* Enderlein are described, *P. darlingi, P. angelae*, and *P. paropposita*. Descriptions of the male of *Liosphex trichopleurum* Townes and *Paniscomima seyrigi* Berland and the female of *Paniscomima opposita* Townes are provided. Keys to the genera of Rhopalosomatidae and species of *Paniscomima* and *Liosphex* Townes are also provided. A cladistic analysis of the Rhopalosomatidae (Hymenoptera: Vespoidea) was performed to test the monophyly of the family, the monophyly and relationships of included genera and to determine the relationships between the species of the genus *Paniscomima*. Sixty-three morphological characters were used in the analysis. Exemplars from the families Pompilidae, Bradynobaenidae and Sierolomorphidae were used as outgroups. The phylogenetic analysis supports: (1) the monophyly of the Rhopalosomatidae; (2) a monophyletic extant macropterous branch of rhopalosomatids; (3) the sister relationship of *Liosphex* to *Rhopalosoma/Paniscomima* and; (4) the monophyly of each of *Olixon, Liosphex*, and *Rhopalosoma*. This study questions the monophyly of *Paniscomima*.

ACKNOWLEDGEMENTS

Thanks to all the institutions who loaned specimens for this project. Particularly helpful were John Huber at CNCI, Matt MacGowan at Mississippi State and David Wahl at AEIC.

Thanks to my supervisor D.C. Darling and adjunct supervisor D.C. Currie for their support and guidance through the duration of this work. I have relied on their expertise more times than I can count. This work was supported in part by an NSERC operating grant to D.C. Darling. Thanks to my committee members Darryl Gwynne and Jim Rising of the Department of Zoology, University of Toronto.

It has been an honour to be a part of the Royal Ontario Museum during this time. The accessibility of the insect collection was invaluable. The resourceful librarians meant I rarely had to leave the building. The security guards were most helpful when I locked myself out. The Centre for Biodiversity and Conservation Biology made it possible to discuss similar problems with others working on less interesting taxa. It was nice to have people around who could make you laugh and whom you could talk to at lunch. Thanks to Amy Lathrop, Tanya Trépanier, Raoul Bain and Brad Hubley. Thanks to Francesco Santini for his comments on the manuscript and discussions on biodiversity.

For artistic counsel and for reminding me that it's O.K. to ask questions, thank you Cara Gibson. For answering all of those innumerable questions, for being the best sounding board, and for editing early versions of this manuscript, Andy Bennett. I can't thank you enough for asking me those questions that I couldn't answer (now I mostly can!).

For being a good friend, soccer mate and keeping my spirits up during the course of this project, thanks to Christina Canil.

Thanks to John Swann for finding more specimens, and allowing me to learn from his

experience.

For technical artistic help and for making me see things a little differently, thanks to Patrice Stephens-Bourgeault.

Thanks to Charmaine Condy, whose strong spirit and positive attitude always lifted me.

Thanks to the Romulan volleyball team, you know who you are, I had fun.

Thanks to my family, who never really has figured out exactly what I've been doing ("playing with bugs"), but supports me none-the-less.

I would like to dedicate this work to my husband Chris Walton, whose dedication to his own work makes me proud, who tolerated my late nights and whose support throughout this project meant I was able to complete it.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF APPENDICES

1. INTRODUCTION

1.1 TAXONOMY

The Rhopalosomatidae (Hymenoptera) (Fig. 1- 4) is a small family of 38 species currently classified in five genera: *Liosphex* Townes, *Olixon* Cameron, *Paniscomima* Enderlein, *Rhopalosoma* Cresson, and the fossil *Mesorhopalosoma* Darling (Townes 1977; Darling and Sharkey 1990). It is predominantly a tropical family, and recorded from Africa, Australia, the Neotropical and Nearctic regions, and Southeast Asia (Table 1); it is absent from the Palaearctic region. *Liosphex* occurs in the Philippines, Indonesia and the Neotropical and Nearctic regions from the Eastern United States to Southern Brazil. *Paniscomima* has African and Southeast Asian species while *Rhopalosoma* occurs in the Nearctic and Neotropical regions. *Olixon* species also occur in most of these areas except for Southeast Asia (excluding one record from India) and is also found in Australia. Although the family is not common in collections around the world, an increase in the use of Malaise and pitfall traps is yielding a greater number of specimens for study.

There has been very little work on either the phylogenetic affinities of the Rhopalosomatidae or on the relationships among the genera. Previous studies have attempted to determine the placement of the Rhopalosomatidae in relation to other Aculeata. Brothers (1975) placed the Rhopalosomatidae as the sister group of the Pompilidae. Brothers and Carpenter (1993), in their phylogeny of the Aculeata, proposed the Rhopalosomatidae as the sister group to the (Bradynobaenidae (Formicidae (Scoliidae, Vespidae))) clade (Fig. 5) and the genus *Olixon* was placed as the sister taxon to the rest of the rhopalosomatids. Historically, *Olixon* has also been placed in numerous different families (e.g., Ichneumonidae (Cresson 1865), Braconidae (Cameron 1887), Dryinidae (Perkins 1908), Bethylidae (Ashmead 1900, Kieffer 1911), and

Pompilidae (Reid 1939)).

The family was originally called "Rhopalosomidae" by Ashmead (1896). In stating that he preferred this form to "Rhopalosomatidae", Ashmead recognized that his term for the family was linguistically incorrect and not in accordance with the code of nomenclature; the nominative plural must be used to create a family name (ICZN 1985). Since Brues (1922), the family has been correctly referred to as the Rhopalosomatidae. The etymology for each generic name has Greek roots: *Rhopalosoma* (club-like body) (Brown 1954), *Paniscomima* (like a little god of the forests or hills) (Brown 1954), *Olixon* (to make a little less) (Jaeger 1955), *Liosphex* (smooth wasp) (Townes 1977), and *Mesorhopalosoma* which is in reference to the Mesozoic era.

The last taxonomic revision of the family was by Townes (1977). In addition to describing new species, he also examined the genus *Rhopalosoma* in detail with accompanying illustrations. Key generic and species characters, as identified by Townes, were sometimes unclear and difficult to interpret. Taxonomic work on the family since Townes has been limited to the description of a fossil genus by Darling in (Darling and Sharkey 1990). *Mesorhopalosoma* Darling was described from fossils in the Santana Formation, Lower Cretaceous (90-140 mybp), Ceará, Brazil. A revision of the Australian *Olixon* is currently being undertaken by Austin and Naumann (pers. comm.).

Recent collections from Vietnam, Malaysia and Thailand have resulted in 59 specimens of Rhopalosomatidae: 19 male and 2 female *Liosphex* from Indonesia; 6 female and 4 male *Paniscomima* from Thailand; and 25 male and 3 female *Paniscomima* from Vietnam. In addition, one female *Paniscomima* was collected from Laos. There are no previous records of either of these genera from any of these countries. A male and a female from Sri Lanka and a male from Madagascar were also examined. Three new species of *Paniscomima* are described herein and the previously unknown males of *Liosphex trichopleurum* Townes and *Paniscomima seyrigi* Berland and the previously unknown female of *P. opposita* Townes are also described. A phylogeny of the species of *Paniscomima* is proposed.

The biogeographic implications of the phylogeny with respect to the disjunct distribution of *Liosphex* are explored. One species of *Liosphex* (*L. varius*) ranges from southeastern United States to southern Brazil while the other species (*L. trichopleurum*) has been collected from Mindanao (Philippines) and Borneo (Indonesia).

1.2 BIOLOGY

There is very little known about the biology of these wasps. Two reports have identified rhopalosomatids as ectoparasitoids of crickets. Perkins (1908) reported *Harpagocryptus (=Olixon) australiae* Perkins from a trigoniidine cricket. He described the "larval sac being of the same form as that of *Aphelopus*" (a dryinid). No other description of the larva or larval sac is given. Hood (1913) reared *Rhopalosoma nearcticum* Brues (as *R. poeyi* Cresson) from a jumping tree cricket, *Orocharis saltator* Uhler (Gryllidae). The sac-like structures (Fig. 6) formed by the larvae on the abdomen of the host were described by Gurney (1953) who also found rhopalosomatid larvae on species of the gryllid *Hapithus* Uhler. The lack of host information for other species of rhopalosomatids (Table 1) precludes host-parasitoid comparisons until more biological data are available. It should be noted that the degree of endemism of the species in the Rhopalosomatidae is hard to assess because this family has not been well-collected and is poorly represented in collections.

There is also very little known about the behaviour and life history of rhopalosomatids. *Rhopalosoma* have been observed flying in a group of about 10 at twilight (H. Townes quoted in

Gurney 1953), and their large eyes and ocelli suggest that they may be nocturnal. Since *Rhopalosoma* are ectoparasitoids of crickets (that are generally more active at night), it seems logical that they may also be nocturnal. *Rhopalosoma* specimens have been collected in the U.S. from June to September (Gurney 1953). *Olixon banksii* Brues has been observed "running swiftly over sandy barrens" (Krombein 1949) and running faster than a cicindelid (M. MacGowan, pers. comm).

1.3 OBJECTIVES

Through a cladistic analysis of adult morphological characters, this study will address a number of issues on the systematics of the Rhopalosomatidae with the following specific objectives:

(1) examine the monophyly of the Rhopalosomatidae (specifically the placement of *Olixon*);

(2) determine the monophyly of the four extant genera (especially *Liosphex* which has a disjunct distribution);

(3) examine the relationships of the 10 species of *Paniscomima*.

Redescriptions of the family and genera and a taxonomic revision of *Paniscomima* and *Liosphex* are prepared. An objective of this study is also to clarify some characters and simplify species keys for *Liosphex* and *Paniscomima* and to modify the generic key for the family.

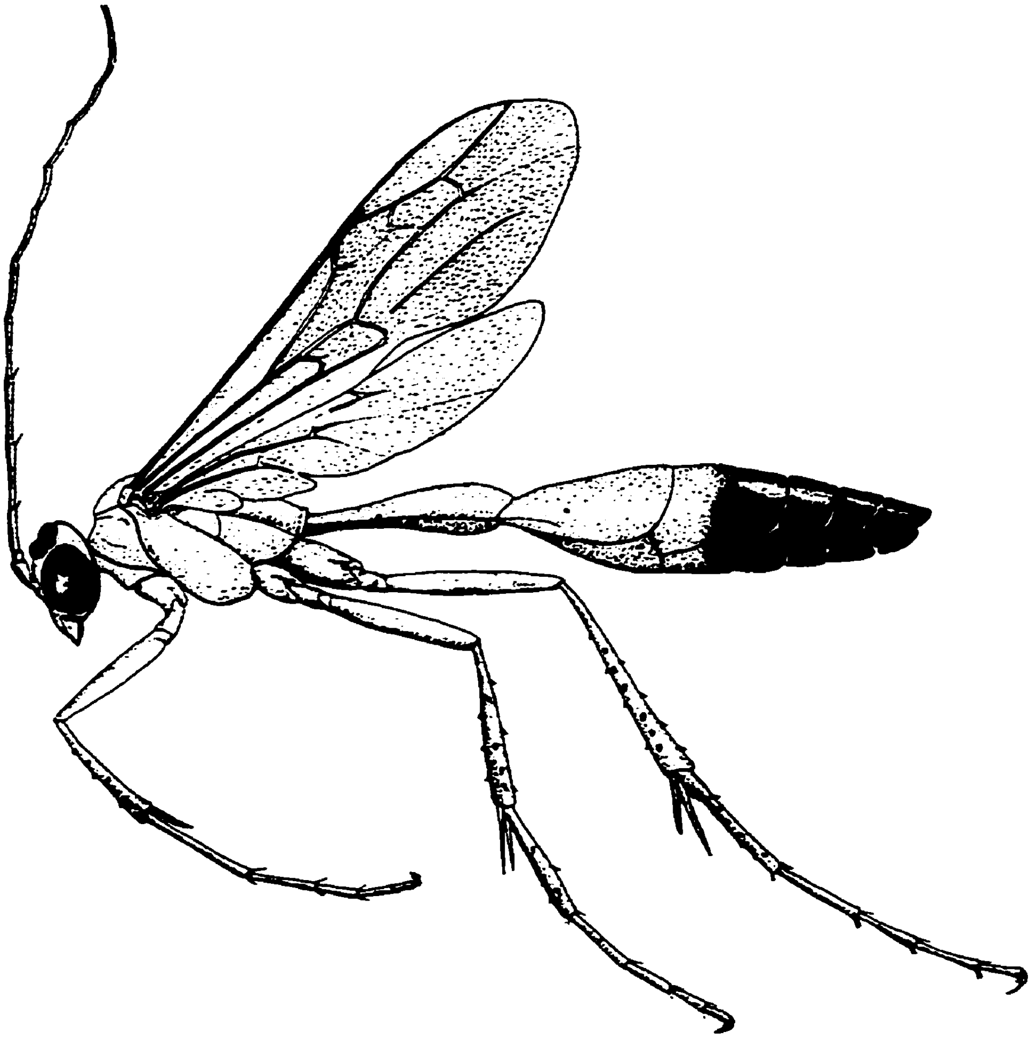

Figure 1: *Rhopalosoma sp.*, ♂. From Hanson and Gauld (1995:549).

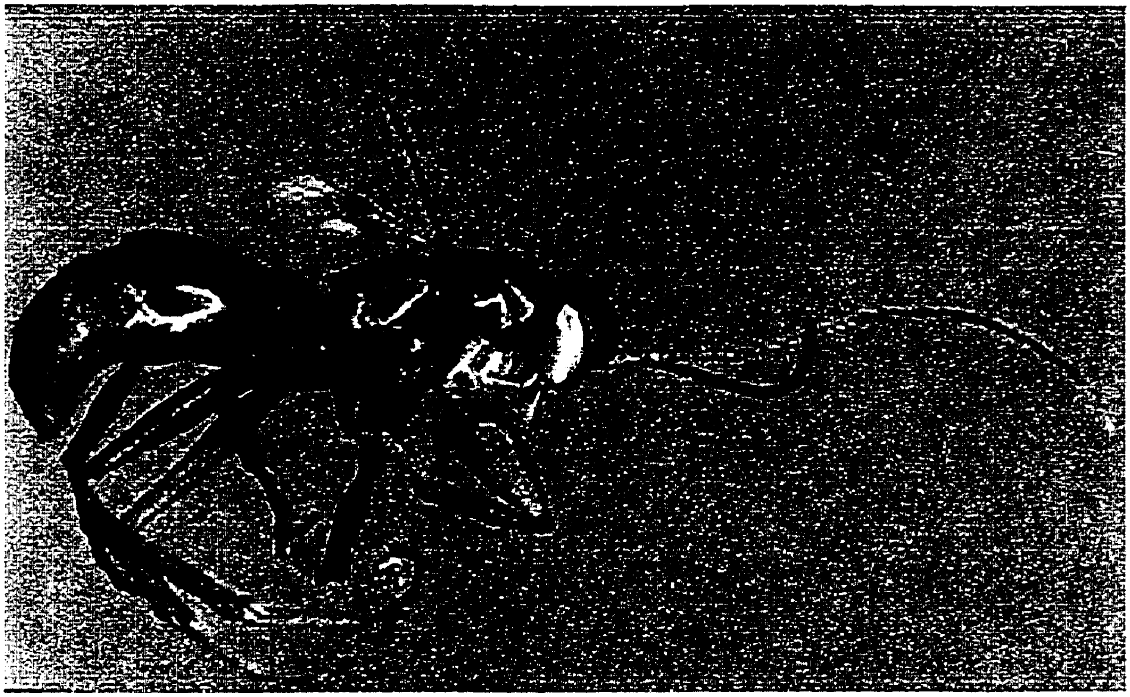

Figure 2: *Olixon testaceum* Cameron, ♀.

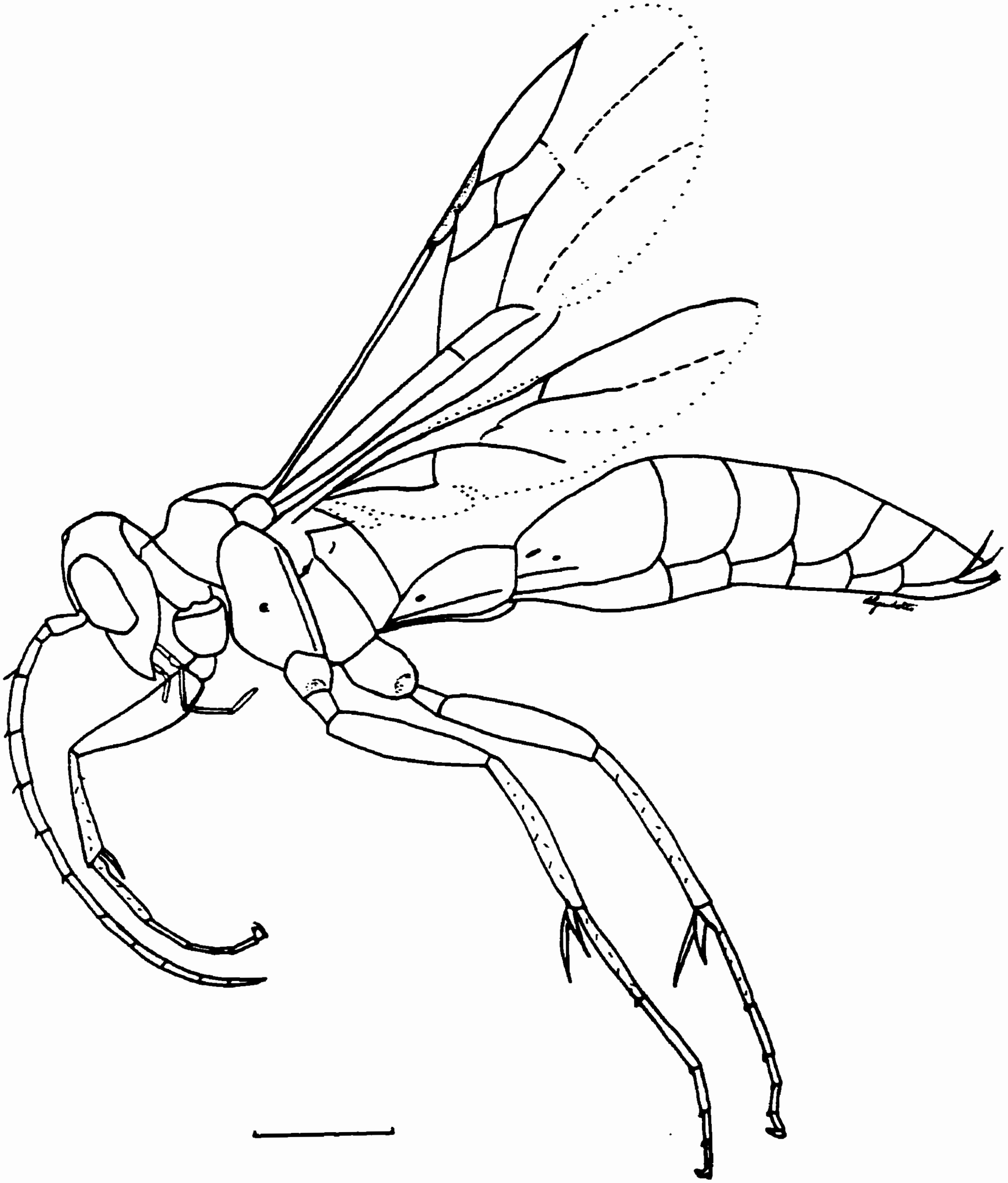

Figure 3: *Liosphex trichopleurum* Townes, ♂. Scale line 1.0 mm.

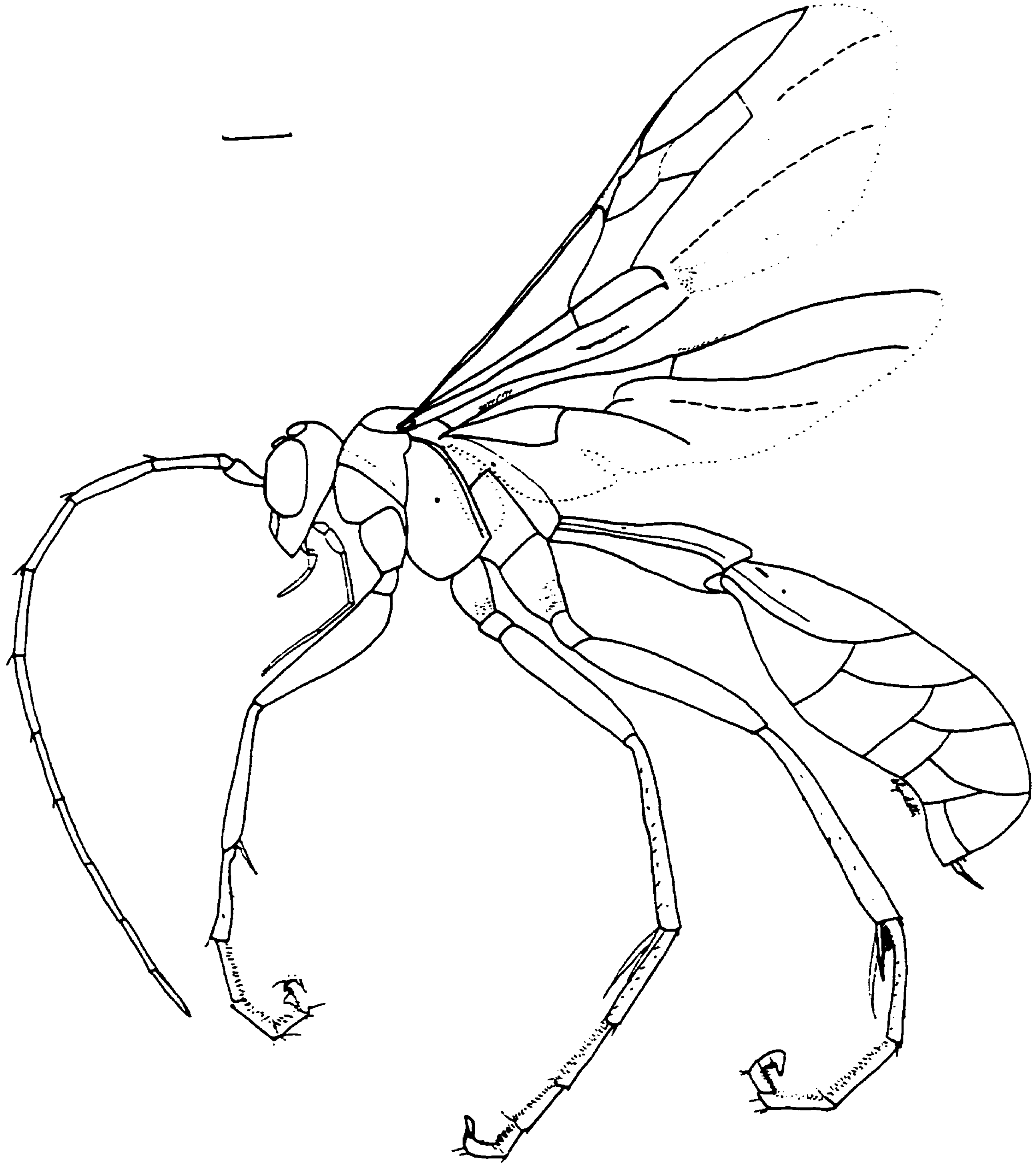

Figure 4: *Paniscomima darlingi* n. sp. Holotype ♀. Scale line 1.0 mm.

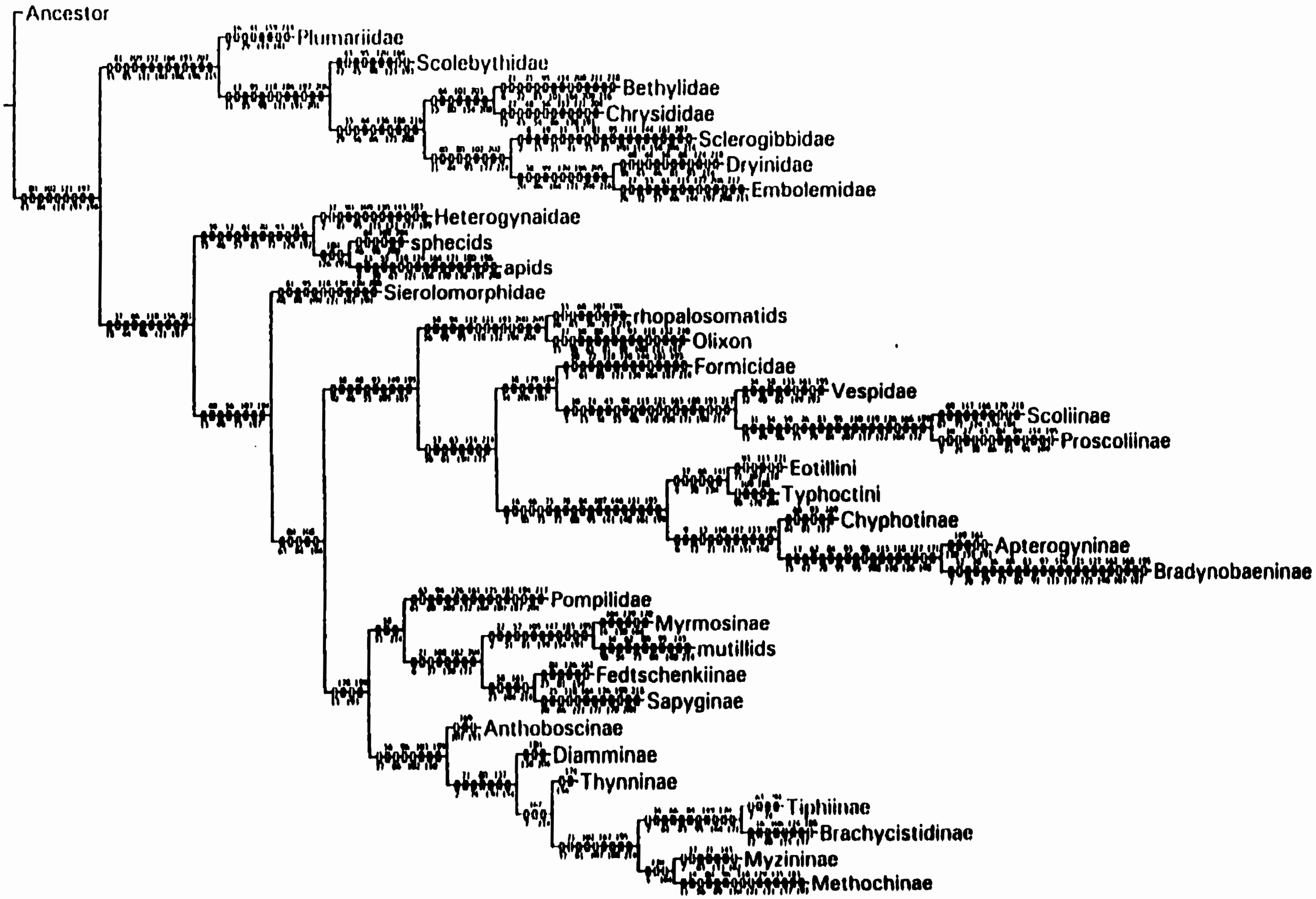

Figure 5: Composite cladogram of Brothers and Carpenter 1993 (fig. 11) based on preferred results of all analyses of Aculeata (length 692, consistency index 0.46, retention index 0.65). Character hashmark shading: black = unique derivation; grey = convergent derivation; open = reversal (unique or convergent).

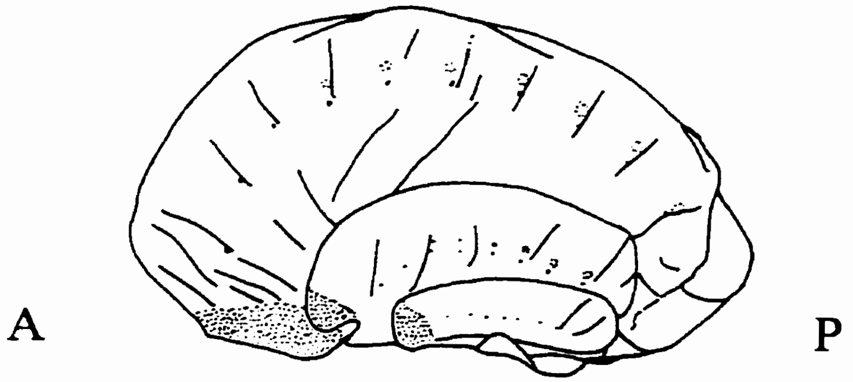

Figure 6: Three layers of exuviae of *Rhopalosoma nearcticum* Brues. A - anterior, P - posterior (after Hood 1913).

Table 1: Distribution and known hosts of Rhopalosomatidae (* indicates circumstantial evidence) (after Townes 1977).

Genus(# spp)	Species	Distribution	Hosts
Rhopalosoma (17)	*alvarengi*	Brazil, Ecuador & Costa Rica	
	angulare	Brazil	
	bahianum	Brazil	
	bolivianum	Bolivia	
	breelandi	Panama	
	guianense	C. America to Bolivia & Surinam	
	haitiense	Haiti	
	isopus	Brazil	
	impar	Brazil, Paraguay	
	lanceolatum	Brazil	
	minus	Argentina, Brazil	
	missionicum	Argentina	
	nearcticum	Eastern US	*Hapithus*, *Orocharis*
	obliquum	Mexico	
	poeyi	Caribbean, Bahamas to Hispaniola	
	scaposum	Bolivia	
	simile	Mexico, Guatemala, El Salvador, Costa Rica, Panama	
Olixon (8)	*flavibase*	Australia	
	majus	Ivory Coast, Burkina Faso, Nigeria	
	banksii	E. US, Mexico, Canada	*Nemobius**
	testaceum	S. Mexico to S. Brazil	*Cycloptilum**
	australiae	Australia	Trigonidiinae
	saltator	South Africa	
	myrmosaeforme	Zimbabwe	
	dentatum	SE. Coast of South Africa	
Paniscomima (10)	*abnormis*	Sri Lanka	
	bekilyi	Madagascar	
	curta	Madagascar	
	erlangeriana	Africa, Botswana, Tanzania	
	opposita	Nepal, India	
	rufoantennata	Madagascar	
	seyrigi	Madagascar	
	angelae	Vietnam	
	darlingi	Vietnam, Thailand, Laos, Sri Lanka	
	paropposita	Thailand	
Liosphex (2)	*varius*	S. US to S. Brazil	
	trichopleurum	Philippines, Indonesia	
Mesorhopalosoma	*cearae*	Brazil	

2.0 METHODS, MATERIAL AND TERMS

2.1 METHODS

2.1.1 Taxonomy

Three new species of *Paniscomima* are described herein based on morphological characters. Descriptions are provided for the previously unknown female of *Paniscomima opposita* Townes, the male of *Paniscomima seyrigi* Berland and the male of *Liosphex trichopleurum* Townes. Exact label data is cited for specimens examined. If additional information is added, it is indicated by {}. Measurements and observations pertaining to holotypes are identified by square brackets [ ]. Characters that were previously reported but were not verified by observation were omitted from these descriptions. In order to have informative characters included in the species descriptions, it was necessary to modify the descriptions of the family and the extant genera. New characters are included in these descriptions. Familial characters are not included in the generic descriptions and generic characters are not included in the species descriptions. The family description is based on extant macropterous females; characters in the brachypterous/apterous genus (*Olixon*) that differ from the macropterous genera are listed separately. The large number of differences in morphology between the extant macropterous species and *Olixon* made it difficult to describe all of the genera together in a single family description. Any differing characters in the extant macropterous male are described at the end followed by the brachypterous and apterous male. Species descriptions and redescriptions are based on the female if both sexes are known. For all descriptions, males are similar to females except as indicated.

Although new species are named, the author intends to publish the species descriptions in a journal and the names should not be cited from this manuscript.

A Wild M5A stereomicroscope and a Zeiss microscope at magnifications from 60X-100X were used for observations. Measurements were taken using the ocular micrometer. For every measurement, the specimen was rotated to a position that was as flat as possible and the point of maximum width or length was measured. For example, lateral ocellar diameter was measured from rim to rim of the ocellus and then rotated to measure ocular ocellar diameter. Eye emargination was measured at the maximum depth. Sections of veins were measured from the centre point of the defining veins. Full veins were measured from end to end. Illustrations were made with the aid of a camera lucida attachment on a stereomicroscope.

2.1.2 **Phylogenetic Analysis**

The phylogenetic method, as first outlined by Hennig (1966), and subsequently modified by several authors, most notably Wiley (1981) and Farris (1983), uses shared derived character states or synapomorphies to elucidate relationships among taxa.

The absence of sufficient behavioural and biological information resulted in the use of morphological data as the sole source of characters for the phylogenetic analysis. A scarcity of specimens made it unfeasible to even consider using molecular data. Homoplasy assumes a character state has evolved independently in different taxa (this may be seen through differences in development) or that a character is lost then reappears. Although it would be convenient from an analytical standpoint for all characters to have a single state for each character, characters in a taxon may have more than one state (i.e. polymorphic). Polymorphic characters show discrete variation within a taxon that is independent of ontogenetic or sexual variation (Wiens 1998). The argument that polymorphic characters are difficult to deal with in analyses has been used to exclude them. They have also been excluded because they are presumed to be less reliable for phylogenetic inferences (Wiens 1998). Neither of these arguments are justification for excluding taxonomic information from an analysis. Studies by Campbell and Frost (1993) and Wiens (1995) have concluded that although polymorphic morphological characters may be more homoplasious (which supports their exclusion from analyses) they contain significant phylogenetic signal and should therefore be included. In taxa with characters exhibiting more than one state, these characters will be treated as polymorphic rather than as uncertainties in these analyses.

A problem has been noted with the successive approximations weighting algorithm in PAUP 3.1.1. "With matrices containing multistate terminals, PAUP, under the "polymorphism" interpretation, will assign higher weight to characters with more within-terminal steps, other things being equal, i.e., to characters with the largest amount of homoplasy." (Rognes 1999). This is not a problem when the uncertainty interpretation for multistate characters is selected. Therefore, some of the analyses will be tested using both options.

Sixty-three characters were coded from the adult external morphology of each taxon (Table 2). The majority of characters were selected based on examination and comparison of specimens. Some characters were initially identified by other authors, e.g., characters 17, 22, 24, 27, 28 and 29 follow Brothers and Carpenter (1993) with some modifications. Some characters were selected based on the basis of their utility in the generic key by Townes (1977). This study examines the generic relationships within the Rhopalosomatidae using exemplars of selected taxa. Eighteen rhopalosomatid (ingroup) species from 5 genera were scored including all species of *Paniscomima* and at least two species from each extant genus of Rhopalosomatidae (Appendix

1). For *Mesorhopalosoma cearae* Darling, character states were determined from the description and illustrations (Darling & Sharkey, 1990). When both sexes of a species were not available for study, character states were determined from drawings or descriptions. All characters were treated as unordered since the direction of evolution is not known. Characters for which information was not available were assigned a missing data (?) code. For taxa with more than one state for a character, characters were interpreted as polymorphic for the first 10 analyses and as uncertainties for analyses 11-14.

Different combinations of outgroups were used to test their effects on the ingroup topology (Table 3). Exemplars of three outgroup families were examined. The outgroup taxa were selected based on the phylogeny of the Aculeata (Fig. 5) proposed by Brothers and Carpenter (1993). The family Bradynobaenidae was selected based on its basal position on the sister branch to the Rhopalosomatidae. *Typhoctes* Ashmead and *Chyphotes* Blake are genera in the two basal subfamilies of the Bradynobaenidae (Brothers and Carpenter 1993). Pompilidae was selected as an outgroup taxon based on a previous study by Brothers (1975) in which this family was proposed as the sister group of the Rhopalosomatidae. Brothers and Carpenter (1993) (Fig. 5), place Pompilidae on the second outgroup branch. A phylogeny of the Pompilidae by Shimuzu (1994) proposes the subfamily Ceropalinae as the sister group to the rest of the Pompilidae. Specimens of *Ceropales bipunctata* Say were chosen as an exemplar of Pompilidae based on this phylogeny. The next outgroup to the Rhopalosomatidae in the phylogeny of Brothers and Carpenter (1993) is the Sierolomorphidae. Specimens of *Sierolomorpha canadensis* Provancher were coded. For simplicity, the outgroups will be referred to by their family group names rather than by their species names.

Cladograms were selected based on the criterion of parsimony using PAUP 3.1.1

(Swofford, 1993). Each outgroup, was assigned as the sole outgroup and a parsimony analysis performed (Analyses 1, 3, 5). An analysis was also performed in which both the Pompilidae and the Bradynobaenidae were selected as outgroups (Analysis 7). Additionally, an analysis using all three outgroups was executed (Analysis 9). In Analyses 2, 4, 6, 8, 10, *Mesorhopalosoma* was excluded because of the large amount of missing data. Heuristic searches were executed. Summary statistics used to describe the trees are total tree length, consistency index (CI), retention index (RI), and rescaled consistency index (RC) (Kluge and Farris 1969; Farris 1989). Character optimizations were done using both ACCTRAN, which accelerates transformations (maximizing reversals and minimizing parallelisms) and DELTRAN, which delays transformations (maximizing parallelisms and minimizing reversals).

Parsimony was relaxed by one and two steps to examine nodal support.

Multistate characters were run unordered, and MacClade (Maddison and Maddison, 1992) was used to examine character state changes on most parsimonious trees.

2.2 MATERIAL

Specimens were borrowed from or are deposited in the following institutions with the curators listed after each institution. Museum acronyms listed in the text follow Arnett *et al.* (1993). Appendix 1 lists the exemplars used in this study, their label information and their repository.

American Entomological Institute (AEIC) 3005 SW 56th Ave. Gainesville, Florida 32608 USA D. Wahl

Bishop Museum (BPBM) P.O. Box 19000-A Honolulu, Hawaii 96817-0916 USA G.A. Samuelson

The Natural History Museum, (BMNH) Department of Entomology, Cromwell Road, London, SW7 5BD England T. Huddleston

California Academy of Sciences (CASC) Golden Gate Park, San Francisco, CA 94118 W. J. Pulawski, B. Zuparko

Bohart Museum of Entomology, University of California, Davis (UCDC) CA 95616 S. Heydon

Canadian National Collections of Insects (CNCI), Arachnids and Nematodes, Eastern Cereal and Oilseed Research Centre, Research Branch, Ottawa, Ontario, Canada K1A 0C6 J. Huber

National Museum of Natural History Leiden (RMNH) Postbus 9517, 2300 RA Leiden, The Netherlands C. van Achterberg

Provincial Museum of Alberta (PMAE) 12845-102 Avenue, Edmonton, Alberta, Canada T5N 0M6 A.T. Finnamore

Royal Ontario Museum (ROME) 100 Queen's Park, Toronto, Ontario, M5S 2C6 D.C. Darling

Smithsonian Institution, National Museum of Natural History (USNM) Department of Entomology, Collections Management Unit NHB MRC 165, 10th & Constitution Ave., N.W.; Washington, D.C. 20560 USA K.V. Krombein

Texas A & M University (TAMU) Insect Collection Department of Entomology, College Station, Texas 77843, USA R.A. Wharton

2.3 MORPHOLOGICAL TERMS

Morphological terms, except wing venation, follow Goulet and Huber (1993) with some terms clarified below as in Finnamore (1995). Wing veins and cells follow Gauld and Bolton (1988). Drawing conventions for wing venation follow Mason (1986). See Figure 7 for terms. Flagellomeres are counted starting at the base F1, F2, etc.

LOD	maximum diameter of lateral ocellus
OOD	shortest distance between lateral ocellus and eye

Other terms used:

apterous	wingless
brachypterous	short-winged, wings not extending beyond apex of tergum 1 (Fig. 2)
fenestra	thin transparent area in the cuticle that transmits light. In macropterous rhopalosomatids, refers to the apilateral sections of the female tarsomeres.
macropterous	full-winged

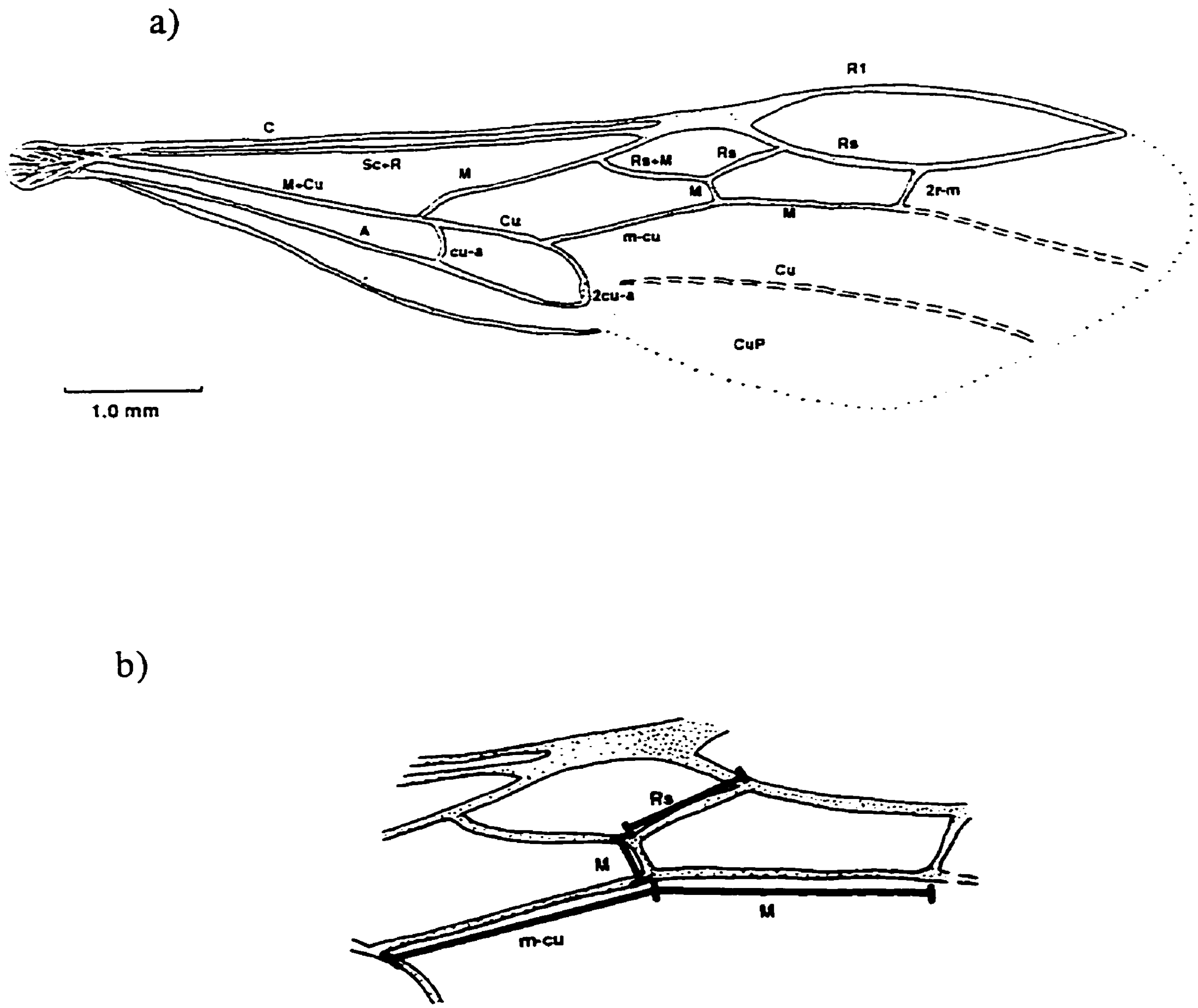

Figure 7: a) Wing venation (after Goulet and Huber 1993).
b) Enlargement of the central part of wing showing where select measurements were taken.

3.0 TAXONOMY

3.1 RHOPALOSOMATIDAE

Rhopalosomidae Ashmead, 1898: 303-309.

Rhopalosomatidae: Brues, 1922: 102.

DIAGNOSIS

Rhopalosomatids belong to the suborder Apocrita, division Aculeata. They are aculeates based on the form of the ovipositor, which is modified for stinging instead of egg laying, and the number of antennal segments: 13 in males and 12 in females. The following combination of characters distinguish rhopalosomatids from other aculeates: female tarsomeres 2-5 or 3-5 wide, flattened and concave ventrally with dense mat of hairs (Fig. 8); forewing with costal cell absent or reduced through fusion of veins C and Sc+R (+Rs) (Figs. 9, 10, 11); and apices of 2 or more basal flagellomeres usually with 2 spines (rarely absent) (Fig. 12). As in the Tiphiidae, posterior edge of mesosternum with a triangular lobe on each side of midline covering bases of coxae (Fig. 13). Rhopalosomatids can be differentiated from most pompilids by a lack of a transverse suture on the mesepisternum.

DESCRIPTION

Three extant macropterous genera and one brachypterous or apterous genus are currently assigned to the Rhopalosomatidae.

Adults are usually tawny yellow with brown markings; if black, then usually with white, red, or yellow markings. Body covered in short, yellow or white hairs. Interocellar area usually dark-coloured (Figs. 14, 15). Mandibles yellow; teeth brown. Forewing length of macropterous species ranges from 4.2 to 17 mm. Sexual dimorphism slight; females are generally larger than males, often more than twice as large.

Head. (Figs. 14, 15, 16) Vertex convex, rounded. Eye emarginate. Ocelli small to large. Dorsal rim of torulus simple. Antenna inserted below emargination of eye. Paired spines present on apices of basal 5 (rarely 6) flagellomeres (Fig. 13). Mandibles tridentate. Clypeus quadrate; apex concave. Labrum exposed, subtriangular, at least twice as wide medially as laterally. Maxillary palp 6-segmented, labial palp 4-segmented (Fig. 18); palpi long and slender, basal 3 labial and 3 maxillary segments shorter and wider than apical segments which are long and narrow.

Brachypterous and apterous species. (Fig. 17) Head with occipital carina and concave posteriorly. Inner eye margin straight. Ocelli reduced or absent. Antenna insertion below lower margin of eye. Spines on flagellomeres often absent or small. Labrum exposed, subtriangular, ventral margin smoothly rounded or weakly bilobed. Mandibles quadridentate (Fig. 17). Basal 2 labial segments shorter and wider than others. Second segment of maxillary palp with thick bristle apically.

Mesosoma. Pronotum shorter than length of head, less than half length of mesoscutum; divided by a transverse groove. Pronotum with posterior margin weakly or deeply concave, and with posterolateral apex weakly truncate anterior to tegula. Prepectus narrow and short, a small elongate strip articulating with or fused to anterior margin of mesepisternum. Mesepimeron narrow, extending full height of mesopleuron and differentiated by complete pleural sulcus. Mesepisternum with a median circular pit. Metapleuron with an endophragmal pit on anterior margin. Posterior edge of mesosternum with a triangular lobe covering mesocoxa, separated from the mesosternum by a transverse suture. Propodeum smoothly convex. Legs long and slender. Metacoxae contiguous. All femora slightly swollen; profemur sometimes more so. Mesofemur and metafemur sometimes with scattered bristles in apical third. Tibial spur formula

1:2:2, inner metatibial spur longer than outer spur, outer spur approximately 2/3 length of inner, with a basal tuft of bristles. Mesotibial spurs simple; inner spur longer than outer spur. Basal quarter of metatarsomere with a comb of hairs on a carinate ridge. In addition to apical bristles, meso- and metatibiae and tarsomeres 1, sometimes 2 and 3 with scattered bristles. Protibia and probasitarsus sometimes with scattered bristles. Tarsomeres 2-5 wide, flat and concave ventrally (Fig. 8). Tarsomeres 2 and 3 (and sometimes 4) with apical lateral fenestrae (Fig. 19). Tarsal claws simple or with median tooth, sometimes with a subbasal low rounded tooth; with a dark, flat, lanceolate bristle usually reaching apex of tarsal claw (Fig. 20). Forewing with 8 or 9 closed cells (Fig. 9, 10, 11); stigma short, narrow and linear; CuP spectral, concave. Hindwing with 2 closed cells, with distinct claval and jugal lobes and with costal vein thick in basal third (Fig. 21); basal cell with densely spaced, very short hairs in anterior and basal part of cell, long sparse hairs in posterior part; other cells with long, densely spaced hairs.

Brachypterous and apterous species. Pronotum longer than length of head, more than twice as long as mesoscutum. Posterolateral apex of pronotum rounded anterior to tegula. Prepectus very short, extending over most of height of mesepisternum, fused with mesepisternum and concealed under posterolateral margin of pronotum. Mesepimeron and mesepisternum fused. Mesopleuron and metapleuron without pits. Rounded lobe covering mesocoxa contiguous with mesosternum, transverse suture incomplete. Propodeum often with posterolateral projections. Profemur swollen and shorter than metafemur. Mesotibial and metatibial spurs subequal in length. Inner metatibial spur pectinate. Tarsomeres 3-5 wide, flat and concave ventrally. Apical fenestrae absent on tarsomeres. Bristles absent on femora and tibiae, sometimes present ventrally on basitarsus. Wings without closed cells. Forewing with costal vein present and some longitudinal skeletal veins. Hindwing, if present, reduced to a short, thread-like vestige.

Metasoma. Six visible terga. Petiole smoothly convex with posterodorsal median pit. Second segment with strong constriction at junction with first. Anterior margin of sternum 1 deeply concave. First tergum with lateral longitudinal carina which may be complete or incomplete, i.e. not reaching posterior margin. Second tergum with an incomplete lateral longitudinal carina, not reaching posterior margin. Paired, oblong-shaped, sculptured, anterodorsal impressions present on tergum II (Fig. 4). Tergum VI exposed with a medial bare area, with an apical depression and weak punctate imbricate sculpture. Tergum VII hidden and considerably desclerotized with a short anterior sclerotized strip connecting lateral spiracular plates. Hypopygium with a longitudinal bare ridge or carina present. Sting short.

Brachypterous and apterous species. Constriction between first and second segments weak. First tergum with complete lateral longitudinal carina but lacking a posterodorsal median pit. Anterior margin of sternum 1 straight or slightly curved. Anterodorsal impressions absent on tergum II. Tergum VI without apical depression.

Male. As in female except for the following. Paired spines may also be present on apices of F6, F7, and F8. Tarsomeres cylindrical, with apical plantar lobes ventrally; without fenestrae or mat of dense hairs. Tarsal claws either with an apical tooth or bifid; claws of similar length and size, without lanceolate bristles or median tooth. Seven terga visible. Bare, medial longitudinal strip usually present on tergum VI but without apical depression or sculpturing. Genitalia with parameres apically produced into elongate, upwardly curved, needle-like processes (Fig. 3). Metasomal sternum VIII (hypopygium) simple, entirely exposed, with 6 or more apical lanceolate bristles in a row (Fig. 22), without longitudinal bare ridge or carina.

Brachypterous and apterous species. As in female except for the following. Tarsomeres not fully cylindrical; slightly flattened. Tarsal claws bifid; inner claw much larger than outer claw;

without lanceolate bristles or teeth. Seven terga visible. Genitalia with parameres apically produced into elongate, upwardly curved, needle-like processes. Plantar lobes absent on tarsomeres and hypopygium simple, entirely exposed, with very short dark hairs apically, without bristles.

BIOLOGY

Where known, the larvae of rhopalosomatids are ectoparasitoids of the Gryllidae. For a description of the larva, see Gurney's (1953) study of *Rhopalosoma nearcticum* Brues. *Rhopalosoma nearcticum* Brues is ectoparasitic on Eneopterinae (species of *Orocharis* Uhler and *Hapithus* Uhler) (Hood 1913; Gurney 1953); *Olixon australiae* Perkins is ectoparasitic on trigonidiine crickets (Perkins 1908). Hosts are unknown for other species. The larva forms a sac-like structure on the abdomen (exuviae Fig. 6). It attaches to the side of the abdomen and feeds through the body wall near the posterior end of the abdomen. The mature larva falls to the ground, burrows into the soil and spins a brownish, parchment-like cocoon. Macropterous species are presumed to be nocturnal. Townes reported seeing *Rhopalosoma* adults in flight at twilight (cited in Gurney 1953). In the same report, Townes also suggests that their preferred habitat is "dense, shrubby vegetation where there is considerable humidity, as along stream bottoms and seashores." Specimens of *Paniscomima* were collected from a dipterocarp forest in Vietnam which was a humid, dense, shrubby location near a river. *Olixon banksii* Brues has been seen "running over sandy barrens" (Krombein 1949).

DISTRIBUTION

Worldwide except for the Palearctic Region and Antarctica.

COMMENTS

For the description of the extinct genus *Mesorhopalosoma* Darling, see Darling and Sharkey

(1990). Evans (1987:680) states that the larval characters do not seem helpful in placing this family in the scheme of Hymenoptera.

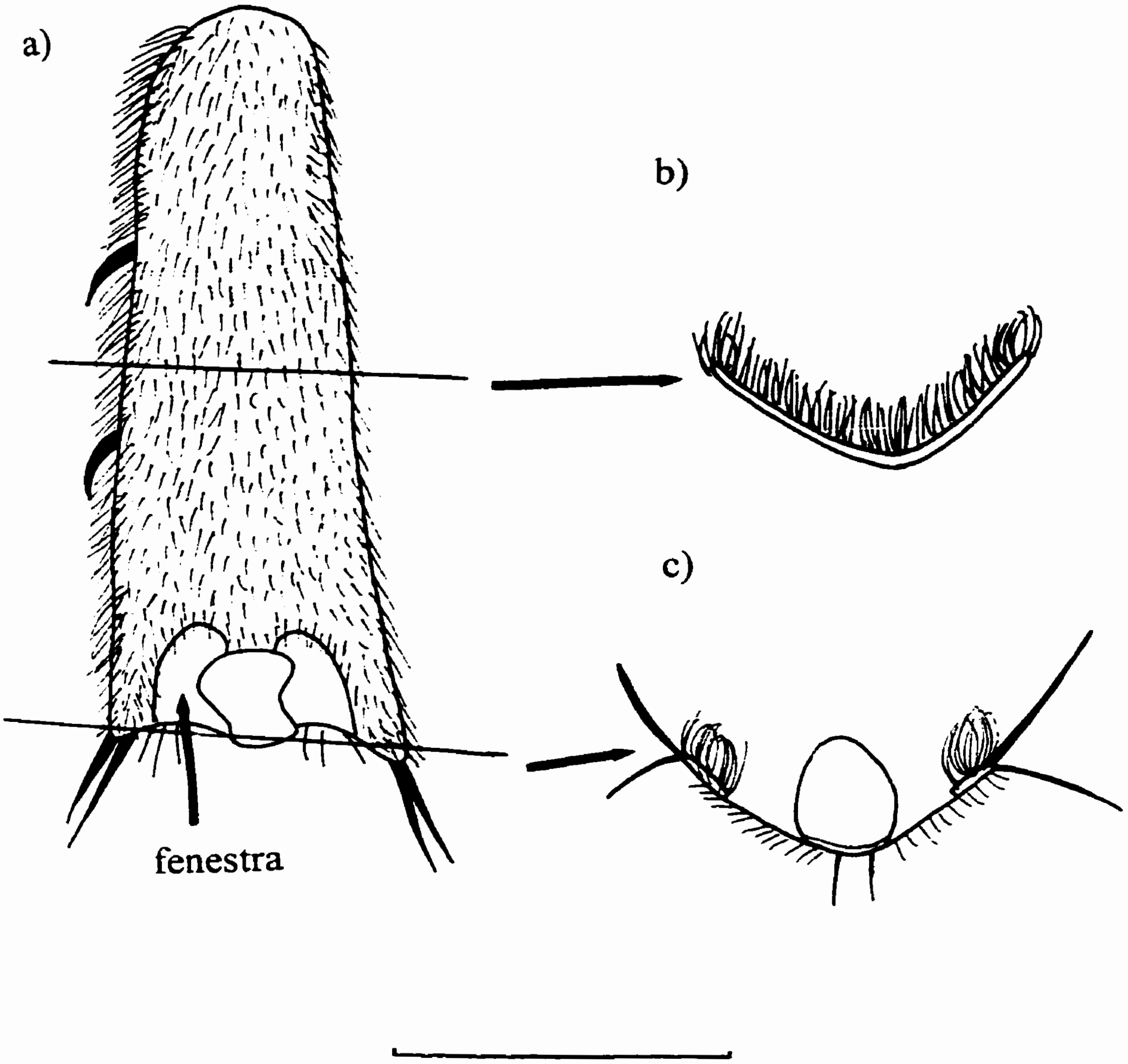

Figure 8: *Paniscomima darlingi* n. sp. Holotype. Scale line 0.5 mm. a) Ventral view of female tarsomere 2, b) Cross section at middle of tarsomere 2, c) Cross section at apex of tarsomere two. Note thin cuticle at fenestrae.

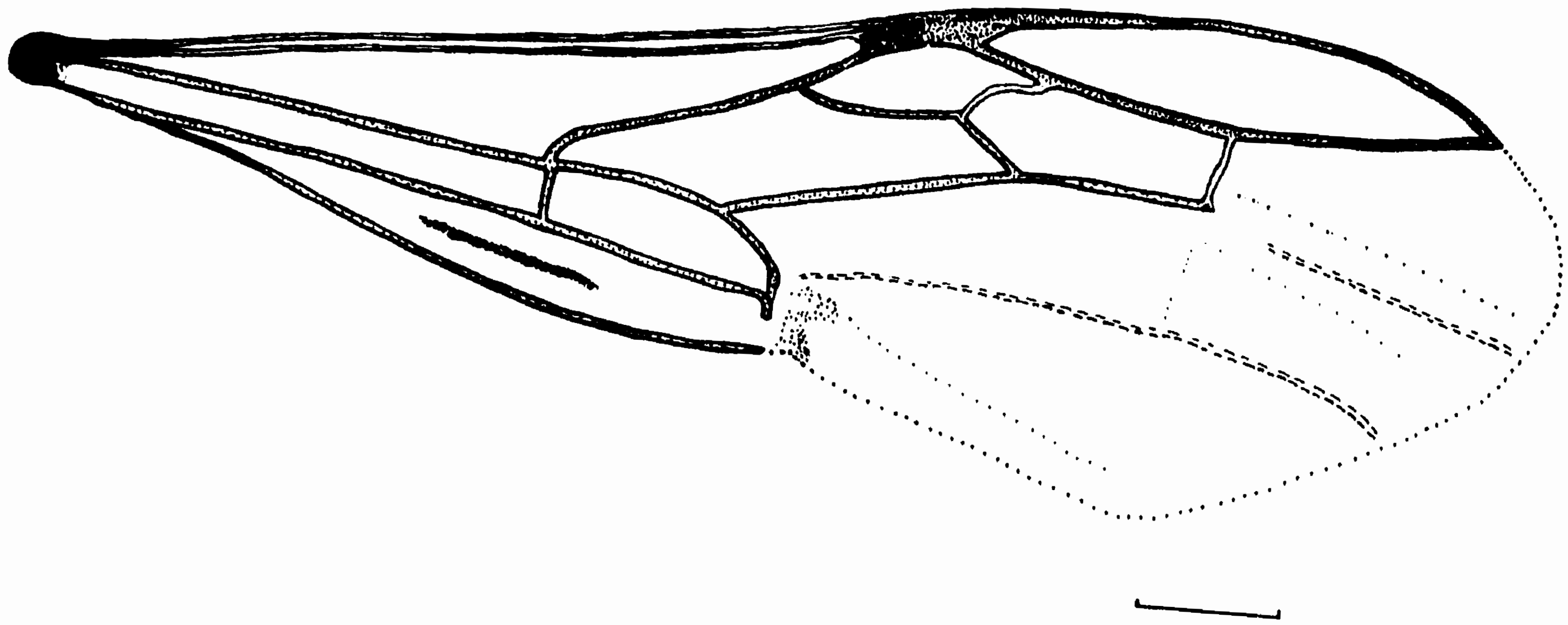

Figure 9: *Paniscomima darlingi* n. sp. Forewing. Holotype ♀. Scale line 1.0 mm.

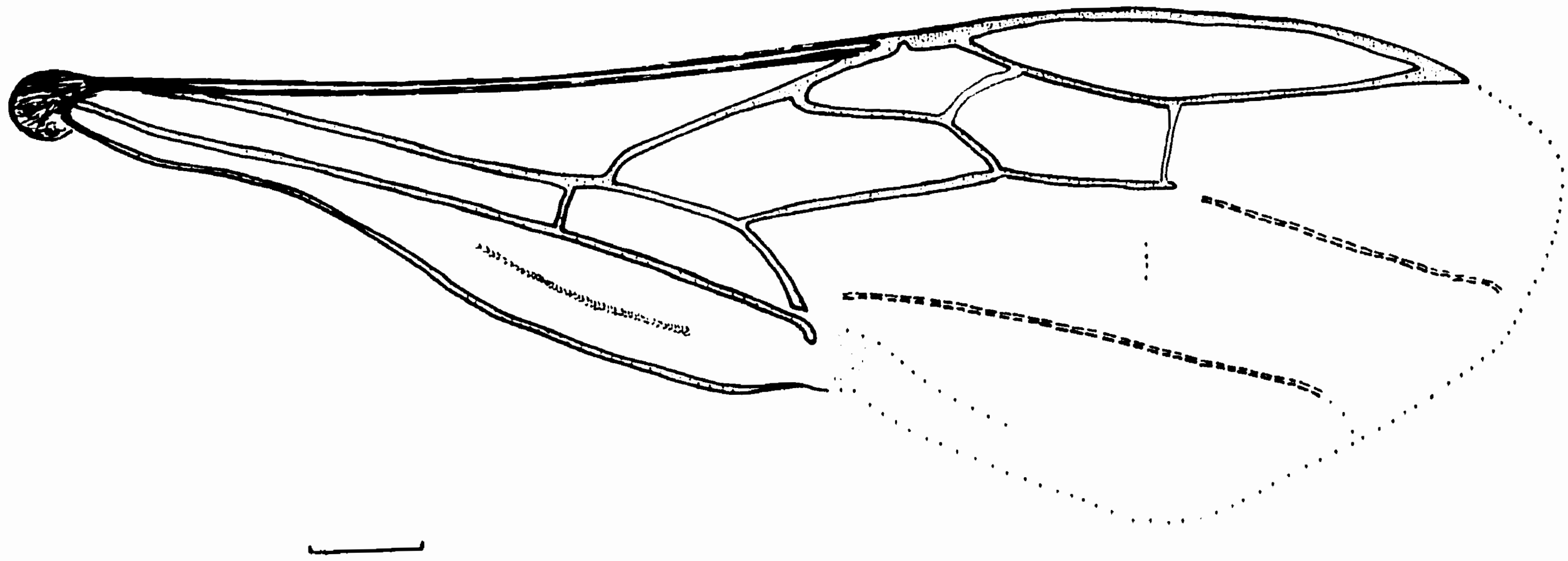

Figure 10: *Paniscomima angelae* n. sp. Forewing. Holotype ♀. Scale line 0.5 mm.

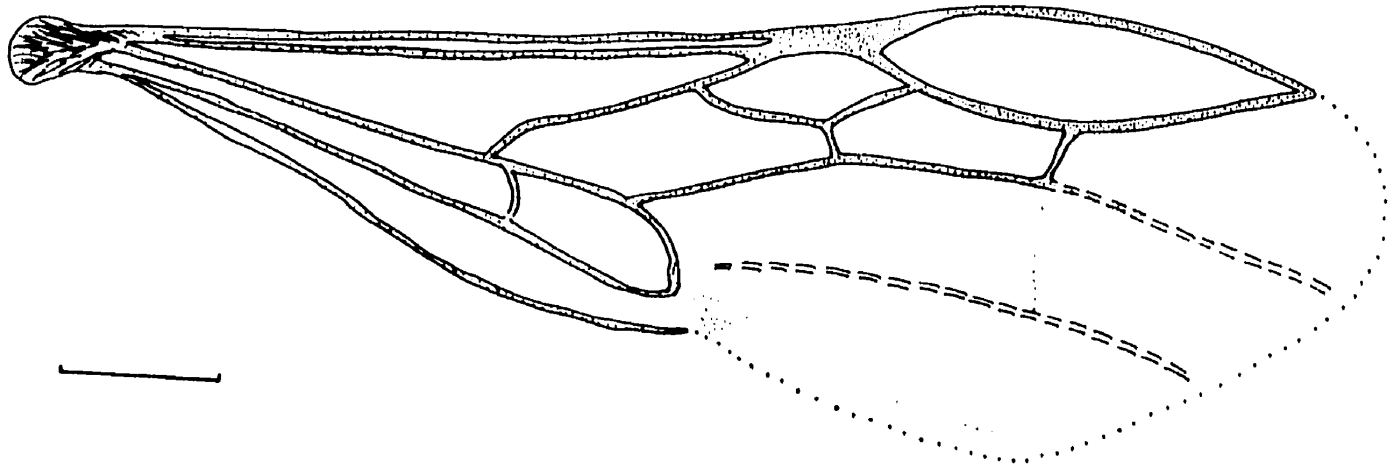

Figure 11: *Paniscomima paropposita* n. sp. Forewing. Holotype ♀. Scale line 1.0 mm.

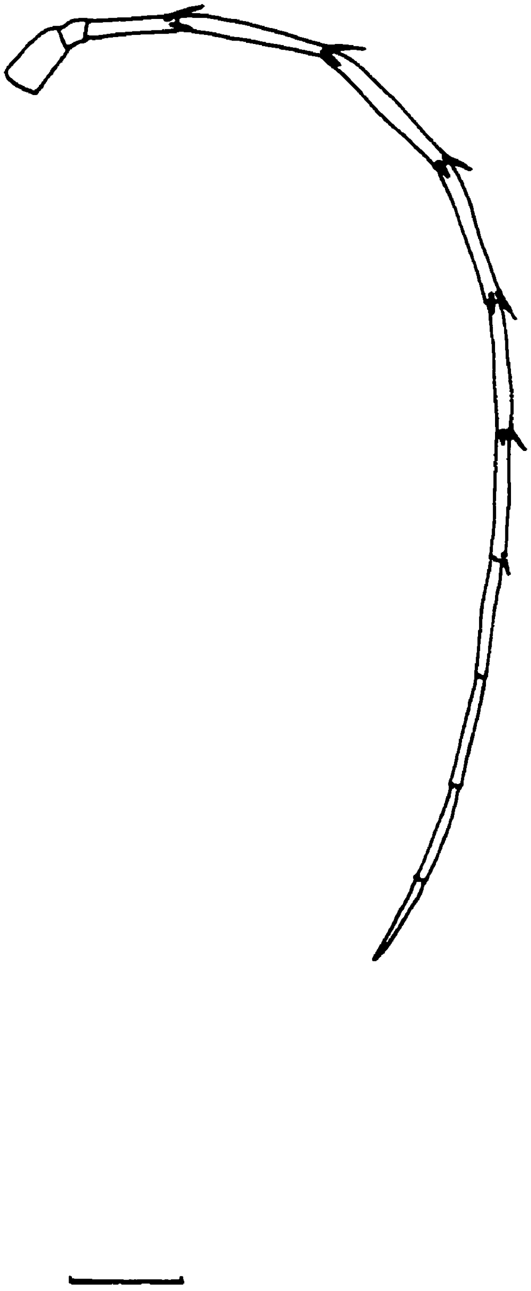

Figure 12: *Paniscomima darlingi* n. sp. Antenna. Holotype ♀. Scale line 1.0 mm.

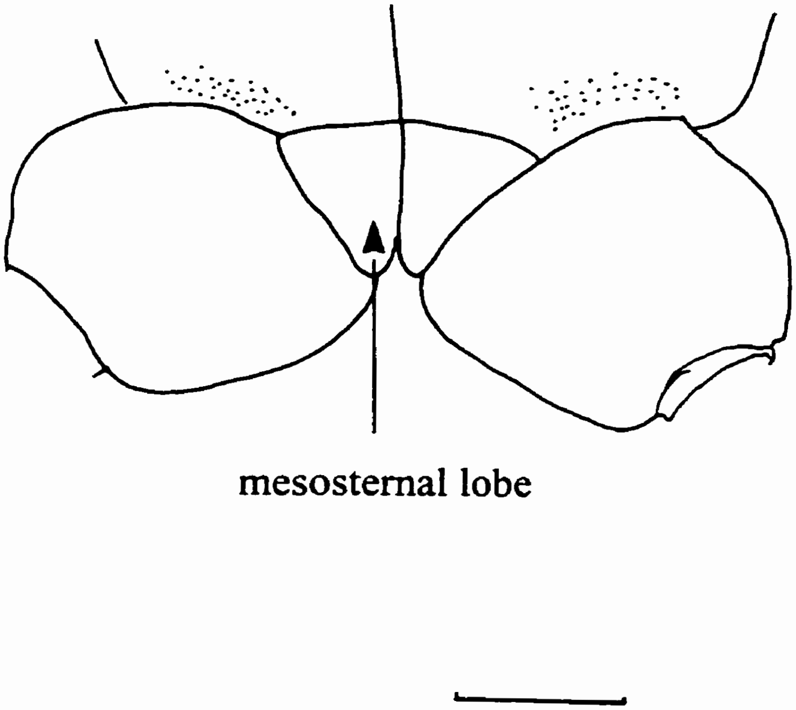

Figure 13: *Paniscomima darlingi* n. sp. Mesosternal lobes. Holotype. Scale line 1.0 mm.

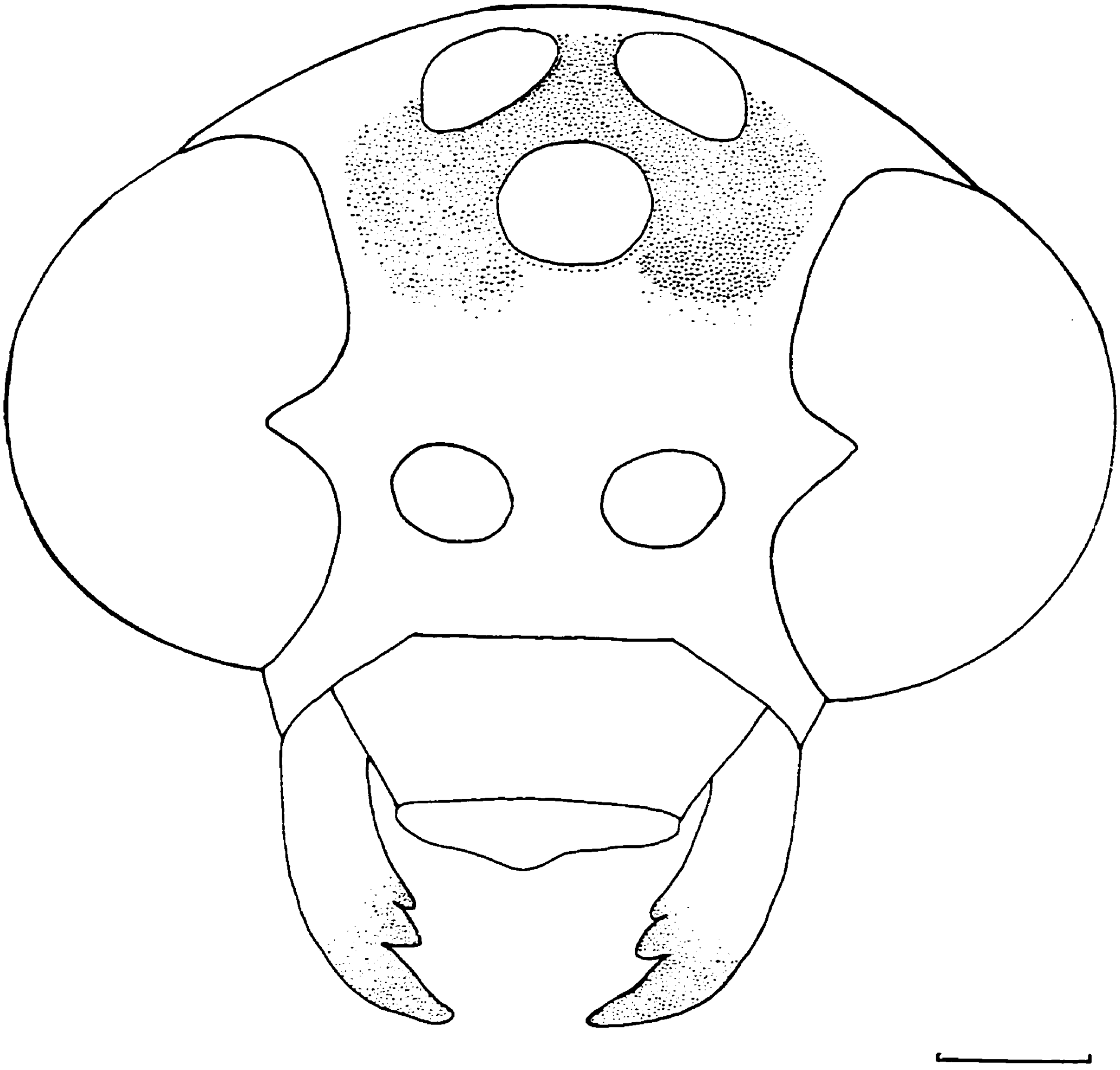

Figure 14: *Rhopalosoma sp.*, ♀. Head. Scale line 0.4 mm.

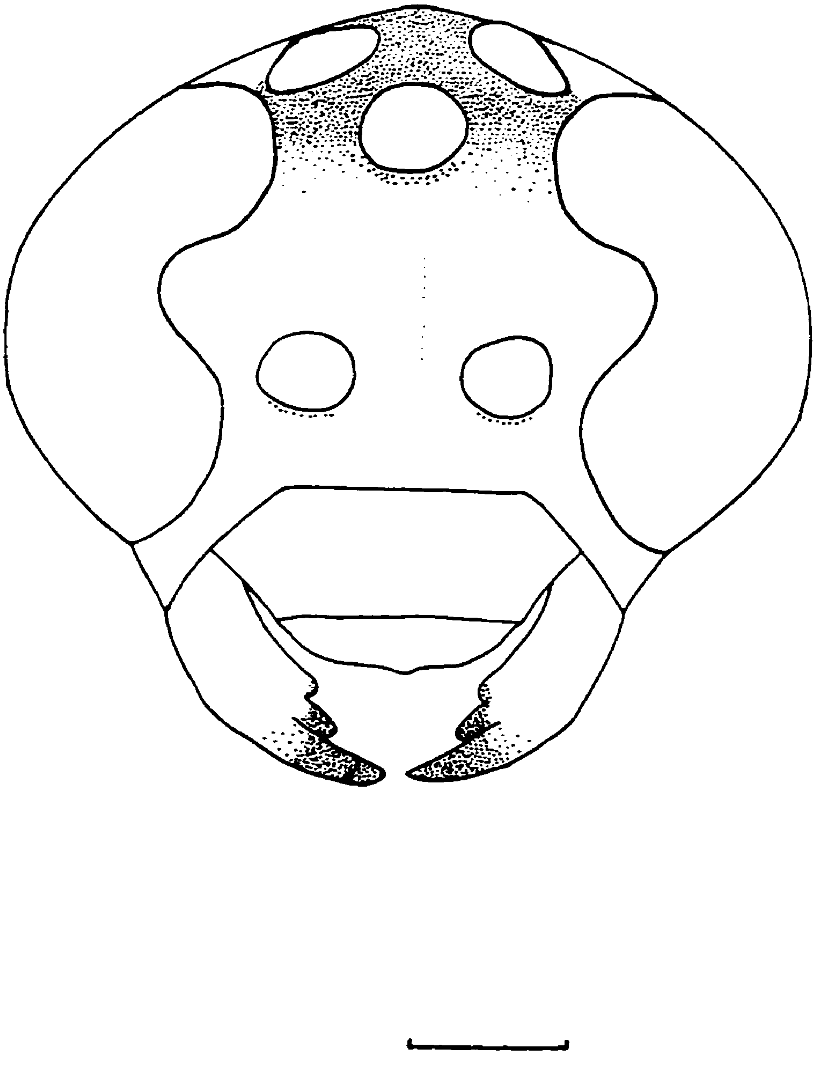

Figure 15: *Paniscomima paropposita* n. sp. Head. Holotype ♂. Scale line 0.4 mm.

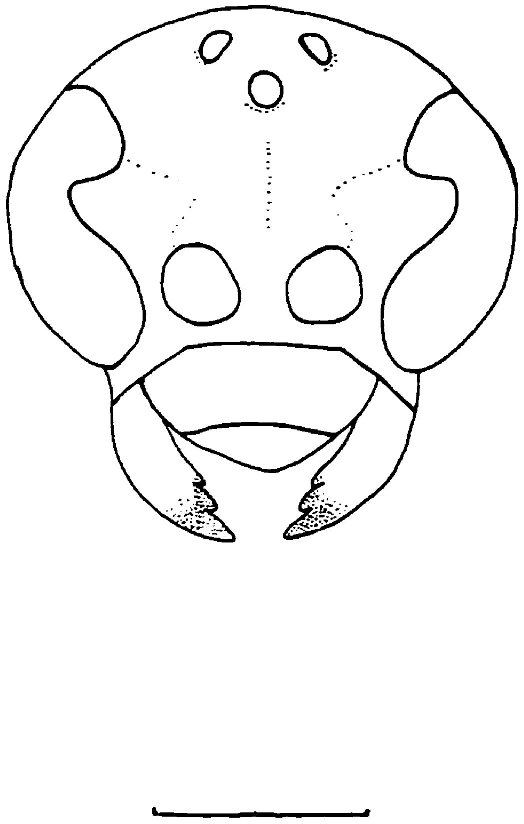

Figure 16: *Liosphex trichopleurum* Townes, ♂. Head. Scale line 0.5 mm.

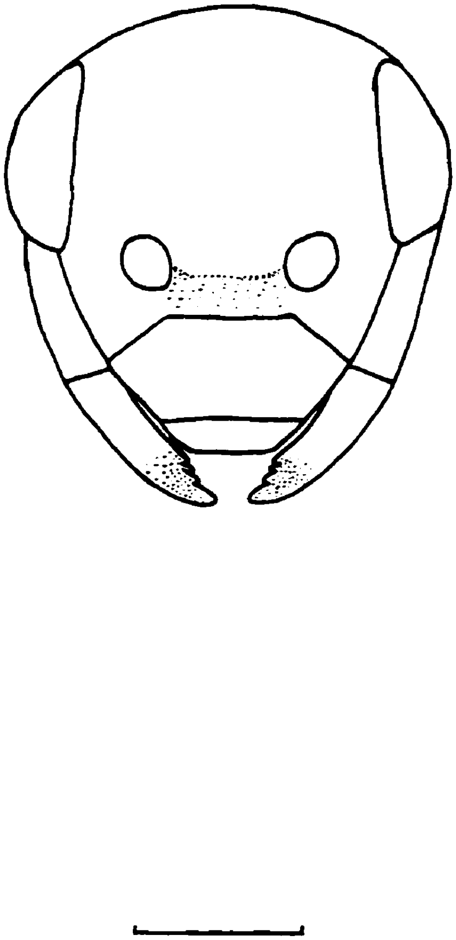

Figure 17: *Olixon testaceum* Cameron, ♀. Head. Scale line 0.4 mm.

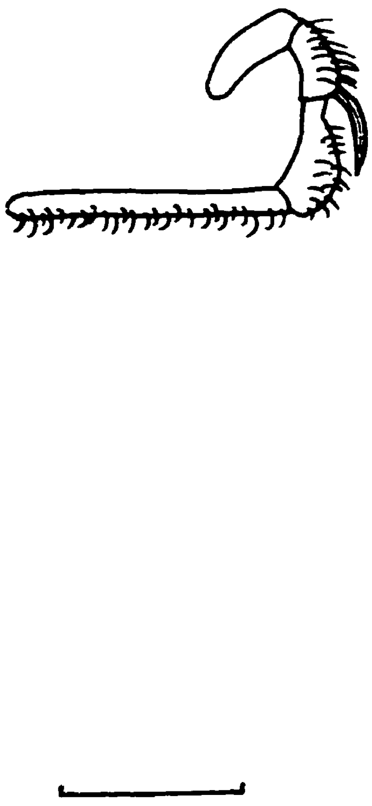

Figure 18: *Liosphex trichopleurum* Townes, ♂. Labial palp. Note bristle on segment 2. Scale line 0.4 mm.

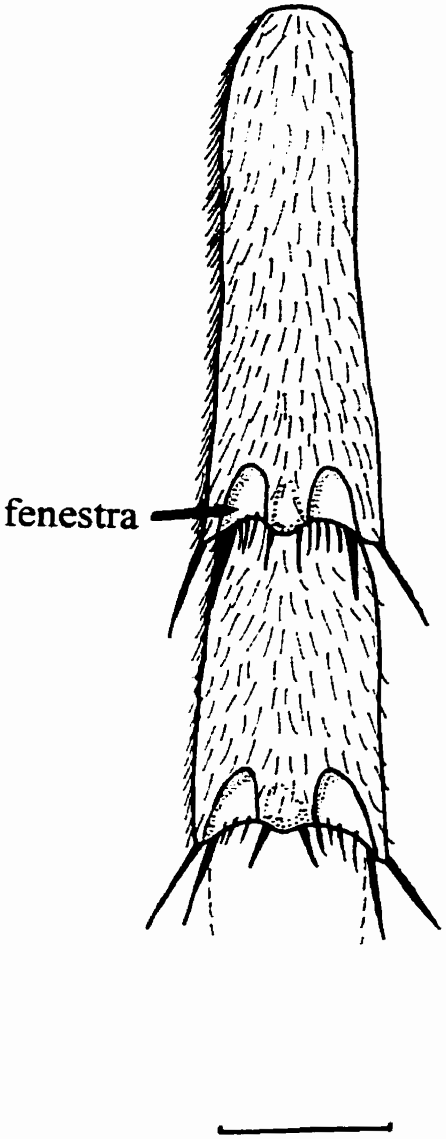

Figure 19: *Paniscomima darlingi* n. sp. Dorsal view of tarsomeres 2 and 3. Fenestrae illustrated. Holotype ♀. Scale line 0.4 mm.

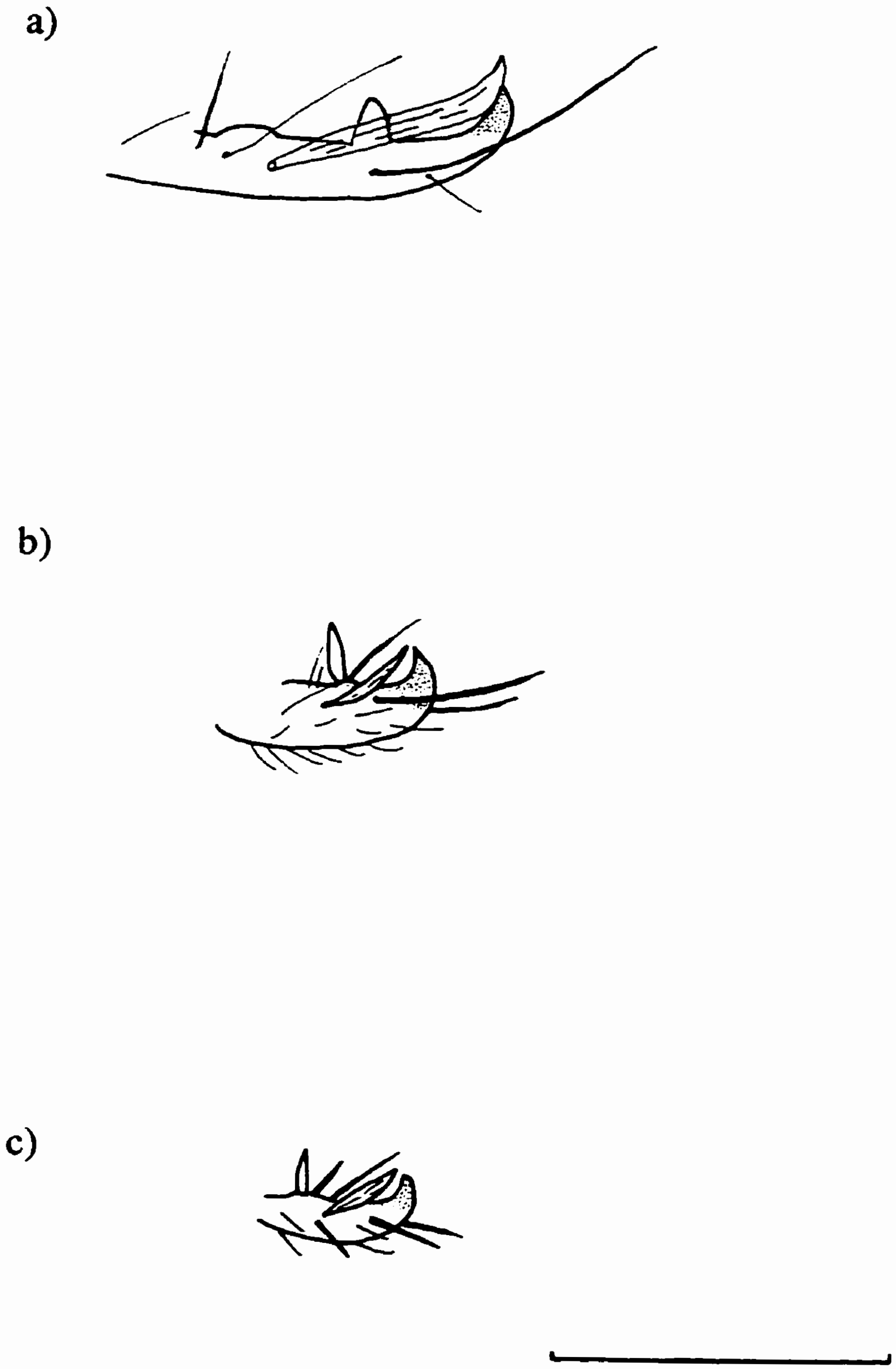

Figure 20: Female tarsal claws a) *Rhopalosoma sp*. b) *Paniscomima darlingi* n. sp. Holotype. c) *Liosphex trichopleurum* Townes. Scale line 0.5 mm.

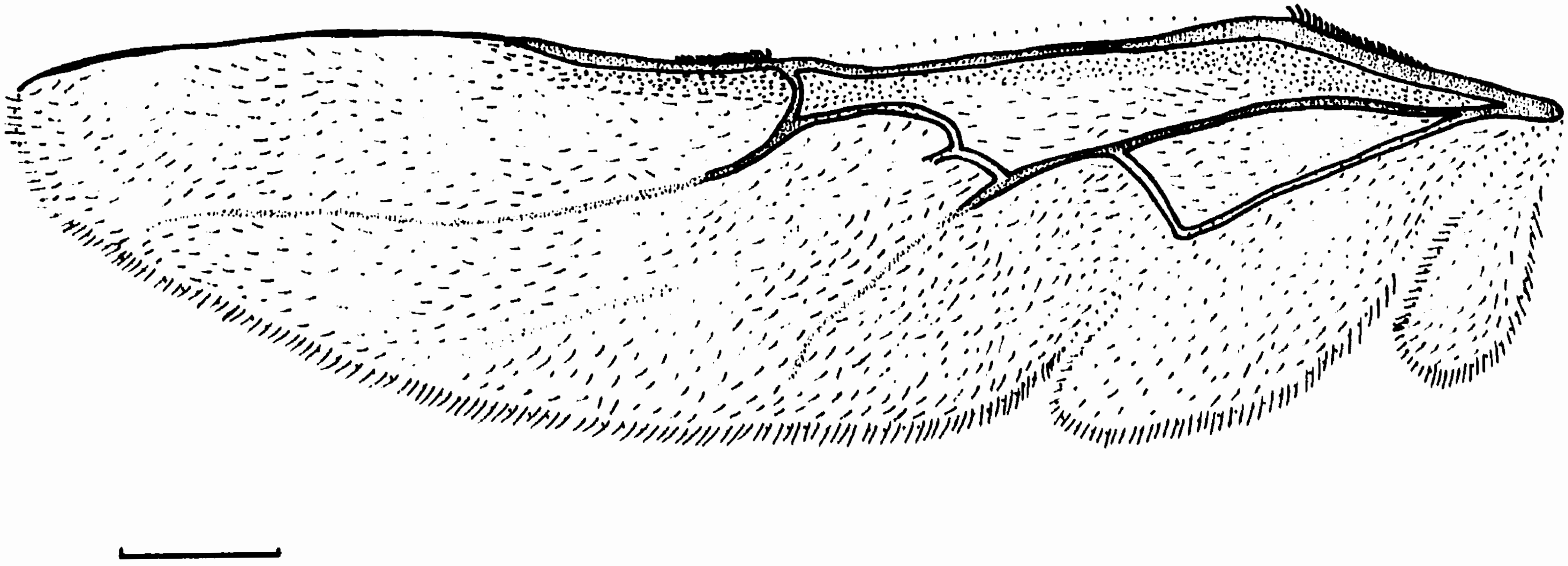

Figure 21: *Paniscomima darlingi* n. sp. Hind wing. Holotype ♀. Scale line 1.0 mm.

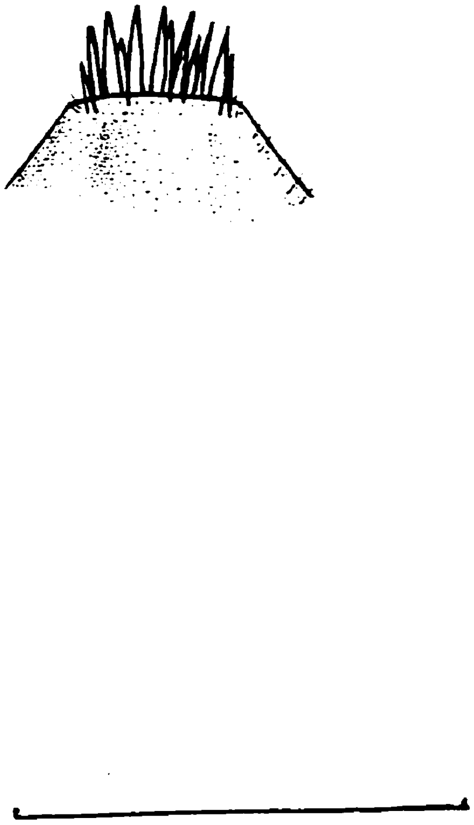

Figure 22: *Paniscomima paropposita* n. sp. Bristles on apex of male hypopygium. Holotype ♂. Scale line 0.5 mm.

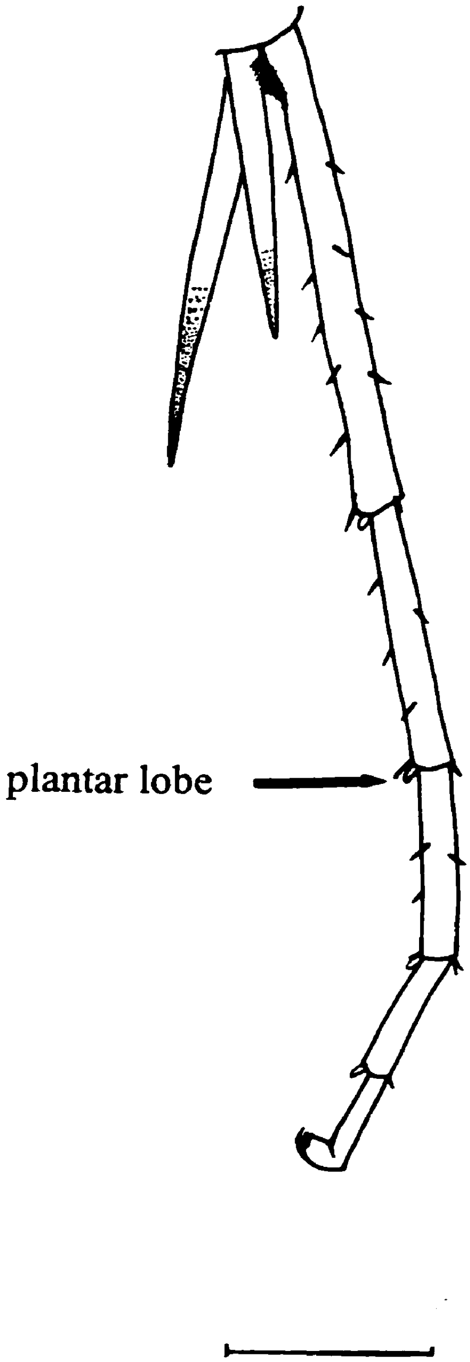

Figure 23: Hind leg of male *Liosphex trichopleurum* Townes. Note plantar lobes at apex of each tarsomere. Scale line 0.5 mm.

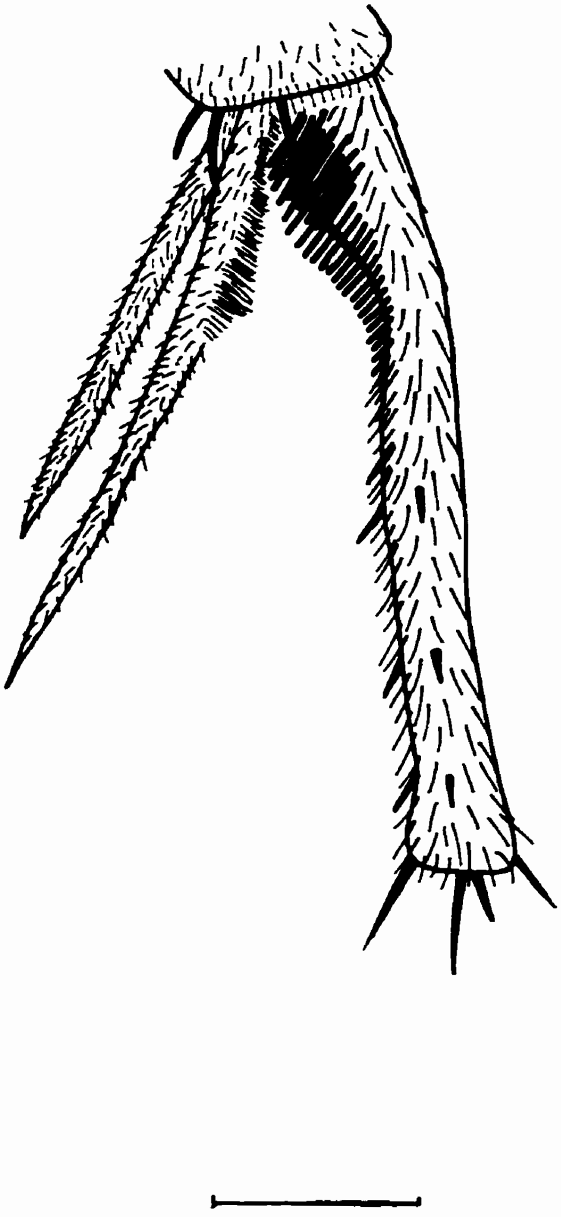

Figure 24: *Paniscomima darlingi* n. sp., ♀. Metatarsomere 1. Holotype. Scale line 0.5 mm.

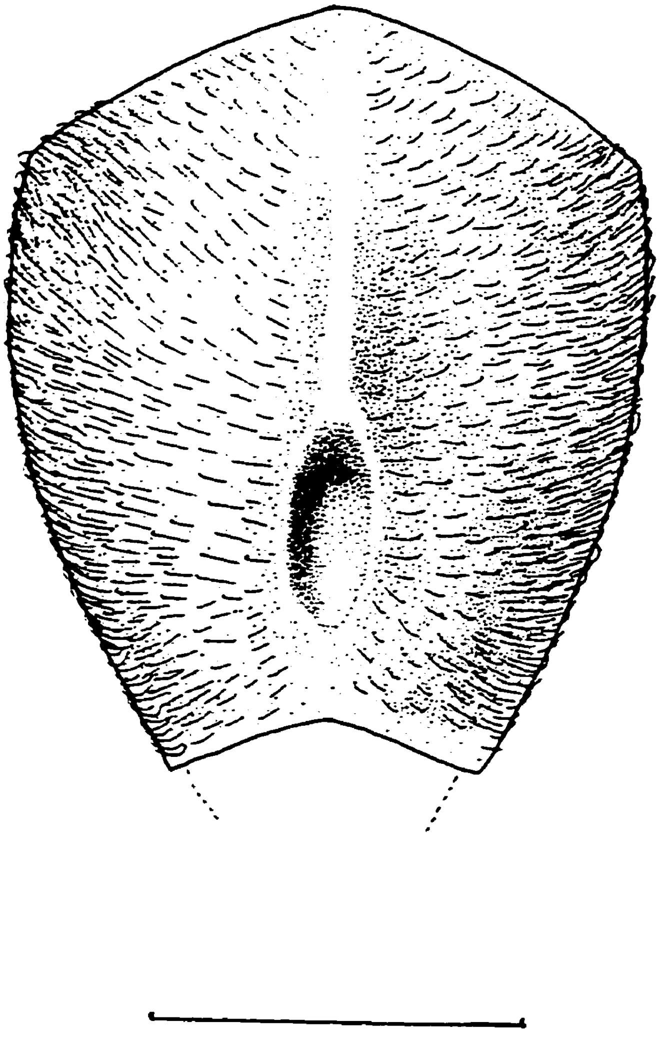

Figure 25: *Paniscomima darlingi* n. sp. Female Tergum VI. Holotype. Scale line 0.5 mm.

3.1.1 REVISED KEY TO EXTANT GENERA OF THE RHOPALOSOMATIDAE

(after Townes 1977)

1. Eye margin smoothly rounded (Fig. 17). Wings absent or shorter than mesosoma. Petiole 0.3 to 0.6 as long as wide. (Americas, Africa, Southeast Asia, Australia).

. . . *Olixon* Cameron

Eye emarginate (Figs. 14, 15, 16). Wings much longer than mesosoma. Petiole 1.3 to 6.8 as long as wide. . . . 2

2. Occipital carina absent. Petiole short, only 1.3-2.0 times as long as wide. Body colour dark and variable. Eye notch asymmetrical (Fig. 16). Eyes with very short setae. (Americas, Indonesia and Philippines). . . . *Liosphex* Townes

Occipital carina present. Petiole short to long, 1.7 to 6.8 as long as wide. Body colour predominantly yellow. Margins of eye notch symmetrical (Fig. 14, 15). Eyes without setae. . . . 3

3. Second segment of labial palpi with a long thick bristle (Fig. 18). Female tarsal claws without a tooth; claws simple, short (Fig. 20b). (Africa & Southeast Asia.)

. . . *Paniscomima* Enderlein

Labial palpi without a thick bristle, possibly with a weak one. Female tarsal claws with a strong medial tooth, often also with a blunt tooth near base; claws elongate (Fig. 20a). (Americas). . . . *Rhopalosoma* Cresson

3.2 LIOSPHEX Townes

Liosphex Townes, 1977: 10. **Type species:** *Liosphex varius* Townes by original designation. [paratype examined, CNCI]

BIOLOGY

Host unknown.

DISTRIBUTION

Indonesia: Borneo, Philippines: Mindanao, Eastern United States to Southern Brazil.

DIAGNOSIS

The two species of *Liosphex* can be differentiated from other genera of the Rhopalosomatidae by the following combination of characters. Occipital carina absent. Eyes usually with sparse short setae. Thick bristle on second segment of labial palp (Fig. 18). Petiole short, length 1.3- 2.0 times width. Female tarsal claws simple (Fig. 20c). Hindwing subbasal cell with sparsely scattered long hairs (~25-40); less dense than the rest of the wing and less dense than other genera.

DESCRIPTION

Female. (Fig. 3) Macropterous. Forewing length 4.2-9.4 mm. Body colour variable; usually dark brown or black with red, white and/or yellow markings; may also be predominantly yellow with brown markings. Antenna colour variable, pale yellow to brown; frequently brown dorsally, yellow ventrally. Clypeus usually pale yellow (or white), rarely with a brown ventral margin or a brown medial spot. Labial and maxillary palpi yellow to brown.

Head. Lateral spine on F1 two to four times longer than the inner spine. OOD 2-3 LOD. Eye margin notch above level of toruli; notch with asymmetrical margins; maximum depth of notch

1-1.5 times width of torulus. Ocelli small (Fig. 16). Smooth, hairless line present on frons, from middle of toruli sometimes reaching median ocellus. Thick bristle on second segment of labial palp long, approximately same length as second labial segment.

Mesosoma. Mesepisternum with at least a small area around pit glabrous, devoid of hair and punctation; weak imbricate sculpture may be present along suture with mesepimeron and around pit. Forewing with 8 or 9 closed cells. Maximum width of claval lobe in hindwing 1-1.5 times the length of cu-a; jugal lobe 0.4-0.5 times length of subbasal cell. Bristles present on mesotibia, metatibia and metabasitarsus and sometimes present on protibia, tarsomeres 2, metatarsomere 3, mesofemur and metafemur. Apical lateral fenestrae of tarsomeres 2 and 3 thin, slit to bell-shaped, distinct only when viewed with transmitted light. Tarsal claws short and stout, simple with a second short, basal, lanceolate bristle.

Metasoma. Lateral longitudinal carina on tergum 2 about half the length of the tergum. Petiole length 1.3- 2 times width.

Male. (Fig. 3). As in female except as follows: presence of apical spines sometimes also on F6 and F7; scattered surface bristles also present on tarsomeres 2 and 3; fenestrae absent; tarsal claws bifid without lanceolate bristle. Plantar lobes on basitarsus absent or present..

3.2.1 KEY TO SPECIES OF *LIOSPHEX*

Metapleuron uniformly covered with hairs except bare medially around pit. M of hindwing tubular or nebulous. Forewing cu-a distad of M by < 0.5 times length of cu-a. Male with plantar lobes on tarsomeres 1-4. (Southeast Asia). . . . *Liosphex trichopleurum* Townes

Metapleuron with short hairs only along lateral margin, the rest bare. M of hindwing spectal or absent. Forewing cu-a distad of M by approximately 1.75 length of cu-a. Male with plantar lobes on tarsomeres 2-4. (Americas). . . . *Liosphex varius* Townes

3.2.2 SPECIES RE-DESCRIPTION

Liosphex trichopleurum Townes

Liosphex trichopleurum Townes 1977: 11. **Holotype:** ♀ Philippines [examined, USNM]

BIOLOGY

Host unknown.

DISTRIBUTION

Indonesia, Borneo; Philippines, Mindanao.

DIAGNOSIS

Liosphex trichopleurum has weak imbricate punctation on the mesopleuron and metapleuron; petiole is always brown or black; M of hindwing tubular or nebulous; forewing cu-a distad of M by ≤ 0.5 times length of cu-a; and male plantar lobes on basal four tarsomeres (Fig. 23). *Liosphex varius* lacks punctation on the meso and metapleura; has a variably coloured petiole; M of hindwing spectral; forewing cu-a distad of M by approximately 1.75 times length of cu-a; and the male has plantar lobes on tarsomeres 2-4 only.

DESCRIPTION

Body colour black to reddish brown and yellow/white. Antenna brown; F1-2, and sometimes F3, F4, F5 yellow ventrally. Scape and pedicel usually yellow, may be brown dorsally. Maxillary palp: second and third segments brown sometimes with yellow; fourth and fifth segments sometimes partially brown, usually yellow; and sixth segment yellow. Clypeus white. Forewing length of females 6.6-8.3 mm[7.5], males 4.2-5.2 mm. Mesosoma dark coloured, black to reddish brown. Foreleg and midleg yellow with some brown markings, tarsi dark yellow posteriorly, brown anteriorly. Tibial spurs pale yellow with brown tip. Hind leg: part of trochanter, coxa and femur dark brown. Petiole dark brown or black with a dorsal yellow band laterally and posteriorly; metasomal segments 2, 3 mostly yellow, partially brown; rest of segments brown.

Head. Outer spine on basal flagellomere 2-3 times length of inner spine. Smooth, hairless line on vertex extends from medial ocellus to middle of toruli.

Mesosoma. Mesepisternum with bare area surrounding pit; partially glabrous (without punctation or hairs); weak, non-uniform, imbricate punctate sculpture present in rest of surface. Metapleuron with bare area surrounding pit, some imbricate punctate sculpture present near lateral ventral margin and posteriorly. Propodeum with small bare area present laterally. Forewing cu-a distad of M by ≤ 0.5 length of cu-a. Maximum width of claval lobe in hindwing approximately the length of cu-a; length of jugal lobe 0.5 times the length of subbasal cell; subbasal cell with more than 25 long hairs scattered on the surface.

Metasoma. Hairless, medial longitudinal depression in tergum VI of female, some imbricate sculpturing in depression; may extend length of tergum, but is usually posteriorly located.

Male. Similar to female except as follows: bristles also present on protibia and tarsomeres 1, sometimes meta- and mesotarsomeres 2 and 3. Plantar lobes present on basal 4 tarsomeres (Fig. 23).

COMMENTS: This species was previously known only from the holotype, a female (Townes 1977) collected in Mindanao (Philippines). Nineteen males and two females have subsequently been collected by the ROME, BMNH and RMNH in Borneo using Malaise traps. Using Townes' key (1977) for *Liosphex*, the specimens key out to *L. trichopleurum* except for the cu-a crossvein in the forewing is **not** always distad of M by 0.5 length of cu-a. I regard this character as variable within this species. Rather than describe a new species, a redescription including male characters is provided and a habitus drawing (Fig. 3) of the male is illustrated.

SPECIMENS EXAMINED

Holotype: ♀ {PHILIPPINES}, "Kolambugan Mindanao {C.F.} Baker" [USNM].

2♂: INDONESIA, W. Kalimantan, Gunung Palung Nat. Pk., 15 June- 15 Aug. 1991, DC Darling, Rosichon, Sutrisno, IIS 910115; ♂ : E. Kalimantan, 38km N. Balikpapan, Samboja I. Darling, Rosichon, Sutrisno, 2-30 Mar 1992. Wanariset Res. Station km 7. 60m 1°2'S, 117°2'E Heavy burnt forest 1983. MT(fine) head. Light gap. IIS 920116. [ROME]. 2♂: SABAH: Danum Valley Field C. 117°48'E 4°58'N vii-viii 1986 E. Smith; ♂ +♀: i-ii.1987 M. Still. [BMNH]. 2♂ : MALAYSIA: SE.SABAH nr Danum Valley Field C. WON1, Mal. trap 5, c 150m 20vi-12vii 1987, RMNH '87 C.v.Achterberg & D.Kennedy; 2♂: 2-23viii.1987, RMNH '87 C.v.Achterberg & D.Kennedy; 4♂: 23.viii-13xi 1987, RMNH '87 C.v.Achterberg & D.Kennedy; 2♂ +♀ : 13.ix-4.x. 1987, RMNH '87 C.v.Achterberg & D.Kennedy; ♂: 5-26.x.1987, RMNH '87 C.v.Achterberg & D.Kennedy; ♂: WO, Malaise trap 5, c 150m 12.vii-2.viii. 1987, RMNH '88 C.v.Achterberg & D.Kennedy;♂: Mal. trap 11, 14-20.III. 1987 RMNH C.v.Achterberg [RMNH].

Liosphex varius Townes

Liosphex varius Townes 1977: 11-12. **Holotype**: ♀ USA, Tall Timbers, Fla. [paratype examined, CNCI]

BIOLOGY

Unknown.

DISTRIBUTION

Southeastern United States to southern Brazil.

COMMENTS

The amount of variation between specimens from different localities suggests that there may be more than one species in the New World. I would like to make a note of one unusual male specimen collected from PANAMA: Las Cumbres 22-28 viii-1982 H. Wolda ground [PMA]. The coloration of this specimen is very close to species of *Paniscomima* and *Rhopalosoma*: yellow with brown between the ocelli and last metasomal segments brown.

SPECIMENS EXAMINED

Twenty six specimens (22♂ and 4♀) of this species were examined. *L. varius*: **Paratype**:♀: LA: Chicot St. Pk. Evangeline Par. 28vi-5vii 71. D. Shanek. MT USA. 5♂: FLA: Alachua Co. Gainesville (DPI) 11-18 VI 1987. DB Wahl MT [CNCI]; 2♂: 1-23-VI-1987, MT J. Wiley [PMA]; ♂: 15-25 VI, 1987; MT Regrown Oak Forest BRC HYM. TEAM [PMAE]; 3♂: Highlands Co. Archbold Biol.Station 1-15.VI.1987 D.B.Wahl.[CNCI]. ♂: Archbold Biol. Sta. Lk. Placid Highlands Co. VII-25-1983 T-2.[UCDC]; ♀: Kentucky: Louisville VII-1982 M.G.Fitton.♂: MEX.:Chis.3000ft. 20 mi N. Huixtla 2 June 1969 W.R.M.Mason [CNCI];♀: Sin.20 mi.E. Concordia,3000' 12Aug 1964. W.R.M. Mason [CNCI]; ♂: PANAMA: Las Cumbres 22-28-VIII-1982 H.Wolda ground [PMAE].♂: BRAZIL, Amazonas Reserva Ducke, km.26

Manaus-Itacoatiara Highway May-April 1972 E.G.,E &E.A. Munroe [CNCI]; ♂: D.F. Cabeco do Veado 3600' 14-30-X-1971 E.Munroe [PMAE]; ♀: PERU: Madre de Dios: Rop Tambopata Reserve, 30 km. (Air) SW Puerto Maldonado, 290m., 12°50'S 069°20'W. [CASC].

3.3 PANISCOMIMA Enderlein

Paniscomima Enderlein, 1904: 465. **Type species**: *Paniscomima erlangeriana* Enderlein. By monotypy.

Hymenochimaera Brues, 1926: 19. **Type species**: *Rhopalosoma abnorme* Cameron = *abnorme* Morley. By monotypy. Synonymy by Townes, 1977.

Rogezia Berland, 1951: 300. **Type species**: *Rogezia seyrigi* Berland. By original designation. Synonymy by Townes, 1977.

BIOLOGY

Host unknown. Some specimens were collected in a riparian dipterocarp forest.

DISTRIBUTION

Africa, Madagascar, Southeast Asia (India, Sri Lanka, Nepal, Laos, Vietnam, Thailand).

DIAGNOSIS

The ten species of *Paniscomima* can be differentiated from those of other rhopalosomatid genera by the following combination of characters. Occipital carina present. Eyes bare. Thick bristle on second segment of labial palp (Fig. 18). Petiole long, length 1.7-3.7 times width. Female tarsal claws with a second short, basal lanceolate bristle (Fig. 20b). Species of *Paniscomima* are very similar in overall habitus to species of the New World genus *Rhopalosoma*.

DESCRIPTION

Female. (Fig. 4) Macropterous. Forewing length 6 to 15 mm. Body slender, dark yellow, metasomal segments V-VII may be brown and intraocellar area brown (sometimes reaching the eyes). Antenna yellow, reddish brown or brown. Clypeus yellow, ventral margin often brown. Labial and maxillary palpi yellow.

Head. Paired apical spines on flagellomeres equal or subequal length, outer spine up to 1.5 times length of inner spine. OOD 0.1-2.1 LOD. Eye margin notch above level of toruli; notch with symmetrical margins; maximum depth of notch 1-1.5 times width of torulus. Ocelli moderately large to very large. Smooth hairless line between toruli on vertex very weak. Thick bristle on second segment of labial palp (Fig. 18).

Mesosoma. Forewing with 8 closed cells (Fig. 9, 10, 11). Maximum width of claval lobe in hindwing 1.3-2.6 the length of cu-a; jugal lobe 0.7-0.9 length of subbasal cell. Bristles present on all tibiae and all basitarsi. Apical, lateral fenestrae of tarsomeres 2, and 3, short, bell-shaped, and delineated by a carina (Fig. 14). At least apical two-thirds of fifth tarsomere parallel-sided. Tarsal claws short and stout, with a second, short, basal lanceolate bristle (Fig. 20b).

Metasoma. Petiole long, length 2.2-3.7 times maximum width.

Male. Similar to female except as follows: flagellomeres usually brown in males; sometimes F6-F8 also with 2 apical spines; bristles also present on metatarsomere 2 and sometimes on pro- and mesotarsomeres 2 and metatarsomere 3; fenestrae absent; tarsal claws bifid, without lanceolate bristles; plantar lobes on tarsomeres 1-4; petiole length 1.7-2.7 times width.

3.3.1 KEY TO SPECIES OF *PANISCOMIMA*

1. Anal cell of forewing with adventitious vein. (Figs. 9, 10) ...2

Anal cell of forewing without adventitious vein (Fig. 11) ...4

2. OOD 1.0 LOD. Forewing cu-a basad M 0.9 length of cu-a. (India and Sri Lanka).
. . . *P. abnormis* Townes

OOD less than 0.6 LOD. Forewing cu-a basad M 0.75 or less length of cu-a.. ...3

3. Female metasoma with brown posterior segments. Forewing cu-a basad 0.75 its length of M (Fig. 10). (Vietnam). . . . *P. angelae* new species

Female metasoma yellow. Forewing cu-a opposite, slightly basad or slightly distad of M (Fig. 9). (Thailand, Laos, Sri Lanka and Vietnam). . . . *P. darlingi* new species

4. M intersects with m-cu at 90° angle (Fig. 11). Forewing cu-a opposite M or slightly distad or basad (less than 0.3 length of cu-a). (Southeast Asia). ...5

M intersects with m-cu at less than 90° angle. Forewing cu-a distad M by 0.4-1.5 length of cu-a. (Africa and Madagascar). ...6

5. Rs about 4 times the length of M distad of Rs+M (Fig. 11). (Thailand).

. . . *P. paropposita* new species

Rs less than 3.3 times the length of M distad of Rs+M. (Sri Lanka).

. . . *P. opposita* Townes

6. Apex of wing infuscate. Ocelli small. OOD 2 LOD. (Madagascar).

. . . *P. seyrigi* Berland

Wing concolorous. Ocelli large. OOD less than 1 LOD. ...7

7. Metasoma yellow. ...8

Metasoma posterior segments brown. (Madagascar). . . . *P. curta* Townes

8. Forewing Cu/2cu-a vein with a swelling at junction of Cu. Forewing cu-a distad M 1.0-1.5 length of cu-a. (Madagascar). ...9

Forewing Cu/2cu-a vein of consistent thickness, there may be some slight thickening of 2cu-a. Forewing cu-a distad M 0.5-1.0 length of cu-a. (Africa).

. . . *P. erlangeriana* Enderlein

9. Antenna brown. (Madagascar). . . . *P. bekilyi* Berland

Antenna reddish yellow. (Madagascar). . . . *P. rufoantennata* Berland

3.3.2 SPECIES DESCRIPTIONS

Paniscomima darlingi new species

BIOLOGY

Host unknown. Collected in dry dipterocarp forest.

DISTRIBUTION

Vietnam, Laos, Sri Lanka, Thailand.

ETYMOLOGY

This species is named for Dr. D.C. Darling (one of the holotype collectors), in recognition of his work on fossil Rhopalosomatidae and in appreciation for his assistance with this project.

DIAGNOSIS

The combination of the following characters distinguishes this species from all other species of *Paniscomima*. Longitudinal adventitious vein present in anal cell of forewing. OOD 0.1-0.5 LOD; differs from *P. abnormis* where OOD is 1 LOD. In forewing, cu-a opposite, slightly basad or slightly distad of M and Rs 0.6 to 1.4 times the length of M distad of Rs+M. Female metasoma yellow; differs from *P. angelae* in which posterior metasoma is brown.

DESCRIPTION

Female. (Fig. 4). Body colour yellow with some brown colouration in the intraocellar area. Flagellomeres dark yellow. Scape yellow.

Head. Interocellar distance approximately one ocellar diameter. Ocelli large. OOD 0.1-0.5[0.3] LOD.

Mesosoma. Tibiae with scattered short bristles on ventral side only. Forewing (Fig. 9): length 6.4-10.8 [10.1] mm.; longitudinal adventitious vein present in anal cell; cu-a basad (less than 0.5 times its length), opposite or slightly distad of M [slightly distad]; Rs 0.6 to 1.4 [0.9] times the length of M distad of Rs+M; M intersects with m-cu at less than 90° angle; m-cu 1.3 to 2.3 [1.6] times the length of M distad of m-cu; terminus of A may have a distinct 3a′ or may end in a knob; r-m and Rs segment distad of Rs+M tubular but pigment reduced or absent. Hindwing cu-a tubular without pigment (Fig. 21).

Metasoma. Petiole length 2.2-3.3 [2.9] times maximum width.

Male. Similar to female except as follows. Flagellomeres brown. Metasomal segments VI and VII (and sometimes V and parts of IV) are dark brown. Petiole length 1.9-2.4 times maximum width.

SPECIMENS EXAMINED

36 specimens: 9♀, 27♂.

Holotype ♀ VIETNAM: Dac Lac: Yok Don N.P. ca. 2 km SE Ban Don, W. bank of Serepok R. 12-28 JUN 1997. DC Darling, A Guidotti, B Hubley. ROM 974113 Malaise trap (fine); no pans near rapids. riparian vegetation 12°53'N, 107°48'E. 100m. [ROME].

Paratypes: 3♂ same data as holotype; 8♂ VIETNAM: Dac Lac: Yok Don N.P., edge of Dak Ken R., 8 km SW Ban Don. 14-22 JUN 1997 B Hubley, A Lathrop, R Bain. ROM 974102. Dipterocarp forest/bamboo thicket. Malaise trap (coarse); no pans. 12°53'N, 107°48'E; ♂ 17-22 JUN 1997 B. Hubley. ROM 974107 Malaise trap (fine); no pans. Dipterocarp forest/bamboo thicket. 12°53'N, 107°48'E.; 7♂ ca. 2 km SE Ban Don, W. bank of Serepok R. 31 MAY- 12 JUN 1997 DC Darling, A Guidotti, B Hubley. ROM 974112 Malaise trap (fine); no pans near rapids. Riparian vegetation 12°53'N, 107°48'E. 100m.; 2♂,♀ 28 JUN-7 JUL 1997 ROM 974114 [ROME]; 5♀ THAILAND: Huai Kha Khaeng, 400m v.1986 M.Allen 1986 [BMNH]; 2♂ KhaoYai Nat. Park 40 km S of Pak Chong Site 4 p.1., Forest Edge 10-17-11-1989 T.W. Thormin [PMAE]; ♀ 800m. KhaoYai N.P. M.G. Allen iv.1988 [BMNH]; ♀ LAOS: Savannakhet Prov.

Savannakhet 15.IV.1967 Native Collector BISHOP MUSEUM [BPBM].

OTHER SPECIMENS EXAMINED

In the four following specimens, the forewing cu-a vein is more basad of M than in the holotype and paratypes. Since there appeared to be no other characters grouping these specimens together and distinguishing them further from the type material, it was presumed that they did not make up a different species.

♂ CEYLON {SRI LANKA}: Kan Dist. Peradeniya. 1-15 Febraury 1971. Piyadasa & Somapala. [USNM]; ♂ THAILAND KhaoYai Nat. Park 40 km S of Pak Chong Site 4 p.1., Forest Edge 10-17-11-1989 T.W. Thormin [PMAE]; 2♂ VIETNAM: Dac Lac: Yok Don N.P., edge of Dak Ken R., 8 km SW Ban Don. 14-22 JUN 1997 B Hubley, A Lathrop, R Bain. ROM 974102. Dipterocarp forest/bamboo thicket. Malaise trap (coarse); no pans. 12°53'N, 107°48'E [ROME].

Paniscomima angelae new species

BIOLOGY

Host unknown. Collected in dry dipterocarp forest.

DISTRIBUTION

Known only from holotype.

ETYMOLOGY

Named in honour of my mother, Angela Guidotti, who has encouraged and inspired my pursuit of learning.

DIAGNOSIS

The following combination of characters distinguishes this species from all other species of *Paniscomima*. Longitudinal adventitious vein present in anal cell of forewing; OOD 0.5 LOD; in forewing (Fig. 10), cu-a basad 0.75 of M; metasomal segments V and VI dark brown. Flagellomeres brown. Depth of eye emargination is approximately the width of the torulus for this species whereas in *P. abnormis* the depth is approximately half the width of the torulus. The females of *P. abnormis* and *P. darlingi* have a yellow metasoma.

DESCRIPTION

Female. Body colour yellow with some dark brown colouration in the intraocellar area. Scape yellow. Metasomal colour dark yellow; segments V and VI are dark brown.

Head. Ocelli very large. OOD 0.5 LOD. Depth of eye emargination approximately width of torulus.

Mesosoma. Tibiae with scattered short bristles on ventral side only. Hindwing cu-a skeletal. Forewing (Fig. 11): length 6.0 mm.; longitudinal adventitious vein present in anal cell; cu-a basad of M 0.75 times length of cu-a; Rs 1.1 times the length of M distad of Rs+M; M intersects with m-cu at less than 90° angle; m-cu 1.4 times the length of M distad of m-cu; r-m and Rs segment distad of Rs+M tubular, pigment absent; 3a′ present at terminus of A.

Metasoma. Petiole length 2.9 times maximum width.

Male. Unknown.

SPECIMEN EXAMINED

Holotype ♀ VIETNAM: Dac Lac: Yok Don Natl. Pk. Edge of Dak Ken R., 8km SW Ban Don 16-22 JUN 1997. B. Hubley. ROM 974104 Malaise trap (fine); no pans dipterocarp forest 12°53'N, 107°48'E [ROME].

COMMENTS

Note that this specimen was collected from the same general area as specimens of *P. darlingi* n. sp.

Paniscomima paropposita new species

BIOLOGY

Host unknown.

DISTRIBUTION

Known only from holotype.

ETYMOLOGY

From the Latin "par" or close to; *opposita* because of this species' similarity to *P. opposita.*

DIAGNOSIS

This species is similar to *P. opposita* except for in forewing Rs is 3.9 times the length of M distad of Rs+M (Fig. 11); petiole length is 2.3 times width. Male of *P. opposita* forewing Rs is 2.5-2.9 times the length of M distad of Rs+M.

DESCRIPTION

Body yellow. Dark brown in the intraocellar area, brown reaches the eye. Flagellomeres dark brown. Scape yellow. Metasomal dark yellow except segments V, VI, VII and posterior half of IV dark brown.

Head. Ocelli large. OOD 0.2 LOD.

Mesosoma. Forewing: length 8.1 mm; cu-a distad M 0.3 times length of cu-a; Rs 3.9 times length of M distad of Rs+M; M intersects with m-cu at 90° angle; m-cu equal length of M distad of m-cu; terminus of A ends uncurved; r-m, Rs segment distad of Rs +M, and cu-a tubular but pigment absent or minimal. Hindwing cu-a tubular, pigment absent.

Metasoma. Petiole length 2.3 times maximum width.

Female. Unknown.

SPECIMEN EXAMINED: **Holotype**. ♂ THAILAND, Sam Lan at light 21-1-78, G.C. Varley. [BMNH].

Paniscomima opposita Townes

Paniscomima opposita Townes, 1977: 14. **Holotype**: ♂ Nepal, near Simra Adhabar [CNCI] [paratypes examined, CNCI]

BIOLOGY

Host unknown.

DISTRIBUTION

India, Nepal.

DIAGNOSIS

This species can be distinguished from other species of *Paniscomima* by the following combination of characters. Forewing Rs 2.5-3.3 times the length of M distad of Rs+M (♀ 3.3, ♂ 2.5-2.9). Petiole length is 2.6-3 times width. M intersects m-cu at 90° angle. Longitudinal adventitious vein absent in anal cell of forewing

DESCRIPTION

Female. Body yellow. Dark brown in the intraocellar area. Antenna yellow brown.

Head. Ocelli large. OOD 0.2 LOD.

Mesosoma. Forewing: length 8.9 mm; cu-a opposite M; Rs 3.3 times length of M distad of Rs+M; M intersects m-cu at 90° angle; m-cu equal length of M distad of m-cu; terminus of A curves up and joins 2cu-a; r-m and Rs segment distad of Rs+M tubular but with little pigment. Hindwing cu-a tubular, without pigment.

Metasoma. Petiole length 3.0 times maximum width.

Male. Similar to female except as follows. OOD 0.1-0.2 LOD. Flagellomeres dark brown. Forewing: length 7.8-10.3 mm; cu-a opposite M or distad by less than 0.25 length of cu-a; Rs 2.5-2.9 times length of M distad of Rs+M; metasomal dark yellow except segments V, VI, VII brown; petiole length 2.6 times maximum width. Hindwing cu-a white, nebulous .

SPECIMENS EXAMINED

♀ India: And.P. Patancheru, VII.82. [BMNH]; 2♂: NEPAL nr. Simra Adhabhar 600ft. 23-28 Aug. 1967 Malaise Trap No.24 Can.Nepal Exped. Paratype *Paniscomima opposita* Tow. No. 13347 and Gen. No. 18 [CNCI]

Paniscomima seyrigi Berland

Rogezia Seyrigi Berland, 1951: 301. ♂, ♀, des., fig. **Holotype**: Madagascar: Ivondro (Paris). The ♂ described by Berland was redescribed as *P. curta* by Townes (1977). Synonomy by Townes 1977.

BIOLOGY

Host unknown.

DISTRIBUTION

Madagascar.

DIAGNOSIS

The following combination of characters distinguishes this species from all other species of *Paniscomima*. Apex of forewing infuscate. Cu/2cu-a vein of forewing with a basal swelling at junction of Cu. Metasomal segments III-VII dark brown. Petiole short: length ♂ 1.7, ♀ 2.4 times width.

DESCRIPTION

Female. Body yellow with some brown colouration in the intraocellar area, metasoma yellow except segments III-VII dark brown. Antenna yellow.

Head. OOD 2 LOD. Eyes small.

Mesosoma. Forewing: length 10.6 mm; apex infuscate; cu-a distad of M 1.5 length of cu-a; Rs 1.25 the length of M distad of Rs+M; M intersects with m-cu at less than 90° angle; m-cu 2 times the length of M distad of m-cu; Cu/2cu-a vein with a basal swelling at junction of Cu; terminus of A ends flat; r-m tubular, pigment absent.

Metasoma. Petiole length 2.4 times maximum width.

Male. Same as female except for the following: OOD 2.1 LOD; forewing length 8.7 mm; Rs 0.8 the length of M distad of Rs+M; cu-a distad of M 1.2 length of cu-a; petiole length 1.7 times maximum width.

SPECIMEN EXAMINED

♂ MADAGASCAR: Antisiranano R:N:I: de Marojejy 8 km NW Manantenina X. 5-13. 1996, 450m E.Quinter & T. Nguyen. Tributary Manantenina River 14°26.2'S, 49°6.5'E Malaise [USNM].

3.3.3 UNTREATED SPECIES

Paniscomima abnormis Morley
Rhopalosoma abnorme Morley, 1910: 386-390. ♂, ♀. Des., fig. **Holotype**: ♀, Sri Lanka: Manklam (BMNH). ♂ India: Calcutta. Synonymy by Townes, 1977: 13. [Type examined]
Hymenochimaera abnormis Brues, 1926: 19. Synonymy by Townes, 1977: 13.

Paniscomima erlangeriana Enderlein
Paniscomima Erlangeriana Enderlein, 1904: 464-466. **Holotype**: ♀ Somali Umfudu
Rhopalosoma erlangerianum Schulz, 1906: 223-225. Key, syn., des. Synonymy by Krombein 1951:771.
Paniscomima erlangeriana Brues 1926: 18. ♂ des.

Paniscomima bekilyi Berland
Rhopalosoma bekilyi Berland, 1951: 297. ♂, ♀. Des., fig. **Holotype**: ♀ Madagascar: Bekily [Paris]. Synonymy by Townes, 1977. [paratypes examined]

Paniscomima rufoantennata Berland
Rhopalosoma bekilyi var. *rufoantennata* Berland 1951: 298. **Syntype series**: Madagascar [Paris].
Paniscomima rufoantennata Townes, 1977. n. comb. [paratype examined]

Paniscomima curta Townes
Rogezia seyrigi Berland 1951: 301. **Holotype**: ♂ Madagascar, Ivondro, Dec. 1938. A. Seyrig [Paris]. Synonymy by Townes, 1977. [paratypes examined]

3.4 RHOPALOSOMA Cresson

Rhopalosoma Cresson, 1865: 58. **Type species**: *Rhopalosoma poeyi* Cresson. By monotypy.

Sibyllina Westwood, 1868:329. **Type species**: *Sibyllina aenigmatica* Westwood = *Rhopalosoma poeyi* Cresson. By monotypy. Synonomy by Westwood 1874.

BIOLOGY

Rhopalosoma nearcticum Brues is ectoparasitic on crickets of the subfamily Eneopterinae (species of *Orocharis* Uhler and *Hapithus* Uhler) (Hood 1913; Gurney 1953). The host is unknown for other species. The larvae form sac-like structures on the abdomen (exuviae Fig.6). The sac is blackish and can be found on the side near the base of the cricket's hind leg, forcing the leg outward in an unnatural position (Gurney 1953).

DISTRIBUTION

New World: Eastern United States to Southern Brazil.

DIAGNOSIS

The eighteen species of *Rhopalosoma* can be differentiated from those of other rhopalosomatid genera by the following combination of characters. Occipital carina present. Eyes bare. Second segment of labial palp without a thick bristle but may have a weak bristle present. Petiole very long, length 4.0 to 6.8 width. Female tarsal claws long, with a sharp, median tooth and sometimes with an additional blunt tooth toward base (Fig. 20a). Species of *Rhopalosoma* are very similar in overall habitus to those of *Paniscomima*.

DESCRIPTION

Female. Macropterous (Fig. 1). Forewing length 4.8-17mm. Body slender, dark yellow; metasomal segments V-VII may be brown. Intraocellar area brown (rarely reaching the eyes).

Antenna yellow or brown. Clypeus yellow. Labial and maxillary palpi yellow.

Head. Paired apical spines on flagellomeres of subequal length. OOD 0.25-1.25 LOD. Small eye margin notch parallel to or above level of toruli; notch with nearly symmetrical margins; maximum depth of notch approximately 0.5-1 times width of torulus. Ocelli moderately to very large. Smooth, hairless line on vertex extending from middle of toruli to median ocellus. Second segment of labial palp may have weak bristle present.

Mesosoma. Forewing with 8 closed cells. Maximum width of claval lobe in hindwing 1.5-2.1 the length of cu-a; jugal lobe 0.8-0.9 length of subbasal cell. Bristles present on all tibiae and tarsomeres 1, sometimes on meso- and metatarsomeres 2. Apical, lateral fenestrae of female tarsomeres 2, 3, and 4 strong and bell-shaped, delineated by a sharp carina. Tarsal claws elongate and narrow (Fig. 20a).

Metasoma. Petiole length 4.0 to 6.8 times maximum width.

Male. Similar to female except as follows: F6-F8 sometimes also with paired apical spines; bristles sometimes also present on protarsomere 2 and meso- and metatarsomere 3; fenestrae absent; tarsal claws bifid without lanceolate bristles; tarsomeres 1-4 with plantar lobes.

3.5 OLIXON Cameron

Olixon Cameron, 1887. **Type species**: *Olixon testaceum* Cameron. By monotypy.

Harpagocryptus Perkins, R.C. L. 1908: 34-35. **Type species**: *Harpagocryptus australiae* Perkins. By monotypy. Brues, 1922. Synonymy by Townes 1977.

Algoa Brues, 1910: 18. **Type species**: *Algoa heterodoxa* Brues. By monotypy. Synonymy by Townes, 1977.

Apteropompilus Cameron, 1904: 176. **Type species**: *Apteropompilus dentatus* Cameron. By monotypy. Synonymy by Reid, 1939.

Algoella: Kieffer, 1914: 473. = *Algoa* Brues. Synonomy by Townes 1977.

Saphobethylus Kieffer, 1911: 200-233. **Type species**: *Saphobethylus pallidus* Kieffer = *testaceum* Cameron. By monotypy. Synonymy by Turner and Waterston, 1917.

Nealgoa Brues, 1922: 101-109. **Type species**: *Nealgoa banksii* Brues. By original designation. Synonymy by Krombein 1949.

Psyllosphex Arnold, 1935: 479. **Type species**: *Psyllosphex saltator* Arnold. By original designation. Synonymy by Townes 1977.

BIOLOGY

Perkins (1908) reported that the larva of *Harpagocryptus* (=*Olixon*) *australiae* Perkins form a sac similar to that of the dryinid *Aphelopus*. Townes (1977) wrote that *Olixon banksii* Brues "has been found active at night as well as by day" but does not provide any more information. He also reports that "there is circumstantial evidence that *O. banksii* parasitizes crickets of the genus *Neonemobius (Nemobius)* [Hebard] and that *O. testaceum* Cameron parasitizes crickets of the genus *Cycloptilum* [Scudder]" but does say where this evidence can be found.

DISTRIBUTION

Of the eight described species, one is found in the U.S., one in Central and South America, four in Africa and two in Australia. (See Table 1).

DIAGNOSIS

The eight species of *Olixon* can be differentiated from those of other genera of Rhoplasomatidae by the following characters. **Brachypterous or apterous: wings vestigial or absent, not extending beyond apex of tergum 1. Eye elliptic, inner margin straight. Thick bristle absent from second segment of labial palp. Mandibles quadridentate.**

DESCRIPTION

Female. Brachypterous or apterous (Fig. 2). Body blackish brown or black or yellow with brown markings. Body length 2.9-7.0 mm. Antenna colour variable. Mesosoma modified as in other apterous Hymenoptera (Townes 1977).

Head. Head with occipital carina and concave posteriorly; the occipital carina incomplete. Eye with inner margin straight. Ocelli reduced or absent. Antennal insertion below lower margin of eye. Spines on apex of flagellomeres absent, if present, weak. Labrum exposed, subtriangular; ventral margin smoothly rounded or weakly bilobed. Mandibles quadentate. Apex of third segment of maxillary palp with thick bristle.

Mesosoma. Pronotum longer than length of head, more than twice as long as mesoscutum. Posterolateral apex of pronotum rounded anterior to tegula. Prepectus, very short but extending over most of height of mesepisternum, fused with mesepisternum and concealed under posteroventral margin of pronotum. Mesepimeron and mesepisternum fused. Mesopleuron and metapleuron without pits. Rounded lobe covering mesocoxa contiguous with mesosternum, transverse suture incomplete. Propodeum often with posterolateral projections. Profemur swollen and shorter than metafemur, especially in female. Tarsomeres 3-5 wide, flat and concave ventrally; apical fenestrae absent. Bristles absent on femora and tibiae, sometimes present ventrally on basitarsus. Tarsal claws short and stout, sometimes with flat lanceolate bristle. No closed cells in wings. Forewing with costal vein present and some longitudinal skeletal veins. Hindwing, if present, reduced to a short, thread-like vestige.

Metasoma. Sessile. Petiole length 0.3 -0.6 times maximum width. Constriction between first and second metasomal segments minimal. First tergum with complete lateral longitudinal carina but lacking a posterodorsal median pit. Anterior margin of sternum 1 straight or slightly curved. Anterodorsal impression absent on metasomal segment 2.

Male. Similar to female except as follows: tarsomeres slightly flat, more rounded than in female. Genitalia with parameres apically produced into elongate, upwardly curved, needle-like processes. Different from other genera as follows: tarsal claws bifid; inner claw much larger than outer claw, may appear as a large tooth. Plantar lobes on tarsomeres absent. Hypopygium with very short dark hairs apically.

COMMENTS

Naumann and Austin (in prep.) are revising the Australian species.

4. PHYLOGENETIC ANALYSIS

4.1 CHARACTERS AND CHARACTER STATES

The following sixty-three characters were used in the analyses. All characters are treated as unordered. Comments are included where relevant. Where clarification is needed, illustrations are included. Equivalent characters from Brothers and Carpenter (1993) are specified BC. The data matrix for character distributions is given in Table 2.

1. Shape of vertex

0: smoothly rounded

1: flat, ending sharply at the occiput

2. Occipital carina

0: present

1: absent

3. Size of ocelli

0: small, OOD$\geq$2 LOD

1: very small or absent

2: large, OOD >0.8 and < 2 LOD

3: very large, OOD between 0.1 to 0.5 LOD

Although the measurement of LOD shows overlap at the length of 2 LOD, the size of the ocelli differentiates the character states. Character state 1 is for *Olixon*; ocelli, if present, are very tiny (almost impossible to see). OOD is much greater than 2 LOD.

4. Shape of inner eye margin

0: rounded, or very weakly emarginate (Fig. 17)

1: emarginate, margins nearly symmetrical (Figs. 14, 15)

2: emarginate margins asymmetrical (Fig. 16)

Symmetry was determined by comparing margins above and below the deepest point of the emargination.

5. Depth of emargination of eye

0: eye rounded or weakly emarginate

1: shallow, approximately half maximum width of torulus

2: deep, approximately maximum width of torulus

3: very deep, 1.5 times maximum width of torulus

The emargination was measured at the maximum depth.

6. Short setae on eye

0: absent

1: present

7. Antennal insertion

0: below or level with emargination, central on frons

1: level with or below lower eye margin

8. Bristle on segment 2 of the labial palp

0: absent

1: present, long and thick (Fig. 18)

2: if present, very weak

State 1 of this character is very distinct in *Paniscomima* and *Liosphex* species. State 2 is for *Rhopalosoma* species in which the bristle appears to blend in with the hairs on the palp.

9. Labial palp

0: segments all about the same length and short

1: 2 basal segments short and thick, 2 apical ones long and narrow

2: 3 basal segments short and thick, apical segment long and narrow

10. Maxillary palp, 6 segmented

0: basal segment (s) short, 4 or 5 apical segments of medium length and width

1: 3 basal segments short and thick, 3 apical segments long and narrow

11. Thick bristle on third segment of maxillary palpi

0: absent

1: present

12. Apex of mandible

    0: bidentate

    1: tridentate

    2: quadridentate

13. Mandible colour

    0: brown

    1: yellow with dark brown teeth

14. Spines on apex of flagellomeres

    0: absent

    1: pair of spines on basal 5-8 segments

Note that some species of *Olixon* may have a short weak spine at apex of some basal segments (Townes 1977). None of the *Olixon* species coded for this analysis had this state.

15. Paired spines on flagelllomeres

    0: absent

    1: one spine 2-4 times the length of the other

    2: subequal length (maximum 1.5 times length of other)

16. Posterior margin of pronotum

    0: weakly or deeply concave and with posterolateral apex rounded

    1: weakly or deeply concave and with posterolateral apex weakly truncate

17. Prepectus

0: free with each half narrowed and widely separated from its counterpart

1: very short but extending over most of height of mesepisternum, fused with mesepisternum and concealed under posterolateral margin of pronotum

2: narrow and short, a small elongate strip articulating with or fused to anterior margin of mesepisternum

BC 48, 50. Brothers and Carpenter coded 6 different variables for the prepectus.

18. Mesepimeron and mesepisternum

0: fused

1: differentiated by a complete pleural sulcus

19. Deep median circular pit on mesepisternum

0: absent

1: present

20. Endophragmal pit on anterior margin of metapleuron

0: absent

1: present

21. Bare (smooth or weakly sculptured), hairless area on the metapleuron

0: absent

1: present

22. Shape of posterior edge of mesosternum

0: smoothly truncate

1: short transverse carina or rounded expansion

2: triangular lobe covering mesocoxa separated from mesosternum by a complete transverse suture (Fig. 13)

3: rounded lobe covering mesocoxa separated by an incomplete transverse suture

Modified BC 56. I have added the sutures to this character because the lobes do not appear to be homologous. This character is also found in Tiphiidae which were not included in this study. One that was examined (*Tiphia* sp.), showed a partial suture on the lobes.

23. Sharp projections on apicodorsal sides of propodeum

0: absent, propodeum smoothly convex or with a carinate ridge

1: present

24. Width of profemur

0: smaller than metafemur

1: approximately the same size or slightly wider than metafemur

2: swollen, much wider than metafemur and slightly shorter

I divided BC 112 into two characters: #24 and #29. The swelling of the profemur is negligible in macropterous rhopalosomatids. The shape of the tarsomeres (#29) does not co-vary with the width of the profemur as suggested by Brothers and Carpenter (1993).

25. Scattered bristles on meso- and metafemora

0: absent

1: present in apical third

26. Basal metatarsomere

0: unmodified, rounded

1: basal quarter with a narrow fringe

2: basal quarter with a comb of hairs on a carinate ridge (Fig. 24)

27. Inner metatibial spur (or calcar)

0: unmodified

1: enlarged at base with a short, dorsal tuft of bristles (Fig. 24)

2: basal dorsal tuft pectinate, extending halfway along length of spur

Modified BC 132. Brother and Carpenter (1993) actually have 5 characters that describe the inner metatibial spur of different taxa. Character state 1 above is shared by the Pompilidae and macropterous rhopalosomatids, whereas character state 2 is the condition in *Olixon*. The condition for *Olixon* is described by Brothers and Carpenter as follows "Inner spur modified as a calcar by formation of dorsal tuft of bristles and development of finely pectinate dorsal carina." I could not verify the dorsal carina.

28. Scattered bristles on surface of meso- and metatibiae and basitarsomeres

0: absent from at least one of these

1: present

Some taxa have scattered bristles on additional parts of the legs. This character does not refer to the bristles that are present at the apices of leg segments. Brothers and Carpenter (1993) used 6 characters (variables) to describe the bristles or spines. However, I found that "very strong", versus "moderately strong" spines was too subjective to quantify. These bristles are absent from *Olixon*.

29. Shape of female tarsomeres

0: cylindrical or conical

1: 3-5 flat, widened, weakly concave ventrally

2: 2-5 flat, widened, weakly concave ventrally (Fig. 8)

Tarsomeres of *Olixon* (state 1) are not as strongly widened as the other genera.

30. Apilateral fenestrae (Fig. 19) on tarsomeres of female

0: absent

1: present

31. Apilateral fenestrae on female tarsomeres

0: absent

1: weak, visible only with transmitted light

2: strong, sharply delineated (Fig. 19)

Character 1 is the state for *Liosphex* spp. The fenestrae appear as slits in these species; their presence is only noted with transmitted light.

32. Apical fenestrae on female tarsomeres

0: absent

1: present on tarsomeres 2 and 3

2: present on tarsomeres 2 - 4

33. Width of female tarsal claws

0: small, long and narrow

1: large, long and narrow (Fig. 20a)

2: stout and short (Fig. 20b,c)

34. Short medial tooth on female tarsal claws (Fig. 20a)

0: absent

1: present

35. Flat lanceolate bristle on female tarsal claws (Fig. 20)

0: absent

1: present

36. Male tarsal claws

0: simple

1: bifid, of approximately equal length and size

2: bifid, one claw much thicker than the other

37. Plantar lobes on male tarsi (Fig. 23)

0: absent

1: present on tarsomeres 1-4

2: present on tarsomeres 2-4

38. Wing development

0: macropterous (unlike state 1)

1: macropterous with eight or nine closed cells in the forewing (Figs. 9, 10, 11)

2: brachypterous or apterous

3: female apterous, male macropterous

39. Forewing M intersects m-cu

0: at less than 90° (Figs. 9, 10)

1: at 90° (Fig. 11)

40. Forewing cu-a position relative to M

0: opposite, slightly distad (up to 0.3 times length of cu-a) or basad slightly (up to 0.5 times length of cu-a)

1: distad 0.4 to 1.5 times length of cu-a

2: distad 1.7 + times length of cu-a

3: basad 0.75 - 0.9 times length of cu-a (Fig. 10)

According to Carpenter (1982), the plesiomorphic position of cu-a is distad of the fork with M+Cu. The apomorphic position is basad.

41. Curvature of cu-a in forewing

0: straight

1: angled forward

2: curved arc

3: angled backward

4: sinuate

The plesiomorphic condition of cu-a in vespoids is curved along its length giving a concave appearance, i.e., character state 2 (Carpenter 1982).

42. Forewing: junction of Cu with 2cu-a

0: a thick distal swelling

1: flat smooth, slightly thickens in 2cu-a

2: a thick basal swelling

3: a smooth flat arc, vein thickness constant

4: sinuate curve, vein thickness constant

43. Costal cell on forewing

0: present

1: C+ Sc+R fused (or appear fused), costal cell, if present, small (Figs. 9, 10, 11)

Note that a reduced costal cell is also found in Ichneumonidae.

44. Presence of longitudinal adventious vein in anal cell of forewing (Fig. 9, 10)

0: absent

1: present

45. Colouration of forewing

0: concolourous

1: apex infuscate

46. Fuscate spot at end of A in forewing (Figs. 9, 10, 11)

0: absent

1: present

47. Terminus of A in forewing

0: curves up and joins cu-a or ends in a straight line

1: ends in a knob or 3a′ present (Fig. 9)

48. Forewing CuP vein

0: not visible

1: concave, spectral

Mason (1990) states that this vein is nebulous or 'plain to see' in rhopalosomatids. I did not find this to be the case and it is here coded as spectral.

49. Apical section of M in hindwing primarily

0: spectral

1: nebulous or tubular

50. Length of jugal lobe in hindwing

0: short, 0.3-0.5 length of subbasal cell

1: long, 0.7-1.0 length of subbasal cell

2: absent

51. Constriction between petiole and metasomal segment 2

0: absent

1: weak (Fig. 2)

2: strong constriction (Figs. 1, 3, 4)

52. Length of female petiole

0: very short, 0.33-0.6 times as long as wide

1: short, 1.3-2.0 times as long as wide

2: long, 2.2-3.7 times as long as wide

3: very long, 4-6.8 times as long as wide

53. Posterior median pit on petiole

0: absent

1: present

54. Lateral longitudinal carina on petiole

0: absent

1: present, incomplete, almost reaching posterior margin

2: present, complete

55. Anterior margin of sternum 1

0: straight edge or weakly concave

1: deeply concave

56. Lateral longitudinal carina on second tergum

0: absent

1: present, incomplete, not reaching posterior margin

57. Paired, hairless, sculptured, anterodorsal impressions on tergum II

0: absent

1: present, longitudinal and cigar shaped

2: present, circular

58. Male metasoma colour

0: other than yellow or yellow with brown in posterior segments

1: yellow

2: mostly yellow, brown/black in posterior segments

59. Female metasoma colour

0: other than yellow or yellow with brown in posterior segments

1: yellow

2: yellow, brown in posterior segments

60. Tergum VI of female

0: evenly haired

1: medial hairless strip present

61. Apical depression (Fig. 25) on tergum VI of female

0: absent

1: present

62. Row of long lanceolate bristles in a row on apex of male hypopygium (Fig. 22)

    0: absent

    1: present

63. Hypopygium of female

    0: smoothly rounded or unlike state 1

    1: with a longitudinal bare ridge/carina medially

Only characters that could be verified were included in the analyses. Using this criterion made it necessary to omit from the analyses three characters that may have been synapomorphies of the family (2 and 3 used by Brothers and Carpenter (1993)).

(1) Of the four species of *Olixon* examined (from Africa and the New World), no trace of a spine could be found on the flagellomeres. However, Naumann (pers. comm.) reports that some Australian *Olixon* may have this character and Townes (1977) includes it in his description of *Olixon*.

(2) The behavioural character of ectoparasitism on the Gryllidae has only been reported in two species of rhopalosomatids, *Rhopalosoma nearcticum* and *Olixon australiae*. No description, lack of illustrations and missing exuviae of the latter species made it impossible to check the homology of this character state. Until more information is known about the hosts of the remaining species, this character is not informative in a species-level phylogenetic analysis.

(3) Brothers and Carpenter (1993) also code larval lifestyle (character 205) of *Olixon* and rhopalosomatids as being 'entirely ectoparasitic with cyst formation'. The difference between state 1 and state 2 of this character is whether the first instar is endo- or ectoparasitic. Perkins'

(1908) only comment about the larval habits of of *Olixon australiae* is that the "larval sac is of the same form as that of *Aphelopus*" (a dryinid). There is insufficient information to conclude whether *Olixon* larvae develop entirely ectoparasitically or endo- and ectoparasitically.

Table 2: Data matrix used in the Cladistic Analysis of Rhopalosomatidae

Sierolomorphidae	000001101?	?000000100	0000002000	0001000000	1100000102
	1002012000	000			
Pompilidae	0000000000	0000000001	0100011100	0000012000	2000010010
	0101000000	001			
Bradynobaenidae	00$_{0/1/2}$000$_{0/1}$020	00100$_{0/1}$200$_{0/1}$	0001000000	0011000300	00001001$_{0/1\ 1/2}$
	2200000110	000			
Liosphex trichopleurum	0102210121	0111112111	1201021121	1120111100	1310010110
	2111111002	111			
Liosphex varius	0102210121	0111112111	1201121121	1120112102	0110$_{0/1}$10100
	2111111002	111			
Rhopalosoma alvarengi	0031200221	0111212111	0201021121	2211111102	4410010111
	2311111112	111			
Rhopalosoma nearcticum	0021100221	0111212111	0201021121	2211111102	4410010111
	2311111112	111			
Mesorhopalosoma	??300?????	??????????	??0?0??0??	???????100	1010?00?1?
	2?????????	???			
Olixon banksii	1010001011	1210001000	0312022010	00200202--	--1-00-0--
	1002010121	000			
Olixon testaceum	1010001011	1210001000	0312022010	00201202--	--1-00-0--
	1002010111	000			
Olixon majus	1010001011	1210001000	0?12022010	00201??2--	--1-00-0--
	1002010001	0?0			
Paniscomima abnormis	002110012?	0111212111	020102112?	2120???103	3311011??1
	221?1?1?1?	???			
Paniscomima angelae	0031200121	0111212111	0201021121	21202??103	0111011111
	221111?22	1?1			
Paniscomima bekilyi	0031200121	0111212111	0201021121	2120211101	1210010111
	2211111112	111			

Table 2: Data matrix used in the Cladistic Analysis of Rhopalosomatidae

Paniscomima curta	0 0 3 1 3 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 ? ?	? ? ? ? ? 1 1 1 0 1	1 2 1 0 0 1 0 1 1 1
	2 2 1 1 1 1 1 2 ? ?	? 1 1			
Paniscomima darlingi	0 0 3 1 2 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 2 1	2 1 2 0 2 1 1 1 0 0	0 1 1 1 0 1 1 1 1 1
	2 2 1 1 1 1 1 2 1 2	1 1 1			
Paniscomima erlangeriana	0 0 3 1 2 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 2 1	2 1 2 0 2 1 1 1 0 1	3 3 1 0 0 1 0 1 1 1
	2 2 1 1 1 1 1 1 1 2	1 1 1			
Paniscomima paropposita	0 0 3 1 2 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 ? ?	? ? ? ? ? 1 1 1 1 0	2 1 1 0 0 1 0 1 1 1
	2 2 1 1 1 1 1 2 ? ?	? 1 1			
Paniscomima opposita	0 0 3 1 2 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 2 1	2 1 2 0 2 1 1 1 1 0	2 1 1 0 0 1 0 1 1 1
	2 2 1 1 1 1 1 2 1 2	1 1 1			
Paniscomima rufoantennata	0 0 3 1 2 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 2 1	2 1 2 0 2 ? ? 1 0 1	1 2 1 0 0 1 0 1 1 1
	2 2 1 1 1 1 1 ? 1 2	1 ? 1			
Paniscomima seyrigi	0 0 0 1 1 0 0 1 2 1	0 1 1 1 2 1 2 1 1 1	0 2 0 1 0 2 1 1 2 ?	? ? ? 0 ? 1 1 1 0 1	2 2 1 0 1 1 0 1 1 1
	2 2 1 1 1 1 1 2 2 ?	? 1 ?			

Table 3: Results of Cladistic Analyses

Analysis	Excluded taxa	outgroups	multistate taxa	# of trees	tree length	CI	RI	RC	# of trees after SW	Strict consensus tree (Figure)
1.	-	Pomp	poly	54	114	0.84	0.89	0.75	42	26
2.	Meso	Pomp	poly	18	112	0.86	0.90	0.77	18	27
3.	-	Brad	poly	234	119	0.84	0.88	0.74	81	28
4.	Meso	Brad	poly	81	118	0.85	0.88	0.75	79	29
5.	-	Sier	poly	42	114	0.83	0.88	0.74	42	30
6.	Meso	Sier	poly	42	112	0.84	0.89	0.74	42	31
7.	-	Pomp, Brad	poly	18	137	0.80	0.85	0.68	18	32
8.	Meso	Pomp, Brad	poly	6	135	0.81	0.86	0.69	6	33
9.	-	Sier, Pomp, Brad	poly	360	153	0.73	0.82	0.60	6	34
10.	Meso	Sier, Pomp, Brad	poly	24	150	0.74	0.83	0.61	6	35
11.	-	Pomp	?	54	113	0.84	0.89	0.75	42	
12.	Meso	Pomp	?	18	111	0.86	0.9	0.77	18	
13.	Meso	Pomp, Brad	?	6	127	0.80	0.86	0.68	6	
14.	-	Sier, Pomp, Brad	?	360	145	0.71	0.82	0.58	6	

Search type heuristic. Characters equally weighted. In #7, #8, #9, #10, #13, #14, OGs considered paraphyletic or basal polytomy. All characters unordered. Each analysis includes all coded species of Rhopalosomatidae unless otherwise indicated. Bradynobaenidae - Brad, Sierolomorphidae - Sier, Pompilidae - Pomp, Meso - *Mesorhopalosoma*, poly- polymorphism, ? - uncertainty, SW - Successive weighting.

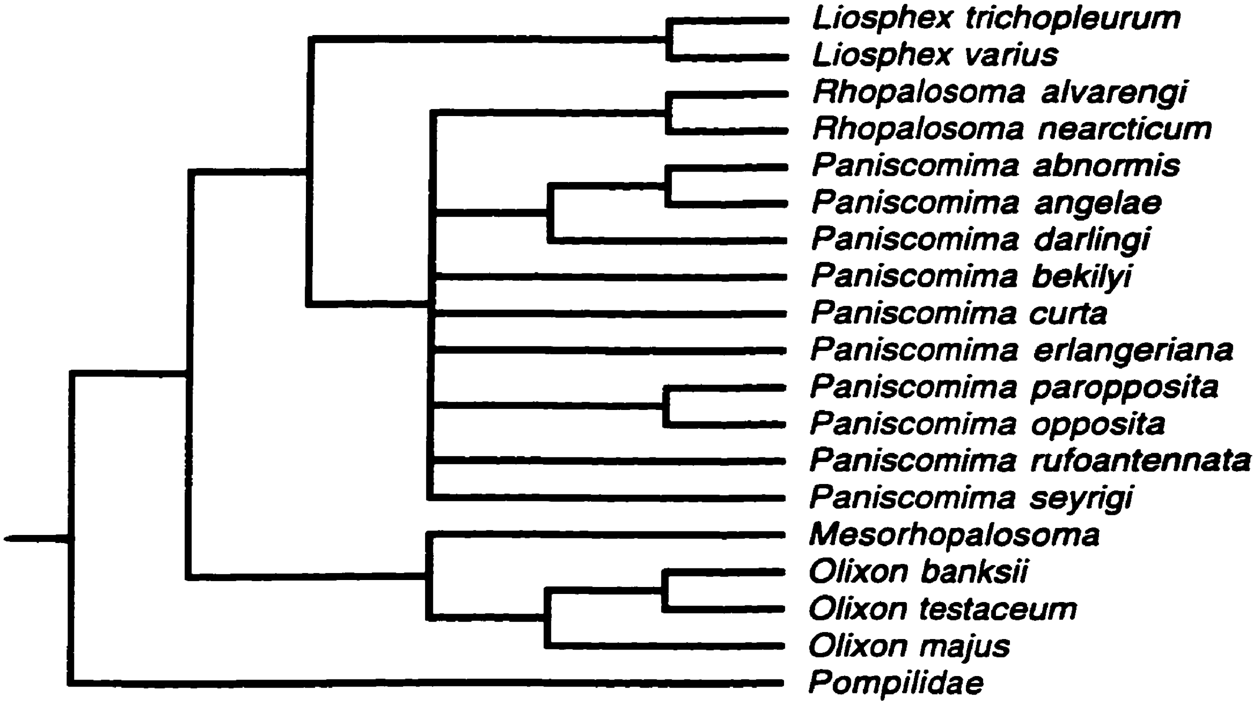

Figure 26: Analysis 1: Strict consensus tree from 54 EPTs

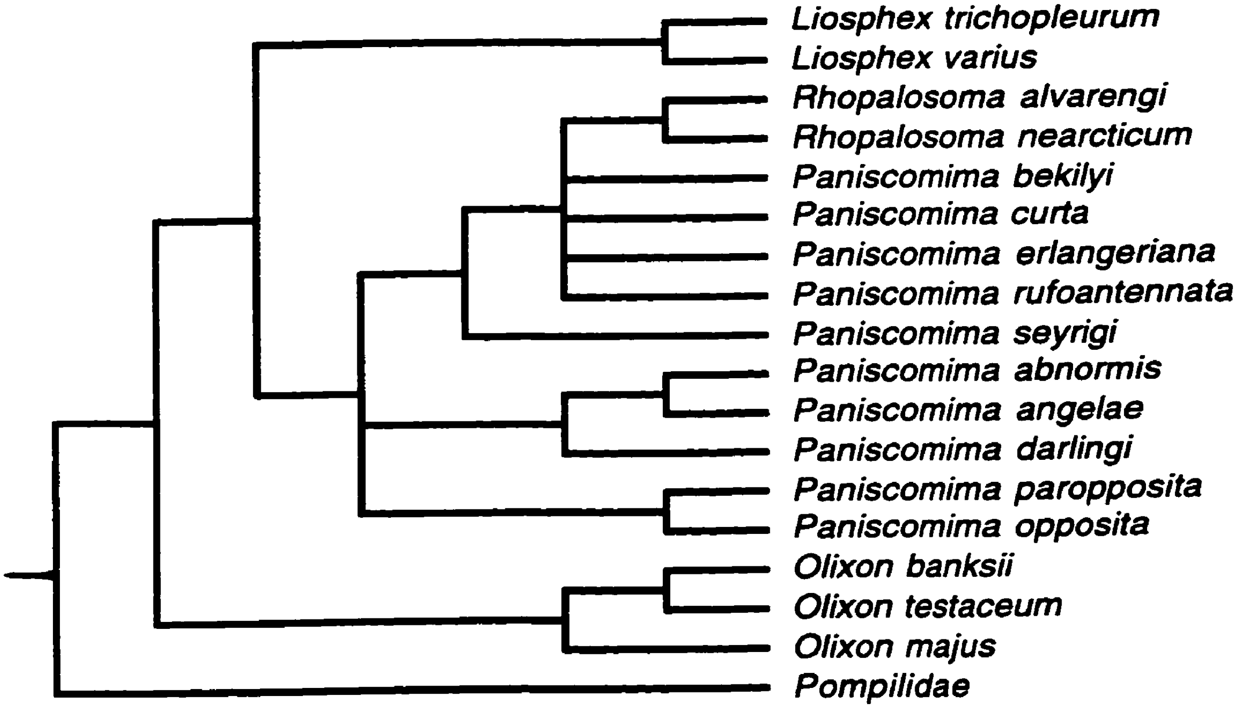

Figure 27: Analysis 2: Strict consensus tree from 18 EPTs

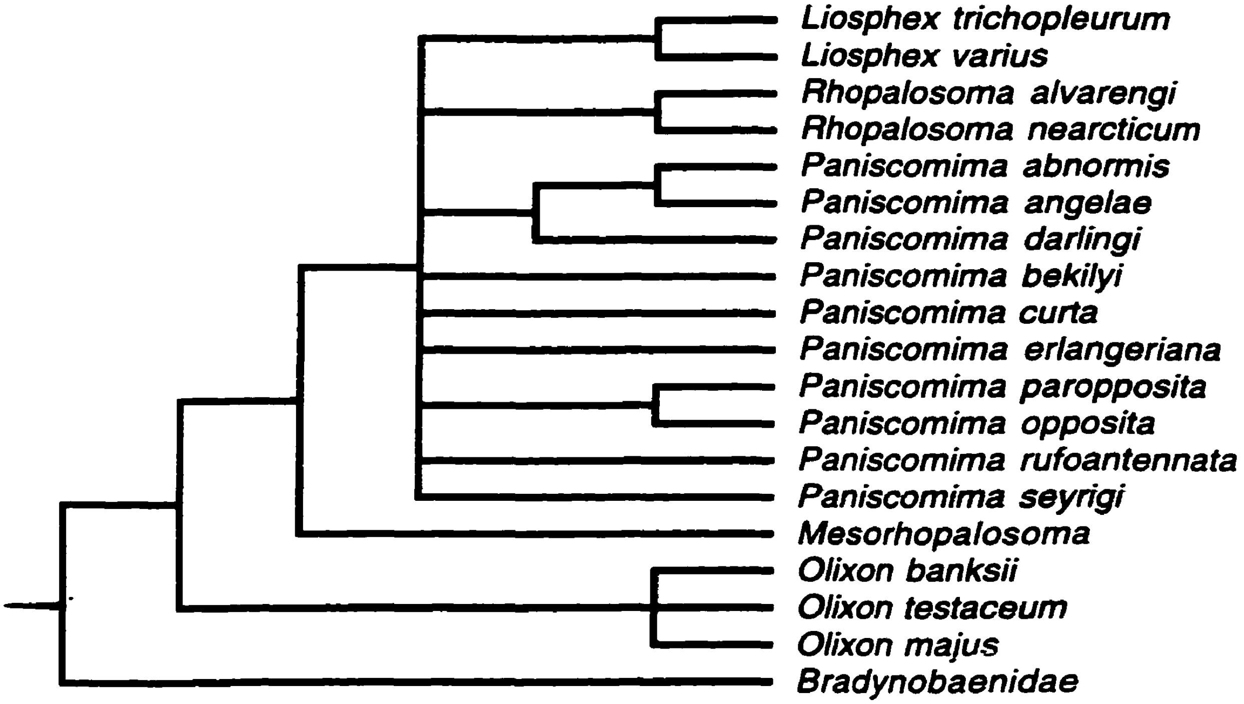

Figure 28: Analysis 3: Strict consensus tree from 234 EPTs

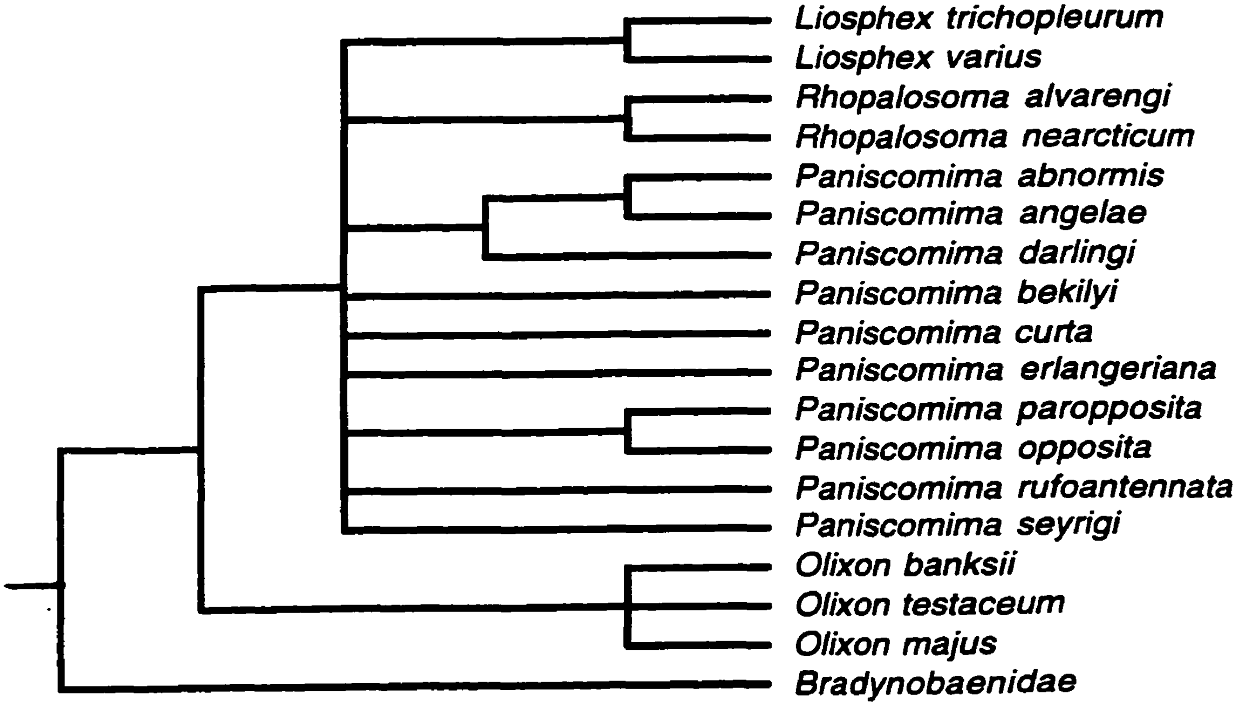

Figure 29: Analysis 4: Strict consensus tree from 81 EPTs

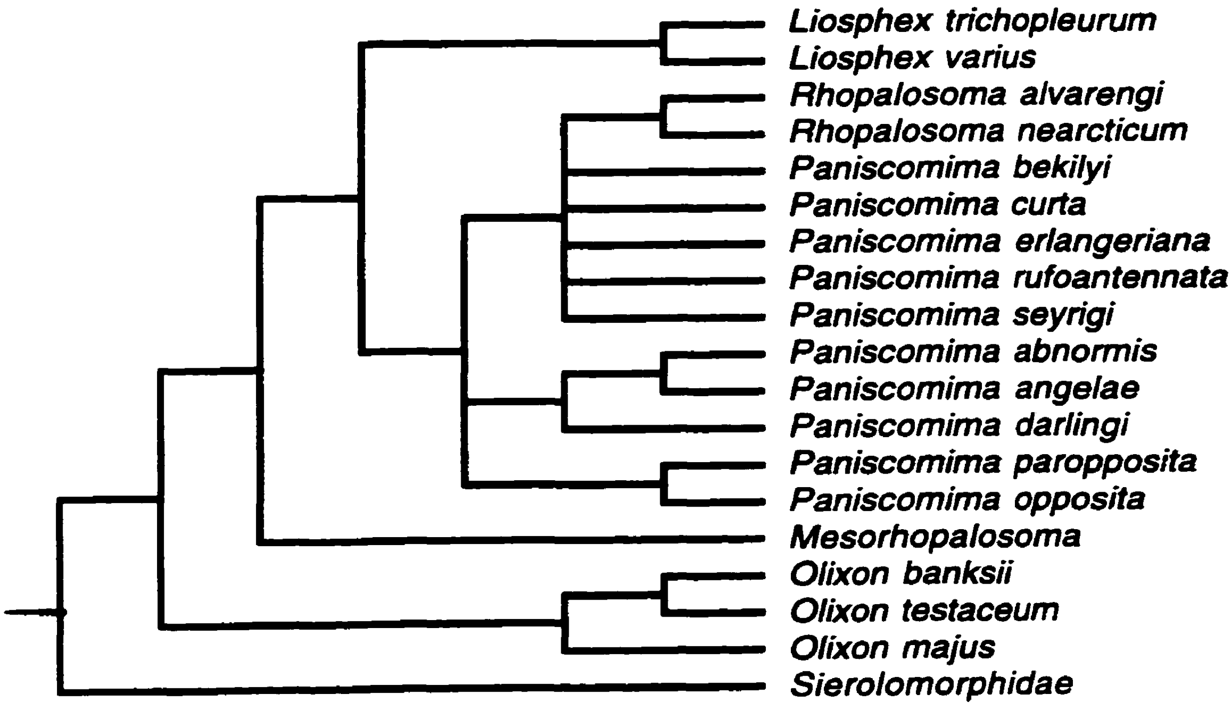

Figure 30: Analysis 5: Strict consensus tree from 42 EPTs

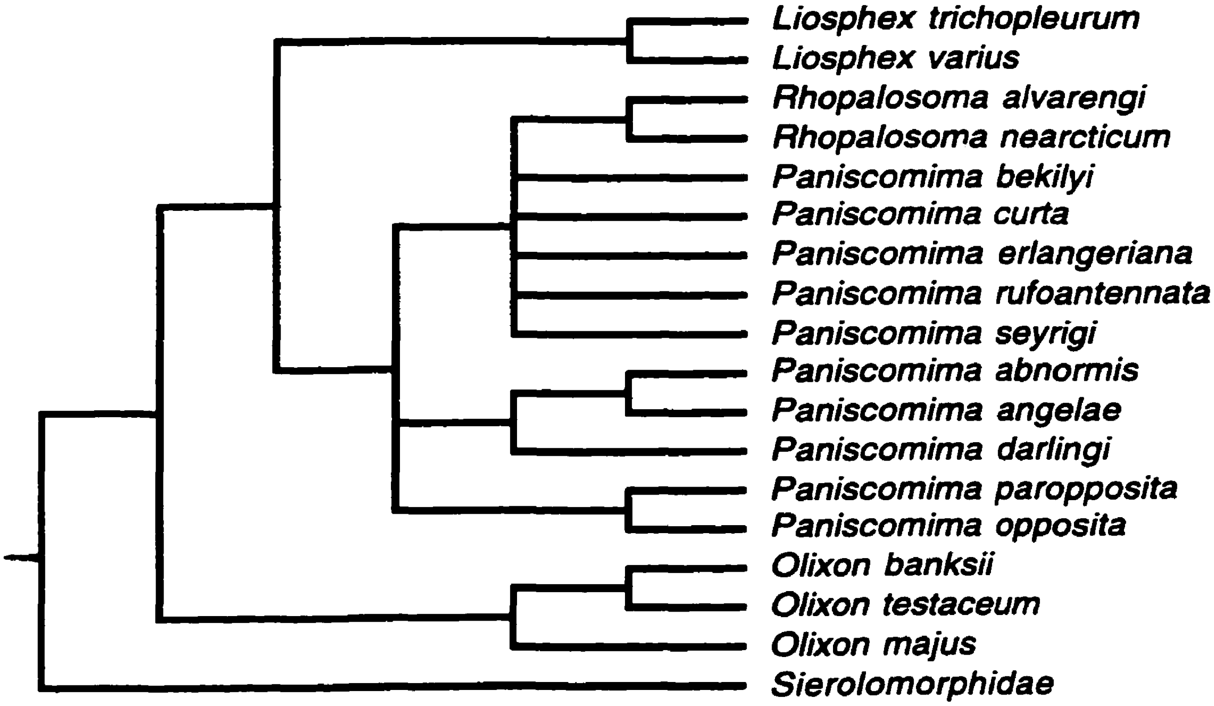

Figure 31: Analysis 6: Strict consensus tree from 42 EPTs

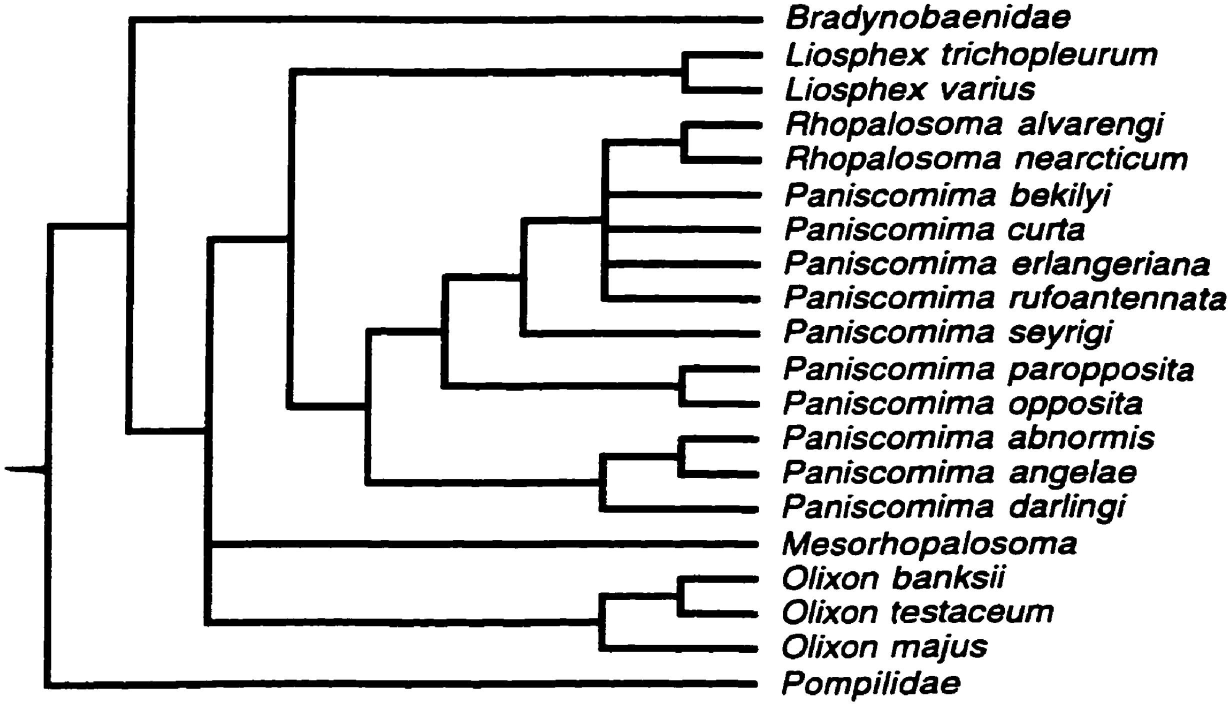

Figure 32: Analysis 7: Strict consensus tree from 18 EPTs

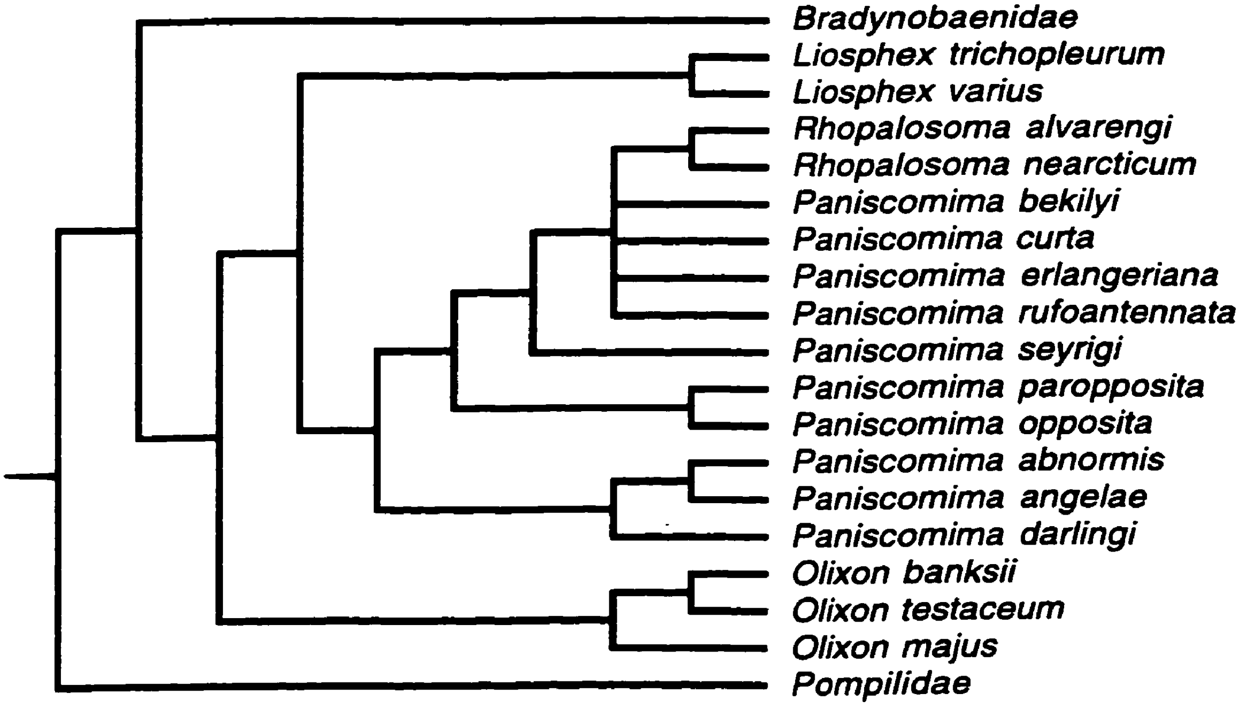

Figure 33: Analysis 8: Strict consensus tree from 6 EPTs

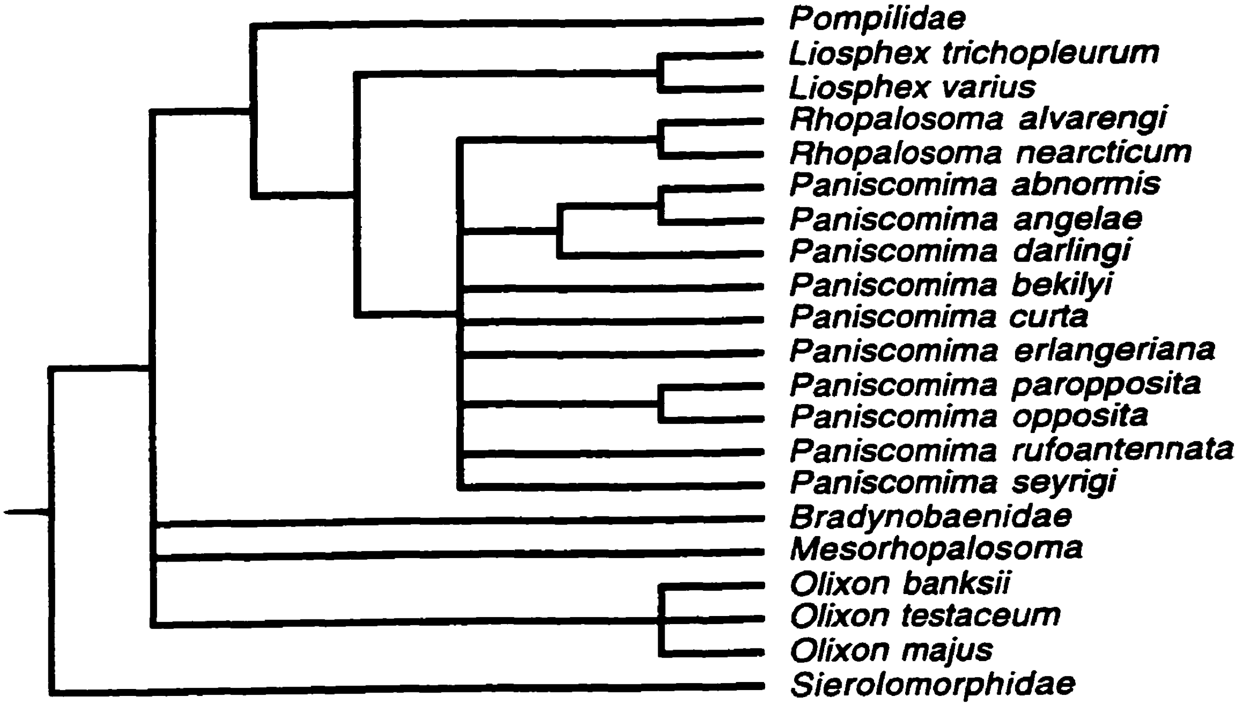

Figure 34: Analysis 9: Strict consensus tree from 360 EPTs

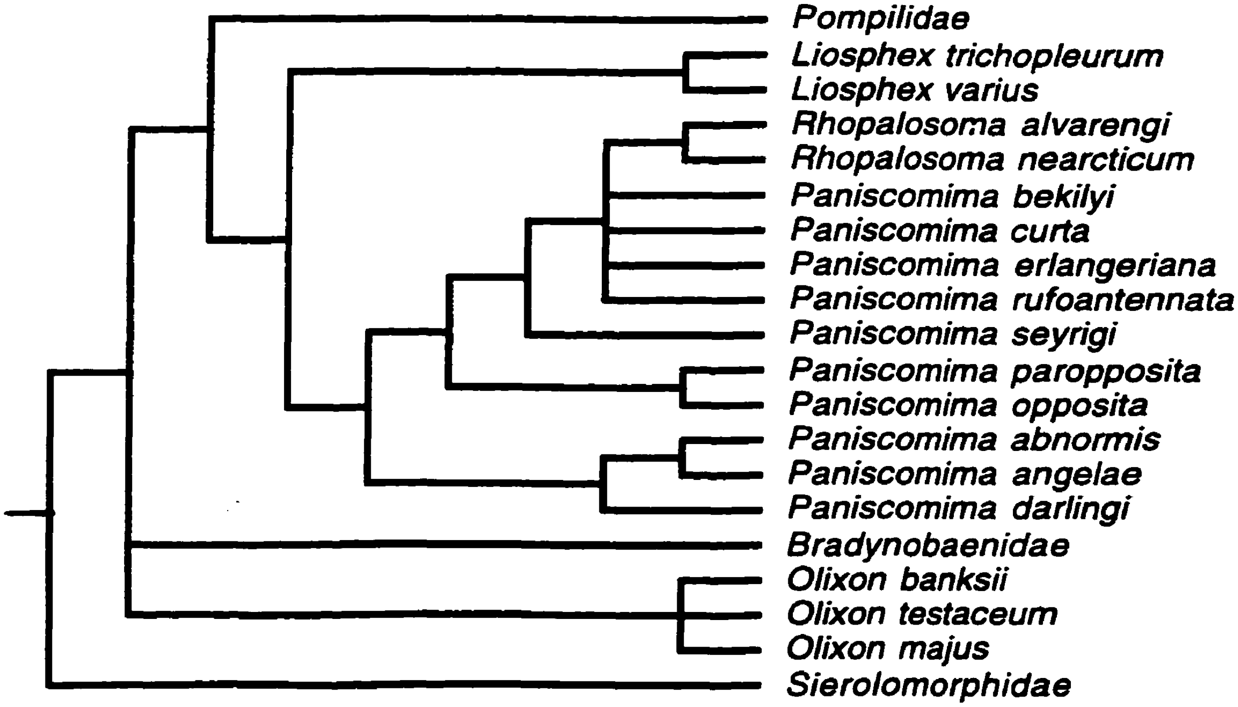

Figure 35: Analysis 10: Strict consensus tree from 24 EPTs

4.2 CLADISTIC ANALYSES

The matrix used to reconstruct the phylogeny of the Rhopalosomatidae is shown in Table 2. Table 3 summarizes the results of each cladistic analysis. Multistate characters were treated as unordered. Each combination of outgroups and taxa resulted in a different number of equally parsimonious trees (EPTs). Each of the combinations was also executed without the fossil *Mesorhopalosoma* because of the high percentage of missing data in this taxon. In every analysis, when more than one most equally parsimonious tree (EPT) was obtained, strict consensus trees were constructed.

Consensus trees may be viewed as a way of reaching the most conservative conclusion possible (Kluge and Wolf 1993). They summarize areas of congruence among equally parsimonious trees, are generally less resolved than any of the EPTs, and consequently have less explanatory power than any of them (Farris 1983). In addition, consensus trees are simply statements about areas of agreement among trees; they should not be interpreted as phylogenies (Swofford 1991). Polytomies on a consensus tree are areas of uncertain resolution, they usually do not indicate simultaneous cladogenetic events. Consensus trees may not be a precise hypothesis, but by restricting the hypothesis to points in which conflicting hypotheses agree, there is less risk of proposing an incorrect hypothesis. "Consensus trees cannot faithfully produce parsimonious solutions from multiple character sets because they cannot resolve conflict and ambiguity according to evidence. Consensus cladograms are generated from fundamental cladograms instead of original information." (Miyamoto 1985). Because there is a large number of analyses in this study, a comparison of strict consensus trees was deemed the most expedient way of determining congruence among analyses. However, because consensus trees are not phylogenies (Swofford 1991), one of the equally parsimonious trees is selected as a solution cladogram in order to examine character evolution and biogeographical implications.

EPTs were subjected to successive approximations character weighting using the rescaled consistency index (Farris, 1989) to reduce the number of trees. This technique selects cladograms based on the set of most consistent characters (Carpenter 1988), i.e., those that provide the strongest evidence. Resultant trees were examined in order to determine whether successively weighted trees were identical in topology to the original trees. The majority of analyses were performed selecting the polymorphism option for multistate characters. The last four analyses (Table 3: 11-14) were executed selecting multistate characters as uncertainties. Trees that resulted from successive weighting of EPTs had the same topology as trees from the analyses in which multistate characters were treated as polymorphisms (analyses 1, 2, 8, 9).

Resolution of *Olixon* species will not be addressed in these analyses. There are additional species in the genus not coded here. The purpose of including multiple species of *Olixon* in this exercise was not to resolve intrageneric relationships but only to confirm monophyly. Any relationship between the three taxa arising from these analyses should be viewed with caution.

In comparing the analyses where all taxa and a single outgroup is used (Table 3: Analyses 1, 3, 5), the shortest length was found when the Pompilidae or the Sierolomorphidae are selected (Analyses 1 and 5: 114 steps). Summary statistics for the Pompilidae as outgroup (CI 0.84, RI 0.89, RC 0.75) are marginally better than those for the Sierolomorphidae as outgroup (CI 0.83, RI 0.88, RC 0.74). A strict consensus tree of the 54 EPTs (Fig. 26) shows that the monophyly of *Liosphex* and *Rhopalosoma* is supported but that *Paniscomima* species form a polytomy with *Rhopalosoma*. Based on this tree, *Paniscomima* could theoreticallt be resolved as monophyletic. This relationship ((*Mesorhopalosoma*, *Olixon*) (*Liosphex* (*Rhopalosoma* +*Paniscomima*))) of the genera is proposed. Successive weighting produced 42 trees. A strict consensus tree produced from 18 EPTs (Fig. 27) after removal of *Mesorhopalosoma* from the matrix (Analysis 2) suggests that the genus *Paniscomima* is paraphyletic.

Analysis 3, where the Bradynobaenidae was selected as outgroup, produced 234 EPTs of 119 steps (summary statistics: CI 0.84, RI 0.88, RC 0.74). In this analysis, a strict consensus of EPTs resulted in the following relationships (*Olixon* (*Mesorhopalosoma* (*Liosphex* + *Rhopalosoma* + *Paniscomima*))) (Fig. 28). While this consensus tree supports the monophyly of *Liosphex* and *Rhopalosoma, Paniscomima* species form a polytomy with these genera. Successive weighting produced 81 trees. Removal of *Mesorhopalosoma* from the matrix (Analysis 4) did not change the topology (Fig. 29) of the consensus tree.

Analysis 5, where the Sierolomorphidae is outgroup, resulted in 42 EPTs of 114 steps (summary statistics: CI 0.83, RI 0.88, RC 0.74). As in Analysis 2, the strict consensus of these trees (Fig. 30) suggests that *Paniscomima* is not monophyletic. The strict consensus tree when *Mesorhopalosoma* is removed from the matrix (Analysis 6; Fig. 31) shows the same topology.

Differences in the summary statistics (CI, RI and RC) for analyses 1-6 were minimal (Table 3). The node joining the three extant macropterous genera (*Liosphex, Paniscomima, Rhopalosoma*) is common to all these analyses.

In Analysis 7, both the Pompilidae and the Bradynobaenidae were designated as outgroups. The resulting analysis produced 18 EPTs of 137 steps (summary statistics: CI 0.80, RI 0.85, RC 0.68). A strict consensus shows a polytomy of *Olixon*, *Mesorhopalosoma* and the extant macropterous branch (Fig. 32). As in analyses 2, 5, 6, monophyly of *Liosphex* and *Rhopalosoma* is maintained but *Paniscomima* is paraphyletic. Analysis 8, when *Mesorhopalosoma* is excluded from the analysis produced 6 EPTs of 135 steps (Fig. 33). The strict consensus tree exhibits the same topology as the strict consensus of Analysis 7. The strict consensus trees from these analyses show more resolution than consensus trees from all other analyses.

Inclusion of all the outgroups (Analysis 9) produced 360 EPTs of 153 steps (summary statistics: CI 0.73, RI 0.82, RC 0.60). Addition of a third outgroup compromises the monophyly of the family. Strict consensus of these trees (Fig. 34) does not support the monophyly of the family. An outgroup taxon (Pompilidae) is proposed as the sister group of the extant macropterous genera and *Olixon* forms a polytomy with *Mesorhopalosoma*, the Bradynobaenidae and the Pompilidae/extant macropterous branch. *Liosphex* is proposed as the sister group of a polytomy of *Paniscomima* species and *Rhopalosoma*. Six trees resulted from successive weighting. These trees also do not support the monophyly of *Paniscomima* which is paraphyletic with respect to *Rhopalosoma*. Strict consensus of Analysis 10 (Fig. 35), where *Mesorhopalosoma* was excluded, shows identical topology to the strict consensus trees of Analyses 7 and 8 (except for the Pompilidae in the ingroup).

One of the 54 EPTs from Analysis 1 was chosen as the solution cladogram. The choice of a tree from this analysis is based on a number of factors. When compared to the other analyses where one outgroup was selected and all taxa were included, it is one of two analyses with the shortest EPTs (114 steps). Furthermore, a previous study (Brothers 1975) and the results of Analysis 9, also suggest that the Pompilidae may be the sister group of the Rhopalosomatidae. Figure 36 is one of the 54 EPTs of Analysis 1; it was one of the EPTs that retained the monophyly of the genera.

Character optimization is an *a posteriori* procedure that does not build trees but allows one to evaluate character evolution (Wiley et al. 1991). Both ACCTRAN and DELTRAN were used to optimize characters on the EPTs. ACCTRAN appeared to order a number of characters and proposed much stronger nodal support for the *Olixon/Mesorhopalosoma* node than was justified (due to missing characters in *Mesorhopalosoma*). Given that DELTRAN treats characters as unordered (Fitch 1971), and that none of the characters in the analysis were ordered, DELTRAN was used to evaluate nodal support. In the EPT from Analysis 1, the following 11 unambiguous characters define the family: 6 segmented maxillary palp - 3 basal segments short and thick, 3 apical segments long and narrow; mandibles yellow with dark brown teeth; basal metatarsomere with a comb of hairs on a carinate ridge in basal quarter; female tarsal claws short and stout; flat lanceolate bristle on female tarsal claws; macropterous with eight or nine closed cells in the forewing; forewing C+ Sc+R fused (or appear fused), costal cell, if present, small; curvature of cu-a in forewing angled forward; strong constriction between petiole and tergum 2; lateral longitudinal carina on second tergum, incomplete, not reaching posterior margin; and tergum VI of female with medial hairless strip present. Two of these characters (#38, #51) change state at the *Olixon* node: wing development is brachypterous and petiole constriction is weak. Furthermore, the curvature of cu-a in forewing (character #41) cannot be coded because cu-a is absent in forewing of *Olixon*.

The macropterous rhopalosomatids are defined by the following 22 unambiguous synapomorphies: depth of eye emargination approximately maximum width of torulus; long, thick bristle on the second segment of the labial palp; labial palp with 3 basal segments short and stout, apical long and narrow; mandibles tridentate; paired spines on apex of flagellomeres; posterior margin of pronotom weakly or deeply concave and with posterolateral apex weakly truncate; mesepimeron and mesepisternum differentiated by a complete pleural sulcus; deep median circular pit on mesepisternum; posterior edge of mesosternum with triangular lobe covering mesocoxa separated from mesosternum by a complete transverse suture; prepectus narrow and short, a small elongate strip articulating with or fused to anterior margin of mesepisternum; profemur approximately the same size as metafemur; female tarsomeres 2-5 flat, widened, and weakly concave ventrally; apilateral fenestrae on tarsomeres of female; fenestrae present on tarsomeres 2-3; forewing junction of Cu with 2cu-a flat, smooth, slightly thickens in 2cu-a; CuP vein of forewing concave, spectral; posterior median pit on petiole; anterior margin of sternum 1 deeply concave; presence of paired, hairless, long and thin anterdorsal impressions on tergum II; hairless strip medially on tergum VI of female; tergum VI of female with apical depression; and row of lanceolate bristles on apex of male hypopygium.

In trees resulting from parsimony analysis, a simple estimate of branch support is provided by inspecting the number of characters on the branch (Bremer 1994). Another approach increases the number of steps and then examines the branches lost on a strict consensus tree (Bremer 1994). Parsimony was relaxed for Analysis 1 by increasing the length of the trees by one and two steps to examine the strength of the nodes or branch support. A heuristic search produced 1365 trees that were less than or equal to 115 steps in length. A strict consensus of these trees collapsed the nodes for all the species of *Paniscomima*. A heuristic search produced 14119 trees that were less than or equal to 116 steps in length. A strict consensus of these trees collapsed the node for *Liosphex*.

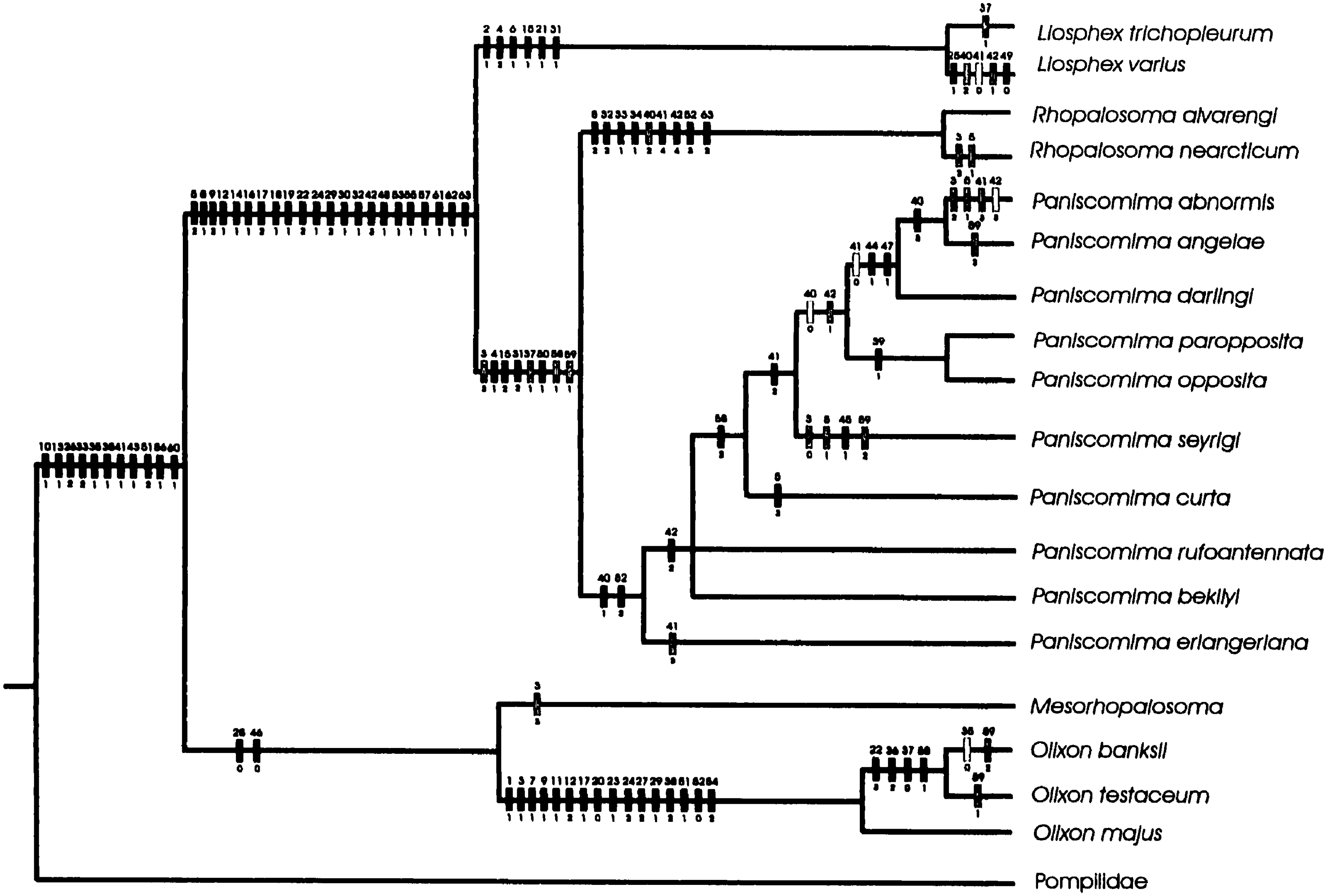

Figure 36: Solution Cladogram. One of 54 EPTs from Analysis 1. Sixty-three characters and states for 18 Rhopalosomatidae taxa (length 114, CI=0.84, RI=0.89, RC=0.75). Character hashmark shading: black=unique derivation, grey= convergent derivation, white=reversal, numbers above hashmark=character number, number below hashmark=character state. See Results for characters and character states. DELTRAN optimization.

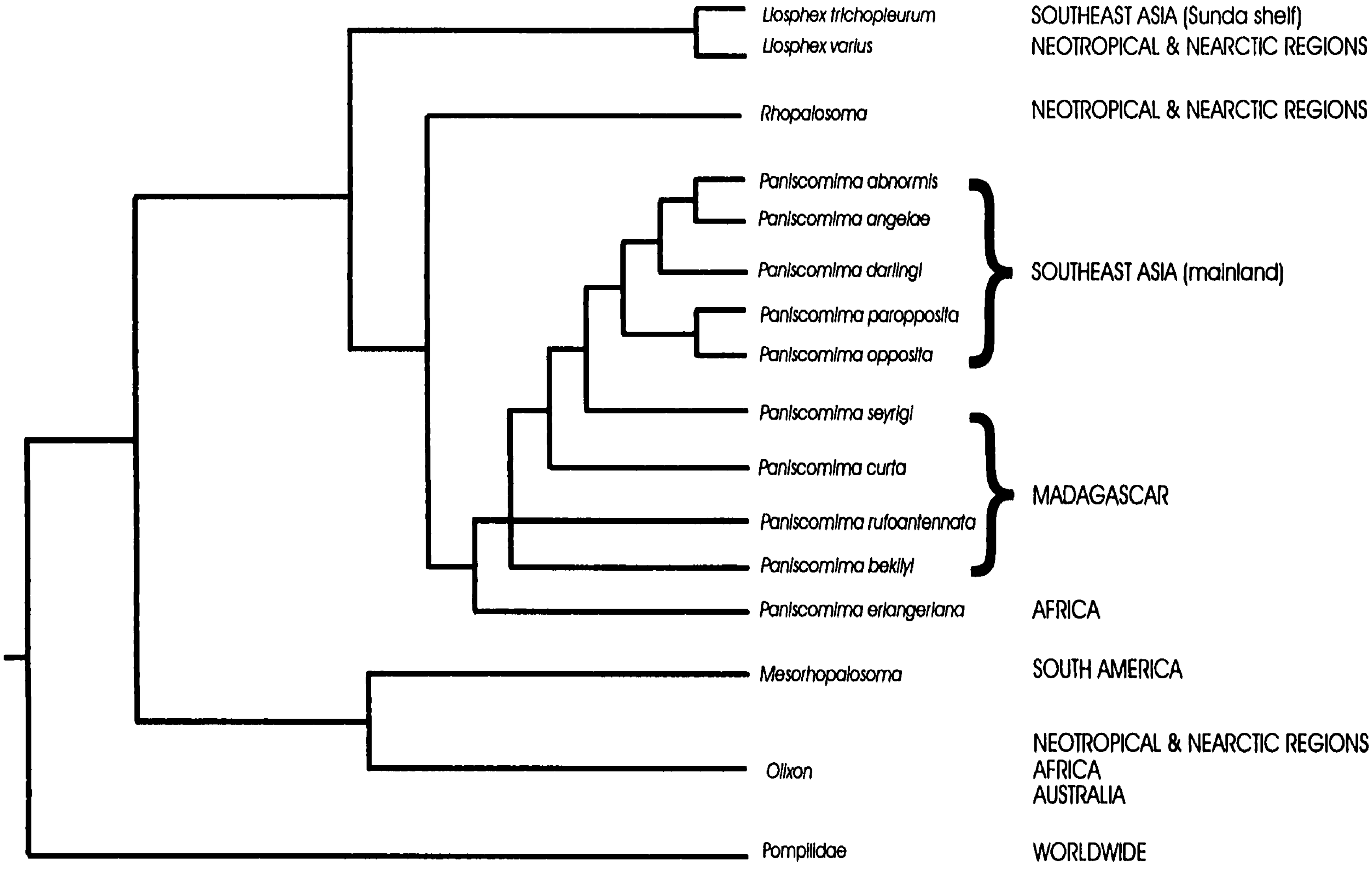

Figure 37: Cladogram from Analysis 1 (length 114, CI=0.84, RI=0.89, RC=0.75) with distribution areas indicated. There is no overlap in Southeast Asia - Sunda shelf (Indonesia, Philippines) and mainland Southeast Asia (India, Nepal, Sri Lanka, Laos, Vietnam, Thailand).

5. DISCUSSION

5.1 **Family integrity**

Is the family Rhopalosomatidae monophyletic? Based on the solution cladogram (Fig. 36) using the Pompilidae as outgroup, there are 11 uniquely derived synapomorphies that unite the family. However, the strict consensus tree produced by the analysis that used 3 outgroups (Analysis 9), suggests that the family may not be monophyletic. Pompilidae are proposed to be the sister group of the macropterous genera of the Rhopalosomatidae (Fig. 34). This is contrary to the phylogeny proposed by Brothers and Carpenter (1993; fig 11) (Fig. 5) where *Olixon* is proposed as the sister taxon of the macropterous group. The key issue is whether *Olixon* should be included in the Rhopalosomatidae.

The hypothesis that *Olixon* may not be a rhopalosomatid is not a new one. *Olixon* has had a volatile taxonomic history. As with other apterous and brachypterous species of Hymenoptera, morphological reductions make it difficult to confidently ascertain its closest relatives. The extreme reductions in morphology of *Olixon* make it an unusual aculeate. Its structural features, combined with a lack of behavioural information (Perkins 1908, notwithstanding) have made it difficult to place this group unequivocally in any family. It is difficult to determine with confidence character state homology, without looking at development, when one group has so many reductions in morphology. The type species *Olixon testaceum* Cameron was originally assigned to the Braconidae, although Cameron (1887) expressed doubt about this placement. Other generic names were recognized as additional species were described: *Apteropompilus* Cameron (1904), *Harpagocryptus* Perkins (1908), *Algoa* Brues (1911), *Algoella* (Kieffer 1914), *Nealgoa* (Brues 1922), *Saphobethylus* (Kieffer 1911), *Psyllosphex* Arnold (1935). These names have all fallen into synonymy. Perkins (1908) regarded *Harpatocryptus* as a dryinid based on the larval habits, "the larval sac being of the same form as that of *Aphelopus*". Ashmead (1900) placed the *Olixon* in the Bethylidae, subfamily Emboleminae, but gives no reason for this assignment (number of antennal segments would exclude *Olixon* from this family). Reid (1939) considered both *Apteropompilus* and *Psyllosphex* to be pompilids. Turner and Waterston (1917) synonymized *Saphobethylus pallidus* and *Olixon testaceum* and suggested that they belonged in the Rhopalosomatidae based on antennal and male genitalic characters but did not elaborate. I have been unable to confidently verify the homology of the behavioural characters that have been used to assign *Olixon* to the family Rhopalosomatidae. Perkins' (1908) report of the larval behaviour is suspect; and it has been suggested that he may have been mistaken (Reid 1939). There are no exuvial remains with the type specimen of *Olixon australiae*. Furthermore, there have been no reports of any other *Olixon* parasitizing crickets. Australia, where the macropterous rhopalosomatid genera have not been collected and are presumed to be absent, would be the ideal region to examine crickets for the distinctive rhopalosomatid larval sacs. If found, this may give support to Perkins' (1908) report. As for morphological similarities between *Olixon* and the macropterous rhopalosomatids, a closer examination of each of these characters reveals problems with homology. The female tarsomeres of *Olixon*, while somewhat widened and flat, lack other features that are characteristic of the rhopalosomatid tarsomeres, e.g., fenestrae and bristles. The mesosternal lobes are distinctly different in *Olixon* than in the other genera of rhopalosmatids; mesosternal lobes are also found in the Tiphiidae. In the macropterous rhopalosomatids, the presence of a narrow costal cell in the forewing is discernible (Fig. 1, 3, 4) while in *Olixon* it is not. This reduced costal cell is also found in the Ichneumonidae; in addition, most cells are reduced or absent from a brachypterous wing. Presence of an occipital carina is plesiomorphic. It may be possible to assign *Olixon* to other families based on some of these characters. Even the larval sac was originally described as being similar to a dryinid sac (Perkins 1908). Unfortunately, there has not been any other larval information available on *Olixon* since Perkins (1908).

Characters of *Olixon* that suggest affinities with the Rhopalosomatidae include: the form of the maxillary palp, colouration of the mandibles, basal metatarsomere with a comb of hairs on a carinate ridge in basal quarter, female tarsal claws short and stout, flat lanceolate bristle on female tarsal claws and the lateral longitudinal carina on tergum II. Thus, there is support for inclusion of *Olixon* in this family. Additional information about behaviour will be necessary before the question of monophyly can be answered. Larval habits and information about the development of *Olixon* may hold the key to resolving the question about whether this genus is a rhopalosomatid or not.

In the analysis using all three outgroups, it is the Pompilidae that renders the Rhopalosomatidae paraphyletic (Fig. 34). Specifically, Pompilidae comes between (*Olixon*, *Mesorhopalosoma*) and the rest of the rhopalosomatids. Following Brothers and Carpenter (1993), the Bradynobaenidae were proposed to be more closely related to the Rhopalosomatidae and would therefore be the group (if any) to align itself closer to the macropterous rhopalosomatids. Morphologically, the macropterous rhopalosomatids are very similar to pompilids. Perhaps Brothers (1975) original theory proposing Pompilidae and Rhopalosomatidae as sister taxa is correct.

In the analyses which include *Mesorhopalosoma*, the fossil genus is variously placed as the sister taxon of *Olixon* (Fig. 26), is left unresolved at the base of the tree with *Olixon* (Figs. 32, 34) or is placed as the sister group to the macropterous rhopalosomatids (Figs. 28, 30). Although analyses were executed without *Mesorhopalosoma*, a total evidence approach should include all the data (including taxa) that are available (Kluge 1989). However, missing data for *Mesorhopalosoma* undermines confidence in any of these relationships. From the solution cladogram, there are two synapomorphies that support a sister group relationship between *Mesorhopalosoma* and *Olixon* (Fig. 36): absence of a fuscate spot at the end of the A vein in the forewing and the absence of bristles on the legs. In fossil specimens, wing colouration may not be retained, making interpretation of this character difficult. As expected with brachypterous species, there is extreme reduction or absence of wing veins and characters in *Olixon*. The absence of leg bristles may be plesiomorphic. In that case, that character would not be a synapomorphy. Of the family level synapomorphies, most of these have been coded as unknown for *Mesorhopalosoma*. The exceptions are: the petiolar constriction (which is found in other aculeates), forewing cu-a is angled forward (this character is variable within this family) and the number of closed cells in the forewing are the same (although wing venation differs so this character may not be homologous to that of the macropterous rhopalosomatid forewing). The synapomorphy that supports inclusion of this fossil in Rhopalosomatidae is a small forewing costal cell, i.e., C+ Sc+R fused (or appear fused). This character, however, is also found in the Ichneumonidae.

There are a number of steps that should be taken before making changes in nomenclature based on this analysis. Although some characters were modified from Brothers and Carpenter (1993), not all of their data was included because my analysis was at the generic and species level, rather than at the family level; some of their characters are uniformative at this level. Brothers and Carpenter (1993) scored *Olixon* separately from the rhopalosomatids in order to check its placement within the Rhopalosomatidae. In their preferred phylogeny, *Olixon* was the sister group to the rest of the rhopalosomatids. An analysis combining the data from my study with Brothers and Carpenter's (1993) data may help to resolve this issue. However, it was not an objective of this study to examine family relationships of the Aculeata and not all of their characters were included. *Olixon* should continue to be coded separately. At present, I prefer to retain this genus within the Rhopalosomatidae based on the following synapomorphies (from Fig. 36): 6-segmented maxillary palp, the 3 basal segments short and thick and the 3 apical segments long and narrow; mandibles yellow with dark brown teeth; basal metatarsomere with a comb of hairs on a carinate ridge in basal quarter; female tarsal claws short and stout; flat lanceolate bristle on female tarsal claws; and lateral longitudinal carina on tergum II, incomplete, not reaching posterior margin.

The solution cladogram (Fig. 36) shows support for the relationship (*Liosphex* (*Rhopalosoma* + *Paniscomima*)). The node supporting this macropterous branch is very well supported by 22 synapomorphies. There is little question that these three genera share a common ancestor.

5.2 **Generic issues**

Are the genera monophyletic? The solution cladogram (Fig. 36) suggests the following relationships: ((*Mesorhopalosoma, Olixon*) (*Liosphex* (*Paniscomima, Rhopalosoma*))). The genera are all monophyletic. However, the strict consensus trees from Analyses 2, 5, 6, 7, 8, and 10 suggest that *Paniscomima* may be paraphyletic. Not surprisingly, choice and number of outgroups has a significant effect on the topology of the cladograms.

Further examination of nodes on the solution cladogram (Fig. 36) show good support for the monophyly of *Olixon*, *Liosphex* and *Rhopalosoma* and the sister grouping of *Liosphex* to (*Paniscomima*, *Rhopalosoma*). The genus *Paniscomima* is the least supported with only 2 uniquely derived characters. Within *Paniscomima*, support for each node varies from 1 to 3 characters but include reversals and convergent derivations as well as unique synapomorphies. The node uniting *Mesorhopalosoma* and *Olixon* is weakly supported by 2 uniquely derived characters. However, when parsimony is relaxed by two steps, the node supporting the species of *Liosphex* and the node supporting the sister relationship of *Olixon* and *Mesorhopalosoma* collapse.

In the solution cladogram there are four uniquely derived synapomorphic characters supporting the node uniting *Paniscomima* and *Rhopalosoma*. The characters are: symmetrical eye margins; paired spines of the flagellomeres of subequal length; strongly delineated apical fenestrae on the female tarsomeres; and a long jugal lobe in the hindwing. There is homoplasy in the four remaining characters on this node. The size of the ocelli is species-dependent and the posterior of the female or male metasoma is brown in some species of *Rhopalosoma* and *Paniscomima*. The male plantar lobes on tarsomeres 1-4 are also found on *Liosphex trichopleurum*.

There are six uniquely derived synapomorphies uniting *Liosphex trichopleurum* and *L. varius* as sister taxa and eight characters uniting *Rhopalosoma nearcticum* and *R. alvarengi*. Since there are 15 other species of *Rhopalosoma* that have not been included in this analysis, I will not suggest that these two are sister species.

5.3 *Paniscomima*

The monophyly of *Paniscomima* is supported by two synapomorphies (Fig. 36): forewing cu-a distad of M 0.4-1.5 times length of cu-a; and female petiole 2.2-3.7 times as long as wide. The weak nodal support for the monophyly of *Paniscomima* and the suggestion of paraphyly from other analyses (Figs. 27, 30, 31, 32, 33, 35), raises the possibility that a single genus should be recognized for *Rhopalosoma* and *Paniscomima*. Although there is a marked geographic disjunction between the two genera, (*Rhopalosoma* are strictly found in the New World while *Paniscomima* are recorded from Africa and Southeast Asia), it is possible that they are a single genus. The results of Analysis 1 question the monophyly of *Paniscomima*. However, there is some support (although weak) for the genus and I am therefore reluctant to synonymize it with *Rhopalosoma* at this time.

The following relationships are as suggested among *Paniscomima* species by the solution cladogram (Fig. 36): (*P. erlangeriana* (*P. bekilyi*, *P. rufoantennata* (*P. curta* (*P. seyrigi* ((*P. opposita*, *P. paropposita*) ((*P. darlingi* (*P. angelae*, *P. abnormis*))))))))). Three characters with multiple transformations are important in this clade. *Paniscomima erlangeriana* is the basal species and forms the sister group of all other *Paniscomima*. Among the latter, the junction of Cu with 2cu-a in the forewing has a thick basal swelling in the four Madagascan species (*P. bekilyi*, *P. rufoantennata*, *P. curta*, *P. seyrigi)*. This junction is flat smooth, and slightly thickens in 2cu-a, or has a thick distal swelling in the rest of the species. *Paniscomima rufoantennata* and *P. bekilyi* form a polytomy with the group (*P. curta* (*P. seyrigi* ((*P. opposita*, *P. paropposita*) ((*P. darlingi* (*P. angelae*, *P. abnormis*)))))). There is only a single colour difference (in antennae) between *P. rufoantennata* and *P. bekilyi* and this character was excluded from this analysis because of the difficulty in coding continuous characters. Monophyly of this latter clade is supported by the colour of the male metasoma, yellow with brown/black in posterior segments. The next node, i.e., the sister clade of *P. curta*, is defined by the curved shape of cu-a in the forewing. In fact, this character has two additional transformations in *Paniscomima*: angled backward and angled forward. The node joining all of the Southeast Asian species of

Paniscomima is supported by two characters: forewing junction of Cu with 2cu-a is flat and smooth at this point with a thickening in cu-a; and forewing cu-a position relative to M is opposite, slightly distad (up to 0.3 times length of cu-a) or basad slightly (up to 0.5 times length of cu-a). Three characters support the node joining *P. darlingi* to *P. abnormis* and *P. angelae*, the presence of an adventitious vein in the anal cell of the forewing; the terminus of the forewing A vein ending in a knob or 3a′; and the forewing cu-a straight. This last character, as has been stated, is homoplasious and changes frequently in this genus. *P. abnormis* and *P. angelae* are sister taxa based on the extreme basal position of cu-a to M in the forewing which is unique to these taxa. One uniquely derived synapomorphy unites *P. opposita* and *P. paropposita*: M vein intersects m-cu at a 90° angle in the forewing.

The results of relaxing parsimony of Analysis 1 by one step collapsed all of the nodes supporting relationships among species of *Paniscomima*. This, in addition to the few characters supporting the nodes, suggests a lack of stability in the relationships proposed by the EPTs.

5.4 **Historical Biogeography**

The investigation of geographical patterns of distribution of organisms in a historical context is being included in the research of numerous systematists and biologists (Brooks and McLennan 1991; Morrone and Carpenter 1994). A goal of these biogeographic studies is to find repetitions in a distribution pattern among different taxa (Seberg 1991). Theories are then proposed to explain the patterns. A robust phylogeny is required before a hypothesis of biogeographic events can be proposed. Determining sister-group relationships is the first step in investigating how speciation events could have occurred.

Although I would not consider the solution cladogram to be a robust phylogeny, it does provide one hypothesis of relationship for the species of *Paniscomima*. From a biogeographic standpoint, the possible dispersion of *Paniscomima* can be traced (Fig. 37). Africa (1 species), Madagascar (4 species), and mainland Southeast Asia (5 speceis) are the three general areas of species distribution. From the solution cladogram, the mainland Southeast Asia clade appears to have evolved most recently. The common ancester of the genus may have had a very wide distribution with subsequent vicariance. However, dispersal from Africa is also a possible evolutionary pattern.

The disjunct distribution pattern of the genus *Liosphex* presents another intriguing problem, one species in the New World and one species in the Philippines and Indonesia. The complexity of southern hemisphere distribution patterns is being investigated by biologists in many different fields (Seberg 1991). Two examples include: the historical links between the Philippines and Sulawesi in the South Pacific (e.g., Kitching et al. 1987; Vane-Wright 1991; Darling 1995) and the faunal relationships between southern South America and New Zealand (Seberg 1991).

Olixon and the *Paniscomima/Rhopalosoma* clade exhibit some overlap in distribution patterns (Fig. 38). The area cladogram (Fig. 37) is consistent with a widespread ancestral species that was fragmented by the geological change that was associated with the break-up of Gondwana which is dated at approximately 200-180 million years before present (Dodson and Dodson 1985).

This may or may not shed some light on the distribution of *Liosphex*. Overall, two general hypothesis can be entertained to explain the distribution of *Liosphex* (Brooks and McLennan 1991; Morrone and Crisci 1995):

(1) Dispersal: A common ancestor arose in one area and then dispersed into another one;

(2) Vicariance and Extinction: A common ancestor originally was widespread when the land

masses were joined and representatives in other areas have become extinct.

In the dispersal explanation, a common ancestor arose in one area and then some members crossed a barrier thus isolating a new population. From this event, the isolated population speciated and a new taxon arose. In this situation, the barrier is the Pacific Ocean. Since it is hypothesized that these insects are not strong fliers (Townes 1977), this scenario is unlikely.

In the vicariance model, the range of the common ancestor is divided by the development of a barrier that prevents gene flow. As can be seen from *Olixon* and the sister group (*Paniscomima/Rhopalosoma*) of *Liosphex*, a widespread ancestor and subsequent vicariance events (e.g., continental drift) are likely to have occurred. If we assume that the ancestor of *Liosphex* was widespread prior to the breakup of Gondwana, and existed in present day Australia and South America, the distribution of the two extant species is less of a mystery. The suggestion is that *Liosphex* were present in Australia during the Cretaceous and have become extinct. The age of the family and a similar pattern in the historical biogeography of *Olixon sp.* give some credence to this theory. The absence of *Liosphex* from Australia could also be a sampling problem; perhaps they just haven't been collected there yet. The vicariance model is the preferred hypothesis to explain this distribution; the two species of *Liosphex* are relicts of a formerly wider distribution.

The absence of the rhopalosomatids from most of the Northern regions (except for the southeastern part of North America) suggests that the distribution into North America may be due to a more recent dispersal event. Alternatively, it could be due to massive extinctions in the northern regions. There is, however, no fossil evidence of this family in Eurasia. The theory of a recent northward dispersal into North America is favoured. The present-day dry land connection between North and South America is a relatively recent feature (in the Pliocene), probably around 3 million years old (White 1986). An earlier Cenozoic landlink also existed. An incomplete fossil record makes it impossible to determine when the dispersal (if it was a dispersal) of the Rhopalosomatidae into North America occurred.

There is a scarcity of rhopalosomatids in collections around the world but it is unknown whether the problem has been one of collecting deficiencies versus rarity of the family. It is possible that entomologists have not used the most efficient techniques to collect these particular insects. It was noted by Townes (1977) that the use of Malaise traps has increased the number of specimens collected in the last 20+ years. The distribution patterns presented here most likely do not accurately reflect the distribution of the Rhopalosomatidae around the world.

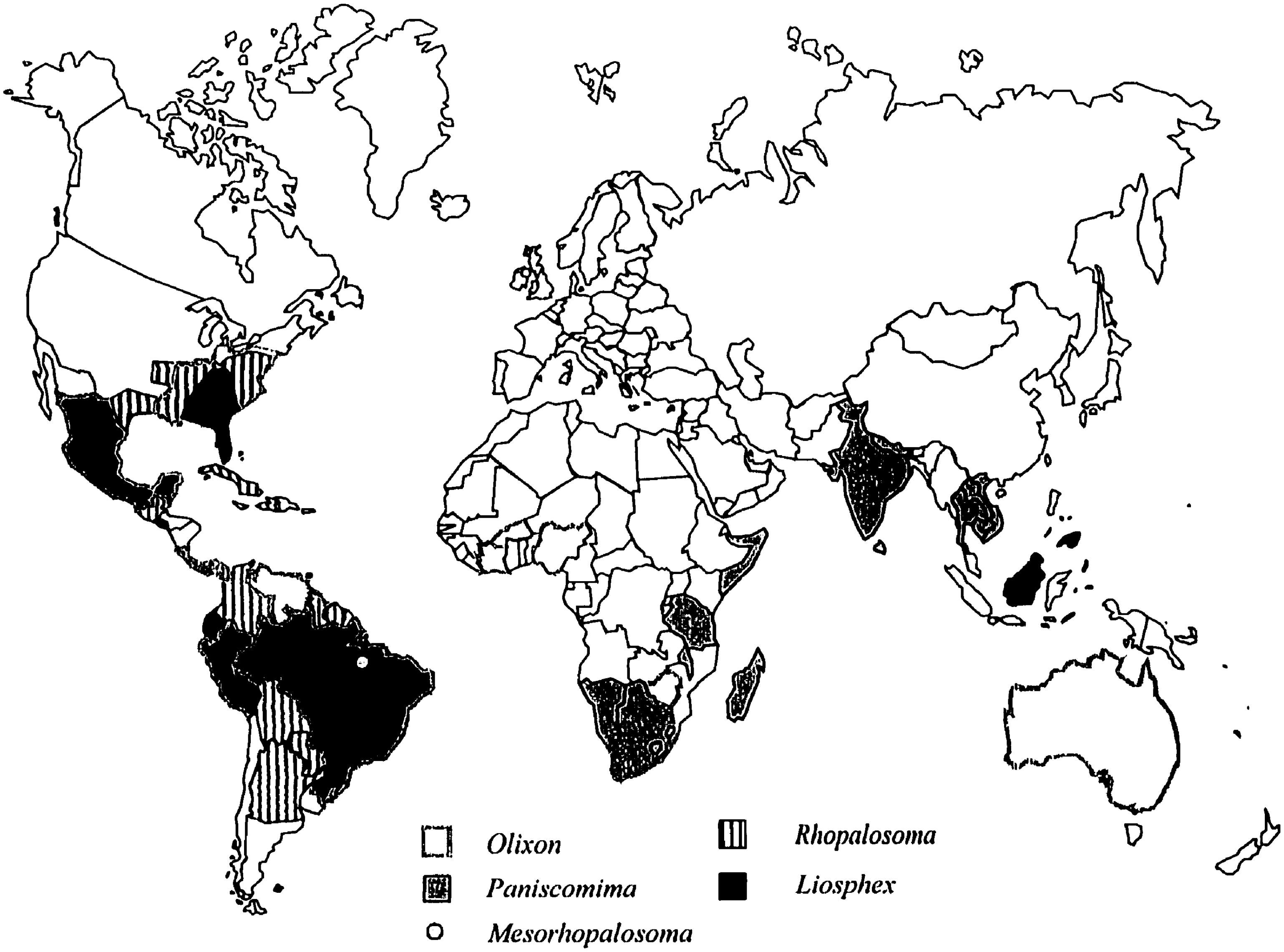

Figure 38: Distribution of Rhopalosomatidae

6. CONCLUSION

Revised descriptions for the family Rhopalosomatidae and its constituent genera are presented. Three new species of *Paniscomima* are described: *P. darlingi, P. angelae*, and *P. paropposita*. Redescriptions of *Liosphex trichopleurum*, *P. opposita* and *P. seyrigi* are presented. New and revised keys for the family, for *Liosphex* and for *Paniscomima* species are included.

The results of the phylogenetic analysis support: (1) a single monophyletic extant macropterous branch of rhopalosomatids; (2) the sister-group relationship of *Liosphex* to *Rhopalosoma/Paniscomima*; (3) the monophyly of each of *Olixon, Liosphex*, and *Rhopalosoma* and; (4) the monophyly of Rhopalosomatidae. However, there is uncertainty about the monophyly of *Paniscomima*. Since behavioural and life history information is mostly unknown, this study was based strictly on morphological characters. Additional information about behaviour or molecular data may be necessary before these questions of monophyly can be answered. Larval habits and information about the development of *Olixon* may hold the key to resolving the question of whether this genus is a rhopalosomatid or not.

The disjunct distribution of *Liosphex* is considered to be a result of vicariance and subsequent extinctions. The present range of the genus is considered to be a relict of a much wider distribution.

Ideally, analyzing this data and additional data (molecular?) and taxa may provide a more robust solution. Combining this data matrix with the Brothers and Carpenter (1993) complete matrix may also resolve the placement of *Mesorhopalosoma* and *Olixon*. It will be interesting to see whether an analysis with additional taxa (i.e. *Rhopalosoma* and *Olixon*) will produce the same relationships.

7. LITERATURE CITED

Arnett, R.H., G.A. Samuelson, and G. M. Nishida. 1993. The Insect and Spider Collections of the World. Sandhill Crane Press, Inc., Florida.

Arnold, 1935. *Psyllosphex saltator. Annals. Transvaal Museum.* 15:479.

Ashmead, W. H. 1896. Rhopalosomidae, a new family of fossorial wasps. *Proceedings of the Entomological Society of Washington.* 3:303-309.

Ashmead, W.H. 1900. Report upon the aculeate hymenoptera of the islands of St. Vincent and Grenada, with additions to the parasitic Hymenoptera and a list of the described Hymenoptera of the West Indies. *Transactions of the Entomological Society of London.* 207-367. (*Olixon*:235)

Berland 1951. *Rogezia seyrigi. Memoires. Institut de Recherche Scientifique de Madagascar* (A) 15: 301.

Bremer, K. 1994. Branch Support and Tree Stability. *Cladistics.* 10:295-304.

Brooks, D.R. and D.A. McLennan. 1991. Phylogeny, Ecology and Behavior. University of Chicago Press.

Brothers, D.J. 1975. Phylogeny and Classification of the Aculeate Hymenoptera, with Special Reference to Mutillidae. *The University of Kansas Science Bulletin.* 50 (11): 483-648.

Brothers, D.J. and J.M. Carpenter. 1993. Phylogeny of Aculeata: Chrysidoidea and Vespoidea. *Journal of Hymenoptera Research.* 2 (1):227-304.

Brown, R.W. 1954. Composition of Scientific Words. Smithsonian Institution Press. Wash. D.C.

Brues, C.T. 1910. *Algoa heterodoxa. Journal of the New York Entomological Society.* 18:18.

Brues, C.T. 1922. On the hymenopterous genus *Harpagocryptus* and its allies. *Psyche.* 29:101-109.

Brues, C.T. 1926. Note on the hymenopterous family Rhopalosomatidae. *Psyche.* 33:18-19.

Cameron, P. 1887. Insecta. Hymenoptera. (Families Tenthredinidae-Chrysididae) Braconidae. *Olixon. Biologia Centrali-Americana.* 1: 412-413.

Cameron, P. 1904. *Apteropompilus dentatus. Zeitshcrift fuer Systematische. Hymenoptera. Diptera.* 4:176.

Campbell, J.A., and D.R. Frost. 1993. Anguid lizards of the genus *Abronia*: Revisionary notes, description of four new species, a phylogenetic analysis, and key. *Bulletin American Museum of Natural History*. 216:1-121.

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

Carpenter, J.M. 1988. Choosing among multiple equally parsimonious cladograms. *Cladistics*. 4:291-296.

Cresson, E. 1865. *Rhopalosoma*. *Proceedings of the Entomological Society of Philadelphia*. 4:58.

Darling, D.C. 1995. New species of *Krombeinius* (Hymenoptera: Chalcidoidea: Perilampidae) from Indonesia, and the first description of first-instar larva for the genus. *Zoologische Mededelingen. (Leiden)*. 69 (17): 209-229

Darling, D. C. and M.J. Sharkey, 1990. *Order Hymenoptera* in D.A. Grimaldi (ed.), 1990. Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History*. Number 195. pp.123-153.

Dodson, E.O. and P. Dodson. 1985. Evolution: Process and Product. 3rd edition. Wadsworth Publ. Co. Belmont, Calif.

Enderlein, G. 1904. *Paniscomima*, eine neue von Herrn Baron von Erlanger aufgefundene Rhopalosomiden - Gattung. *Zoologische Anzeiger*. 27:464-466.

Evans, H. E. 1987. Rhopalosomatidae (Pompiloidea). *In:* Immature Insects. F.W. Stehr (ed). Vol 1. Kendall/Hunt Publishing Co. pp. 679-680.

Farris, J. S. 1969. A successive approximations approach to character weighting. *Systematic Zoology*. 18:374-385.

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

Farris, J.S. 1989. The retention index and rescaled consistency index. *Cladistics*. 5:417-419.

Finnamore, A.T. 1995. Revision of the World Genera of the Subtribe Stigmina (Hymenoptera: Apoidea: Sphecidae: Pemphredoninae), Part 1. *Journal of Hymenoptera Research*.. 4:204-284.

Fitch, W.M.1971. Toward defining the course of evolution: Minimum change for a specific tree topology. *Systematic Zoology*. 20:406-416.

Gauld, I. and B.Bolton. 1988. The Hymenoptera. Oxford: Oxford Univ. Press.

Goulet, H. and J.T. Huber (eds.). 1993. Hymenoptera of the world: An identification guide to families. Agriculture Canada. Publication 1894/E. pp. 161-278.

Gurney, A. B. 1953. Notes on the Biology and immature stages of a cricket parasite of the genus *Rhopalosoma*. *Proceedings of the United States National Museum*. 103:19-34.

Hanson, P.E. and I.D. Gauld, 1995. The Hymenoptera of Costa Rica. The Natural History Museum, London. Oxford Scientific Publications. pp.548-552.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Urbana.

International Trust for Zoological Nomenclature (ICZN). 1985. International Code of Zoological Nomenclature. 3rd Edition. BMNH.

Jaeger, E.C. 1955. A Source-Book of Biological Names and Terms. 3rd Edition. C.C. Thomas Publisher.

Kieffer, J. J. 1911. Nouveaux Bethylides et Dryinides exotiques du British Museum de Londres. *Annales. Societe Scientifique de Bruxelles*. 35:200-233.

Kieffer, J.J. 1914. *Algoella*. Bethylidae. *Das Tierreich*. 41: 473

Kitching, I.J., R.I. Vane-Wright and P.R. Ackery, 1987. The Cladistics of Ideas (Lepidoptera, Danainae). *Cladistics*. 3 (1):14-34.

Kluge, AG. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematic Zoology*. 38:7-25.

Kluge, A.G. and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology*. 18:1-32.

Kluge, A.G. and A.J. Wolf. 1993. Cladistics: What's in a Word? *Cladistics*. 9:183-199.

Krombein, K.V. 1949. An Annotated List of Wasps from Nags head and the Kill Devil Hills (Hymenoptera Aculeata). *Elisha Mitchell Scientific Society Journal*. 65:262-272.

Maddison, W.P. and D.R. Maddison. 1992. MacClade: Analysis of phylogeny and character evolution, Version 3.04. Sinauer Assoc., Sunderland, Massachusetts.

Mason, W.R.M. 1986. Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. *Proceedings of the Entomological Society of Washington*. 88(1):1-7.

Mason, W.R.M. 1990. Cubitus Posterior in Hymenoptera. *Proceedings of the Entomological Society of Washington*. 92 (1): 93-97.

Miyamoto, M.M. 1985. Consensus Cladograms and General Classifications. *Cladistics*. 1(2):186-189.

Morley, C. 1910. On the Position of the Rhopalosomidae with a Description of a Second Species. *Transactions of the Entomological Society of London*. IV: 386-390.

Morrone, J.J and J.M. Carpenter. 1994. In Search of a Method for Cladistic Biogeography: an empirical comparison of Component Analysis, Brooks Parsimony Analysis and Three-area statements. *Cladistics*. 10 (2):99-153.

Morrone, J.J. and J. V. Crisci. 1995. Historical Biogeography: Introduction to methods. *Annual Review of Ecology and Systematics*. 26:373-401.

Perkins, R.C. L. 1908. Some remarkable Australian Hymenoptera. Dryinidae. *Harpagocryptus australiae*. *Proceedings of the Hawaiian Entomological Society*. 2:34-35.

Reid, J.A. 1939. On the Relationship of the Hymenopterous genus *Olixon* and its Allies, to the Pompilidae (Hym.). *Proceedings of the Royal Entomological Society of London* (Series B). 8:95-102.

Rognes, K. 1999. Successive Weighting and Polymorphic Terminals - A Warning to PAUP Users. *Cladistics*. 15: 69-72

Schulz, 1906. *Rhopalosoma erlangerianum*. *Spolia Hymenopterologica* p. 223-225.

Seberg, O. 1991. Biogeographic Congruence in the South Pacific. *Australian Systematic Botany*. 4:127-136.

Shimuzu, A. 1994. Phylogeny and Classification of the family Pompilidae. *Tokyo Metro University Bulletin of Natural History*. 2:1-142.

Swofford, D.L. 1991. When are phylogeny estimates from molecular and morphological data incongruent? *In*: M.M. Miyamoto and J. Cracraft (eds). Phylogenetic Analysis of DNA Sequences. Oxford Univ. Press, New York, pp.295-333.

Swofford, D.L. 1993. PAUP: Phylogenetic analysis using parsomony, Version 3.1.1. Computer program and user's manual (264 pp.). Illinois Natural History Survey, Champaign, IL.

Townes, H.K. 1977. A Revision of the Rhopalosomatidae (Hymenoptera). *Contributions of the American Entomological Institute*. 15(1):1-34.

Turner, R.E. and J. Waterston. 1917. On the Families Bethylidae and Rhopalosomidae. *Annals and Magazine of Natural History* 8 (20): 101-108.

Vane-Wright, R.I. 1991. Transcending the Wallace Line: do the Western edges of the Australian Region and the Australian Plate Coincide? *Australian Systematic Botany*. 4: 183-197.

Westwood, J.O. 1874. Thesaurus Entomologicus Oxoniensis. pp. 130-132.

White, B.N. 1986. The Isthmian Link, Antitropicality and American Biogeography: Distributional History of the Atherinopsinae (Pisces: Atherinidae). *Systematic Zoology*. 35 (2): 176-194.

Wiens, J.J. 1995. Polymorphic characters in phylogenetic systematics. *Systematic Biology*. 44:482-500.

Wiens, J.J. 1998. Testing Phylogenetic Methods with Tree Congruence: Phylogenetic Analysis of Polymorphic Morphological Characters in Phrynosomatid Lizards. *Systematic Biology*. 47(3): 427-444.

Wiley, E.O. 1981. Phylogenetics. The Principles and Practice of Phylogenetic Systematics. John Wiley & Sons, New York.

Wiley, E.O., D. Siegel-Causey, D.R. Brooks and V.A. Funk. 1991. The Compleat Cladist. Univ. of Kansas Museum of Natural History Special Publication No. 19.

Appendix 1: List of exemplars used in Cladistic Analyses

Species name	Label data
Olixon banksii Brues	♂ USA: GA. Tifton Co. 13km NW Tifton Aug 1985. PT M Keller [PMAE]
	♀ USA: LA. Chicot State Park Evangeline Co. 8 vi - 6 vii 71 [AEIC]
Olixon testaceum Cameron	♀ COSTA RICA La Selva 40m 17-23-V-1988 B.V. Brown MT 2° rainforest [PMAE]
	♂ BELIZE: Orange Walk District. Rio Bravo Cons. Area. Well Trail near "Texas Camp" 11-18.vii 1996 P.W. Kovanik [CNCI]
Olixon majus Townes	♀ BURKINA FASO: Gourma Kimplenga (20km.S.Pama) 1-16.VI.1988. Sanborne, Landry & Tou, Savane, lit de rivière, p. à intercept. [CNCI]
Liosphex varius Townes	♀ Paratype: USA: LA Chicot St. Pk. Evangeline Par. 28vi-5vii 71. D. Shanek. MT [CNCI]
	♂ USA: FLA. Alachua Co. Gainesville (AEI) 15-25 VI, 1987; MT Regrown Oak Forest BRC HYM. TEAM [PMAE]
Liosphex trichopleurum Townes	♀ SABAH: Danum Valley Field C. 117°48'E 4° 58'N i-ii.1987 M. Still [BMNH]
	♂ INDONESIA: W. Kalimantan Gunung Palung Nat. Pk. 15 JUN - 15 AUG 1991 Darling, Rosichon, Sutrisno. IIS 910115. Cabang Panti Res. Sta. 1° rainforest 100m Granite-light gap 1°15'S, 110°05'E Malaise trap pans [ROME]
Rhopalosoma nearcticum Brues	♀ USA: Georgia, McIntosh Co., Sapelo Island, MT 20-VI-18-VII-1981 Live Oak Forest BRC.HYM. TEAM [PMAE]
	2♂ USA: Missouri Williamsville, MT VII-1987 J.T.Becker [PMAE]
Rhopalosoma alvarengai Townes	♀ Paratype: BRAZIL: Encruzilhada Bahia; XI.'72 960m. M. Alvarenga [UCDC]
	♂ Paratype: BRAZIL: Encruzilhada Bahia; XI.'74. 980m. M. Alvarenga [UCDC]
Paniscomima bekilyi Berland	2♂ MADAGASCAR BEKILY Reo Sud de L'ile Museum Paris XI-36 A. Seyrig Gen No. 23 Paratype Rhopalosoma bekilyi Berl. [AEIC][USNM]
	2♀MADAGASCAR BEKILY Reo Sud de L'ile Museum Paris XI-36 A. Seyrig Paratype Rhopalosoma bekilyi Berl. [AEIC][USNM]
Paniscomima curta Townes	♂ MADAGASCAR Ivondro Muséum Paris XII-38 A.Seyrig. Paratype [AEIC]
Paniscomima erlangeriana Enderlein	♀ ULUGURU 700-1800m Tanganyika XII 1961-I 1962 Gerd Heinrich [AEIC]
	♂ TZANEEN, Trvl. I-II-71 So. Africa H. & M. Townes Gen No.11 [AEIC]

Appendix 1: List of exemplars used in the Cladistic Analysis

Species name	Label data
Paniscomima opposita Townes	2♂ NEPAL nr. Simra Adhabhar 600ft. 23-28 Aug. 1967 Malaise Trap No.24 Can.Nepal Exped. Paratype Paniscomima opposita Tow. No. 13347 and Gen No. 18 [CNCI] ♀ India: And.P. Patacheru vii.82 [BMNH]
Paniscomima darlingi n.sp.	♀, ♂ VIETNAM: Dac Lac: Yok Don N.P. ca. 2 km SE Ban Don, W. Bank of Serepok R. 12-28 JUN 1997. DC Darling, A.Guidotti, B. Hubley. ROM 974113 Malaise trap (fine); no pans near rapids, riparian vegetation 12°53'N, 107°48'E. 100m. [ROME]
Paniscomima angelae n.sp.	♀ VIETNAM: Dac Lac: Yok Don Natl. Pk. Edge of Dak Ken R., 8km SW Ban Don 16-22 JUN 1997. B. Hubley. ROM 974104 Malaise trap (fine); no pans Dipterocarp forest 12°53'N, 107°48'E [ROME]
Paniscomima paropposita n. sp.	♂ THAILAND Sam Lan at light. G.C. Varley 21-1-78 [BMNH]
Paniscomima rufoantennata Berland	♀ MADAGASCAR: Fort Dauphin Museum Paris XII 36 A. Seyrig [AEIC]
Paniscomima seyrigi Berland	♂ MADAGASCAR: Antisiranano R:N:I: de Marojejy 8 km NW Manantenina X. 5-13. 1996, 450m E.Quinter & T. Nguyen. Tributary Manantenina River 14°26.2'S 49°6.5'E Malaise [USNM]
Mesorhopalosoma cearae Darling	Ceará, Brazil AMNH 43266, AMNH 44103 from description (Darling & Sharkey, 1990, pp. 136-143)
OUTGROUPS	
Bradynobaenidae	
Chyphotes sp.	♀ 94mi south of Parral, Chib Mex. 5800' 30Apr 1953 Creighton [CNCI]
Chyphotes mickeli mickeli Buzicky	2♂ Indio, Cal. 12-11-1955 W.R.M. Mason [CNCI]
Typhoctes williamsi Krom. & Schus.	♂ {USA} Thousand Palms Cal. 7-iv-1955. W.R.M. Mason [CNCI]
Pompilidae	
Ceropales bipunctata Say	2♀ Canada: Ont. Toronto 3.9. (18)82. Wm. Brodie Collection. [ROME] ♂ Canada: Ont. Toronto 24-8-(18)94. Wm. Brodie Collection. [ROME] ♂ Canada: Ont. Port Hope ix-4-25. N.K. Bigelow [ROME]
Sierolomorphidae	
Sierolomorpha canadensis Provancher	♀ Ann Arbor Mich. Aug 1958 H.& M. Townes [AEIC] ♂ Takoma Park IV.16.1942 Md. H.& M. Townes [AEIC] NY: Tompkins Co. Ithaca X-76 Andow 1981 [ROME]