

AN ABSTRACT OF THE THESIS OF

Gerasimos Cassis for the degree of Doctor of Philosophy
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Title: A Systematic Study of the Subfamily Dicyphinae
(Heteroptera: Miridae).

Abstract approved: _____


John D. Lattin

A systematic study of the subfamily Dicyphinae Reuter (Heteroptera: Miridae) resulted in a redefinition of the subfamily and included genera, and a revision of the genus Dicyphus Fieber in the Western Hemisphere. The study entailed examination of about 14,000 specimens, including numerous non-dicyphine, cimicomorphan taxa to assess character transformations. New character sources, such as the thoracic pleura, were investigated to test current classifications, establish the present classification, and perform a preliminary phylogenetic analysis with included consideration of host associations and biogeography.

In the first chapter, general information about the family Miridae is given and the systematic problems of the Dicyphinae and the objectives of the study are elucidated.

In the second chapter, a diagnosis of the subfamily is provided with some discussion of the intrafamilial relationships. Also the genera of the subfamily are

redefined, redescribed, and included species for each genus are listed. Sixteen genera are recognized and one new genus, Glarisia n. gen., and one new subgenus, Uhlerella n. sgen., of the genus Dicyphus, are described. The six subgenera of Cyrtopeltis Fieber: Cyrtopeltis, Engytatus Reuter, Nesidocoris Kirkaldy, Singhalesia China and Carvalho, Tupiocoris China and Carvalho, and Usingerella China and Carvalho are elevated to generic rank, whereas the subgenera of Dicyphus are retained.

Chapter three is a revision of the genus Dicyphus in the Western Hemisphere which contains nine species. There are eight endemic species belonging to the endemic subgenus D. (Uhlerella), including two new species nigracorium n. sp. and occidentalis n. sp.. A key is given to the species.

A Systematic Study of the Subfamily Dicyphinae
(Heteroptera: Miridae).

by
Gerasimos Cassis

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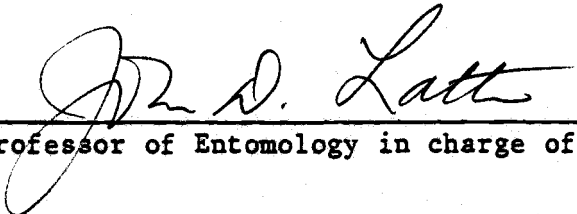
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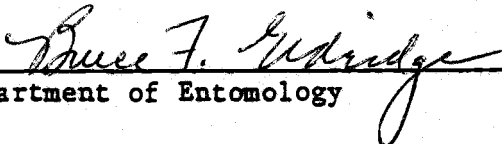
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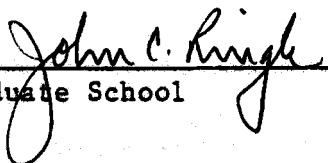
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TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1. GENERAL INTRODUCTION.....	1
CHAPTER 2. A Generic Reclassification of the Subfamily Dicyphinae Reuter (Heteroptera: Miridae)	
INTRODUCTION.....	6
MATERIALS.....	9
METHODS.....	11
TERMINOLOGY.....	16
NOMENCLATURE.....	18
HISTORICAL REVIEW.....	19
BIOLOGY.....	22
SUBFAMILY DICYPHINAE REUTER.....	25
SYNOPSIS OF SUBFAMILY DICYPHINAE REUTER..	34
KEY TO GENERA OF SUBFAMILY DICYPHINAE....	36
TAXONOMY OF THE GENERA OF DICYPHINAE....	42
Genus <u>Campyloneuropsis</u> Poppius.....	42
Genus <u>Campyloneura</u> Fieber.....	49
Genus <u>Chius</u> Distant.....	55
Genus <u>Cyrtopeltis</u> Fieber.....	58
Genus <u>Dicyphus</u> Fieber.....	64
KEY TO THE SUBGENERA OF THE GENUS <u>DICYPHUS</u> FIEBER.....	71

	<u>Page</u>
Subgenus <u>Brachyceraea</u> Fieber.....	72
Subgenus <u>Dicyphus</u> Fieber.....	79
Subgenus <u>Idolocoris</u> Douglas and Scott....	88
Subgenus <u>Mesodicyphus</u> Wagner.....	94
Subgenus <u>Uhlerella</u> Cassis.....	95
Genus <u>Engytatus</u> Reuter.....	101
Genus <u>Glarisia</u> Cassis.....	112
Genus <u>Macrolophus</u> Fieber.....	117
Genus <u>Nesidocoris</u> Kirkaldy.....	128
Genus <u>Setocoris</u> China and Carvalho.....	137
Genus <u>Singhalesia</u> China and Carvalho....	143
Genus <u>Tupiocoris</u> China and Carvalho.....	148
Genus <u>Usingerella</u> China and Carvalho....	160
GENERA RETAINED IN SUBFAMILY (NOT EXAMINED)	
.....	164
GENERA REMOVED FROM THE SUBFAMILY	
DICYPHINAE.....	166
PHYLOGENETIC ANALYSIS OF THE GENERA OF THE	
DICYPHINAE.....	173

CHAPTER 3. A Systematic Study of the Genus

Dicyphus Fieber in the Western

Hemisphere

INTRODUCTION289

MATERIALS291

	<u>Page</u>
METHODS	294
SYNOPSIS OF THE GENUS <u>DICYPHUS</u> IN THE	
WESTERN HEMISPHERE.....	294
KEY TO SPECIES OF <u>DICYPHUS</u> FOR WESTERN	
HEMISPHERE.....	295
TAXONOMY	299
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>discrepans</u> Knight	
.....	299
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>famelicus</u> (Uhler)	
.....	306
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>gracilentus</u>	
Parshley.....	310
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>hesperus</u> Knight	
.....	314
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>nigracorium</u> Cassis	
.....	320
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>occidentalis</u> Cassis	
.....	325
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>paddocki</u> Knight	
.....	329
<u>Dicyphus</u> (<u>Uhlerella</u>) <u>vestitus</u> Uhler	
.....	336
<u>Dicyphus</u> (<u>Idolocoris</u>) <u>pallicornis</u>	
(Meyer-Dur).....	338
LITERATURE CITED	359

List of Figures

Page

CHAPTER 2.

II.1-II.16. Dorsal and lateral view of head and pronotum	237
II.17-II.32. Dorsal and lateral view of head and pronotum	239
II.33-II.47. Thoracic structures.....	241
II.48-II.77. Femoral trichobothria	243
II.78-II.92. Wings	245
II.93-II.110. Wings	247
II.111-II.127. Pygophore	249
II.128-II.167. Left and right claspers	251
II.168-II.186. Aedeagus	253
II.187-II.201. Aedeagus	255
II.202-II.221. Female bursa copulatrix	257
II.222-II.225. Thoracic pleura	259
II.226-II.230. Thoracic pleura	261
II.231-II.236. Thoracic pleura	263
II.237-II.242. Thoracic pleura	265
II.243-II.248. Pretarsus	267
II.249-II.256. Pretarsus	269
II.257-II.262. Pygophore	271
II.263-II.268. Pygophore	273
II.269-II.271. Pygophore	275

II.272. Habitus of <u>Dicyphus</u> (<u>Idolocoris</u>)	
<u>regulus</u>	277
II.273. Habitus of <u>Dicyphus</u> (<u>Uhlerella</u>)	
<u>paddocki</u>	279
II.274. Habitus of <u>Tupiocoris californica</u>	281
II.275. Cladogram showing the distribution of synapomorphies in Dicyphinae genera	283
II.276. Cladogram showing the regional distribution of Dicyphinae genera	285
II.277. Cladogram showing the host plant family associations for Dicyphinae genera	287

CHAPTER 3. Diagnostic characters of Dicyphus

(Uhlerella) species and D. (Idolocoris)

pallicornis

III.1-III.25.	357
--------------------	-----

List of Tables

	<u>Page</u>
CHAPTER 2.	
Characters and character states for the genera of Dicyphinae	174
Raw data for the cladistic analysis of the genera of the Dicyphinae.....	180
Regional distribution of the Dicyphinae genera, and the outgroup <u>Felisacus</u>	193

List of Maps

Page

CHAPTER 2.

II.1	<u>Campyloneuropsis</u>	203
II.2	<u>Campyloneura</u>	205
II.3	<u>Chius</u>	207
II.4	<u>Cyrtopeltis</u>	209
II.5	<u>Dicyphus</u> (<u>Brachyceraea</u>)	211
II.6	<u>Dicyphus</u> (<u>Dicyphus</u>)	213
II.7	<u>Dicyphus</u> (<u>Idolocoris</u>)	215
II.8	<u>Dicyphus</u> (<u>Mesodicyphus</u>)	217
II.9	<u>Dicyphus</u> (<u>Uhlerella</u>)	219
II.10	<u>Engytatus</u>	221
II.11	<u>Glarisia</u>	223
II.12	<u>Macrolophus</u>	225
II.13	<u>Nesidocoris</u>	227
II.14	<u>Setocoris</u>	229
II.15	<u>Singhalesia</u>	231
II.16	<u>Tupiocoris</u>	233
II.17	<u>Usingerella</u>	235

CHAPTER 3.

III.1	<u>D. (Uhlerella) discrepans</u>	339
III.2	<u>D. (Uhlerella) famelicus</u>	341
III.3	<u>D. (Uhlerella) gracilentus</u>	343
III.4	<u>D. (Uhlerella) hesperus</u>	345
III.5	<u>D. (Uhlerella) nigracorium</u>	347

Page

III.6	<u>D. (Uhlerella) occidentalis</u>	349
III.7	<u>D. (Uhlerella) paddocki</u>	351
III.8	<u>D. (Uhlerella) vestitus</u>	353
III.9	<u>D. (Idolocoris) pallicornis</u>	355

A Systematic Study of the Subfamily Dicyphinae
(Heteroptera: Miridae).

CHAPTER 1

GENERAL INTRODUCTION

The Miridae is the most speciose family in the Heteroptera and exhibits a wide diversity in morphology, biological habits, and host plant associations. Many of the species are phytophagous, although mycetophagy (e.g. Cylapinae, Schuh, 1976) and predation (Deraeocorinae, Razafimahatratra, 1980) are known, and it is quite probable that oligophagy, which is common in the Dicyphinae (Cobben, 1968), is prevalent in other mirid taxa.

At present, the systematic knowledge of the family is based chiefly on the fauna of the Palearctic and eastern Nearctic regions. Knowledge of the mirids of the Ethiopian (Odhiambo, 1962; Linnavouri, 1975), Australasian (Carvalho and Gross, 1979), and Oceanic (Carvalho, 1956) regions is limited. Carvalho and his students (1945-present) have contributed greatly to the description of the Neotropical mirid fauna, however, much remains to be accomplished. The family is cosmopolitan in distribution.

Much of the systematic work on mirids is regional in scope, however with the invaluable addition of the mirid

world catalogue of J. C. M. Carvalho (1955-1960) more attention has been paid to classification, phylogeny, and host associations (China and Carvalho, 1952; Carvalho and Leston, 1952; Leston, 1957; Leston, 1961; Schuh, 1974, 1975, 1976; Akingbohunge, 1974, 1983). Carvalho's classification is the more generally accepted and is based on the original classification of Reuter (1910), who emphasised pretarsal structure, pronotal structure and general body characteristics. Of late, Carvalho's classification has been questioned, and Schuh (1976) has offered an alternative classification which is based on new character sources and derived from a phylogenetic analysis. Schuh (1975, 1976) focused on the fine structure of the pretarsus (correctly identifying homologies), and femoral trichobothria number and position. Schuh's classification has not been broadly accepted by miridologists (Carvalho and Gross, 1979; Kelton, 1980b). He also recognized sister-group relationships that have not been previously recognized such as the placement of the dicyphines (sensu Carvalho, 1958) in the subfamily Bryocorinae. This classification has been recently supported by Akingbohunge (1983) on the basis of testicular follicle number of numerous Nearctic mirids.

Much controversy exists concerning the correct placement of the dicyphine taxa, if they constitute a

monophyletic group, what are their sister-group relationships, and what are the included taxa. My study was originally planned as a systematic study of the genus Dicyphus Fieber in North America north of Mexico, but it became apparent after initial investigations that the genera were poorly defined, and that significant taxonomic problems existed in this group at both the species and generic levels.

Considering the instability of the classification, and the numerous species synonyms that existed because of the ill-defined genera, I undertook a generic review with an investigation of most of the genera and included species. This thesis deals only with the generic reclassification and a revision of the Nearctic members of Dicyphus. Other generic revisions are in progress with the objective of completely reviewing all dicyphine taxa.

As I adhere to a phylogenetic approach to classification (sensu Hennig, 1966; Wiley, 1981), it was critical to investigate new character sources and re-examine traditionally used features. The dicyphines have been defined traditionally on obvious attributes such as their fragile, elongate body form, presence of a pronotal collar, two membrane cells in the hemelytra, and the pretarsus structure. The pretarsus structure has been used chiefly in the suprageneric classification of the mirids (Carvalho, 1952; Schuh, 1976). Some authors, like

Kullenberg (1947), have argued that the pretarsus is of questionable taxonomic value as this feature would be highly adaptive and prone to considerable parallelism. I chose to study intensively this feature to assess intergeneric variation and assess consistency and homoplasy. Riedl (1978) has argued that appendage attributes are characters of less genetic burden and their fixation is less than somatic features. For this reason I focused on body characters such as the thoracic pleura which have not been used before in mirid taxonomy. Apart from a brief treatment of the morphology of the thorax of Orthotlyus by Southwood (1953), the taxonomic significance of differences in thoracic structures are little understood and as yet even the correct homologies have not been established. Other characters investigated included the wings, and male and female genitalia.

Although structurally simplified, the dicyphines are most unique biologically. They are only associated with plants that either have glandular trichomes, or are densely pubescent and have toxic qualities (Russell, 1953; China, 1953; Seidenstucker, 1967; Cobben, 1968; Southwood, 1973). Trichomate plants are not phylogenetically restricted within the angiosperms (Levin, 1976), and I investigated the hypothesis that dicyphines may be associated with phylogenetically related plant taxa. This was done by constructing a

phylogeny for the Dicyphinae and listing known host plant groups for each bug genus to see if any coevolutionary pattern existed. A preliminary historical biogeographic analysis was also conducted using the derived dicyphine phylogeny.

In determining generic groups it is essential to investigate interspecific variation. I conducted a revision of the Nearctic Dicyphus species to achieve the original objective of the research and to provide for an observational basis for generic concepts. This revision included a preliminary investigation of phylogeny, distribution, and host plant associations.

CHAPTER 2

A Generic Reclassification of the Subfamily Dicyphinae

Reuter (Heteroptera: Miridae).

INTRODUCTION

The subfamily Dicyphinae is redefined as a monophyletic group comprised of sixteen genera and 178 species, and is regarded as a discrete assemblage of taxa within the family Miridae. The suprageneric group is diagnosed by the following attributes: 1) slender and delicate form, 2) pronotal collar, 3) an external mesepimeric spiracle, 3) scent efferent system subdivided into an osteole, peritremal disc, and evaporative areas, 5) pretarsus usually distinguished by pseudopulvilli and setiform parempodia, 7) the male genitalia are strongly asymmetrical, and 8) the vesica is sac-like.

The dicyphines are a cosmopolitan group with the greatest known taxic diversity in the Palearctic, however, this is most probably a sampling bias as recent studies (Carvalho and Gagne, 1968; Gagne, 1968; Linnavouri, 1975) indicate that the group is well represented in the tropics. The Dicyphinae are characterized by a simplified morphology, i.e. character reductions, and are more distinctive to hemipterists for their peculiar biological habits. They are most often associated with plants that either have glandular

trichomes, or have toxic qualities, such as high concentrations of alkaloids, and densely distributed, non-glandular trichomes (Reuter, 1913; China, 1953; Siedenstucker, 1967; Cobben, 1968; Southwood, 1973).

The suprageneric group has never been studied on a cosmopolitan scale although there are numerous regional works or partial treatments of genera (Poppius, 1914; Knight, 1941, 1943, 1968; Carvalho 1945, 1947, 1956; Wagner and Weber, 1964; Carvalho and Gagne, 1968; Gagne, 1968; Wagner, 1971; Linnavouri, 1975).

This study was initiated as a revision of the Nearctic species of the genus Dicyphus Fieber, however, the apparent inadequacy of the generic classification necessitated a broadening of this work to establish stable generic concepts and proper species placements. Carvalho (1955) provided a key to the genera of the world, and there are numerous regional generic keys (Poppius 1914; Knight 1968; Wagner 1971; Kelton, 1981), however, these keys are unreliable as they are based on characters that are either artificial, or variable within a genus.

In this paper, a revised generic classification is proposed including redescriptions of genera, a generic key, and a listing of included species, host plants and distribution. Intergeneric and intrafamilial relationships are discussed and new character sources

are emphasised to test other classifications and adding new morphological frameworks for studies in the family Miridae and the superfamily Cimicomorpha. Also, a key to the subgenera of Dicyphus Fieber is provided which includes new character information that makes identification more probable than the subgeneric key provided by Wagner (1971).

One new genus, Glarisia, is described for a small group of species found in the south-western United States that are characterized by a very short rostrum and unique features of the male genitalia. A new subgenus, Uhlerella, of the genus Dicyphus, is described to recognize the distinct Nearctic element of the genus which have a unique metaepisternum scent efferent system.

Attention in this paper is limited to the known species. In the material I have examined, numerous new species remain to be described, however, they are not treated here, although they were examined in view of setting the appropriate generic limits. I have commenced a revision of all the genera in the Dicyphinae which will include these new taxa and be presented in separate publications.

MATERIALS:

This study is based on an examination of about 14,000 specimens borrowed from museums and private collections. Institutions and individuals providing material were:

American Museum of Natural History, New York, R. T. Schuh; Arizona State University, Tempe, F. F. Hasbrouck; University of Arizona, Tucson, D. B. Thomas; Bernice P. Bishop Museum, Honolulu, Hawaii, W. C. Gagne; British Museum (Natural History), London, England, W. R. Dolling; University of British Columbia, Spencer Entomological Museum, Vancouver, Canada, S. G. Cannings and G. G. E. Scudder; California Academy of Science, San Francisco, P. H. Arnaud, Jr.; University of California, Berkeley, J. A. Chemsak and J. B. Whitfield; University of California, Davis, D. Ford; University of California, Riverside, J. Pinto and S. I. Frommer; University of Connecticut, Storrs, J. A. Slater and J. E. O'Donnell; Canadian National Collection, Ottawa, L. A. Kelton; Colorado State University, Fort Collins, W. D. Fronk; Cornell University, Ithaca, New York, L. L. Pechuman; Florida Department of Agriculture and Consumer Services, Gainesville, F. W. Mead; University of Georgia, Athens, C. L. Smith; Harvard University, Museum of Comparative Zoology, Cambridge, M. Hathaway; University of Helsinki, Zoological Museum, Finland, A. R. I. Jansson; Humboldt State University, Arcata, California, R. L. Hurley;

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The species which were obtained from each institution are not acknowledged in the following text. In the species listing for each genus the cross symbol, (+), indicates that specimens of that taxon were examined.

METHODS:

Classification and phylogenetic methods:

Decisions on generic delimitations were based on comparative morphological studies of the adults. Some consideration was given to extrinsic character information such as distribution and host plant associations.

I define genera as monophyletic assemblages of species (sensu Hennig, 1966). Autapomorphies are used to define a genus and synapomorphies identify intergeneric relationships. In some instances, however, derived characters intergrade between lineages, i.e. homoplasy occurs (parallelism and reversal). Gauld and Mound (1982) have discussed the problems of recognizing monophyletic supraspecific taxa when considerable homoplasy exists. They recommended that genera be defined

polythetically (i.e. group membership is determined by a suite of characters) which increases the probability of correctly assigning species. In certain insect groups, character reductions are common phenomena and often dominate the character sets that show any variability (Gauld and Mound, 1982). This is the case in dicyphines and polythetic genera are often recognized in the present study. This method also allows the minimization of monotypic groups which are redundant taxa and contribute little information in a phylogenetic analysis (Wiley, 1981).

The proposed phylogenetic hypothesis and classification of the dicyphines are based on cladistic analysis. This was achieved by using the cladistic computer algorithm, PAUP, which is valuable in detecting optimum solutions (see Swofford, 1981). Outgroup comparison was used to root the trees produced, and to polarize character states. The genus Felisacus Distant was used as the outgroup and the reasons for its selection are discussed in the text. Characters were either coded as binary or multistate characters and characters were unweighted, and either ordered or unordered when the direction of a transformation was unknown. The characters and character states used in this analysis are included in Table 1, and the raw data set is presented in Table 2, and the integers in this table

represent the character states, and the polarization when the characters are ordered. Included in Table 1 are the consistency ratios (CR) for each character. The CR is evaluated by the observed changes divided by the expected changes, so that a value of 1.00 represents a fully homologous character, and lower values indicate increasing homoplasy.

In coding characters, I considered it critical that each character was invariant within a genus. However, in the genus Dicyphus, which is widely variable, I used the character state found in the subgenus Dicyphus when there was inter-subgeneric variation. Similarly, in the genus Macrolophus, which is probably polyphyletic, there is considerable interspecific variation, and in such cases I only used the character states found in the Palearctic species that are closely related to the nominal species, nubilus s. s. (Herrich-Schaeffer).

In this analysis, fifty one characters were used, with considerable emphasis on the male genitalia and thoracic pleura characters. The thirteen treated genera were used in this analysis.

This analysis, and a discussion of the phylogenetic relationships of the dicyphine genera, including information gained from extrinsic data such as host plant associations and distribution, are provided after the taxonomic treatments of the genera.

The analysis of extrinsic data such as distribution and host plant associations can only be considered preliminary on the basis of the paucity of empirical data and the lack of any clear methodology. The biogeographic methods used in this analysis follow those proposed by Morse and White (1979), and the host plant associations are based on the recommendations of Mitter and Brooks (1983).

General Procedures:

Each genus is described in a conventional and uniform format. The males and females are not described separately and any morphological dimorphism is indicated. The range of interspecific variation in structure, body length, color, and vestiture was described. For each genus a listing of included species is provided with an account of known host plants and distribution for each species. Where a species is broadly distributed, regional names such as Europe, Middle Asia or Palearctic are used; otherwise country names are used as descriptors. A complete synonymical listing for each species is not provided as Carvalho (1958) has given a thorough listing, and post-1958, all new references are included in this text. In species listings where new synonymies or new combinations are erected, the nomenclatorial changes refer to the previous combinations or species standings proposed by Carvalho (1958), and not to the original

descriptions, unless the species are not treated by Carvalho (1958). If a new combination is proposed the former binominal combination is placed in brackets after the new status statement.

Distribution maps for each genus were constructed from specimens examined and published records (where the latter were considered to involve the correct taxa). Some of the maps indicate new range extensions for certain species or extralimital, new species. Often this information is from unpublished data and is indicated thus in the text for the relevant genera.

The construction of taxonomic keys was made with no intention of expressing phylogenetic information and are formulated for user convenience. Unfortunately, the generic key and the subgeneric key of Dicyphus requires male specimens for positive identification.

The male and female genitalia of all the species available within each genus were examined to assess intergeneric variation. Only dried specimens were used in this study. The dissecting methods developed by Kelton (1959) and Slater (1950) were used, although, they were somewhat adapted for the the delicate genitalic structures found in dicyphines, i.e. the genitalia of both sexes were boiled in 5% KOH for about two to five minutes and transferred to distilled water, and then stained in either acid fuchsin or eosin to highlight the membranous

structures and the ductus seminalis of the males.

Observations were made with either a Zeiss photomicroscope or a Leitz Wetzlar stereomicroscope at various magnifications. Measurements are in millimeters and were obtained with an ocular micrometer. All measurements represent maximum lengths. The scale for each figure is provided in the legend. Illustrations were drawn using an ocular grid and grid paper. Photomicrographs were recorded on Panatomic X film.

SEM Methods:

Both dried museum specimens and live material were used in scanning electron microscope observations. Dried material was sonicated in water and then air dried. Live material was fixed in 0.1M sodium cacodylate buffer, pH 7.2, and dehydrated in ethanol, and then critical point dried. The prepared material was attached to aluminum stubs with silver paint or double-sided sticky tape, and then coated with carbon and gold. An AMR 1000 scanning electron microscope was used to record the images on P/N 55 film.

TERMINOLOGY

I have adopted the terminology of Southwood (1953) for the thoracic pleura pending further examination of these structures and the establishment of homologies within the entire Cimicomorpha. Matsuda (1970) has briefly analyzed the Heteropteran thoracic pleura,

however, his treatment was not considered appropriate for this study as he referred mostly to gerromorphan Heteroptera. In describing the so-called "metathoracic stink-gland" I have used terms from various authors to accomodate the description of the cuticular dissipative system. The "stink-gland" is called the metaepisternum scent efferent system (Staddon, 1979), which is subdivided into the osteole, the peritremal disc which arises laterad to the osteole, and the evaporative areas (see fig. 33). Further, the components of the evaporative areas are referred to as the evaporative bodies which are identical to "le chapeaux" of Carayon (1971).

The mesepimeric spiracle is interpreted by Southwood (1953) and Andersen (1977) in the Heteroptera as the third thoracic spiracle. In dicyphines and phyelines this spiracle is situated on the mesepimeron and is easily identified by the exterior opening and the surrounding evaporative bodies.

I have accepted the pretarsal nomenclature of Schuh (1976), recognizing the distinction between pseudopulvilli and pulvilli (the latter as arising from the ventral aspect of the claw), and I accept the term parempodia over the more traditionally used term, arolia (see Cobben, 1968, and Schuh, 1976, for reasoning).

In describing the various wing polymorphic conditions in dicyphines I have used the nomenclature of Cobben

(1960). When the membrane is absent, or reduced and without veins, the condition is referred to as brachyptery, whereas when the membrane is reduced but the veins are present the character state is termed semibrachyptery. In describing the membrane cells of the hemelytra I refer to the large cell as the major one, and when the small cell is present I call it the minor cell. The homologies for the veins of the hindwings follow those described by Davis (1961).

The terminology of Kelton (1959) for the male genitalia, and that of Slater (1950) and Davis (1955) for the female genitalia, are used in this work.

The remainder of the terminology used in this paper has general acceptance in the modern literature.

NOMENCLATURE:

Carvalho's Catalogue of the genera of the Miridae of the World (Carvalho, 1958) was produced before the most recent International Codes of Zoological Nomenclature (1961, 1964), and does not conform to various recommendations in the present code. These include:

1) Article 51A (d) which states that the author name of a taxon must be in parenthesis when a new combination is proposed. In this treatment all of these cases are corrected. 2) Article 30 deals with the need for agreement in gender between species-group and genus-group names. In dicyphines this is critical as the majority of

species have been proposed in various combinations and few authors have attempted to correct the endings of the species names. This has been dealt with in this study in accordance with the code.

Steyskal (1973) suggested that the gender of numerous genus-group names in the world catalogue (Carvalho, 1958) were incorrectly identified and proposed gender changes in Campyloneuropsis, Cyrtopeltis, and Macrolophidea. I have checked the recommendations of Steyskal (1973) and regard them as correct and therefore I adhere to his proposed changes.

HISTORICAL REVIEW:

Few works have dealt with the intergeneric relationships within the Dicyphinae. Much of the confusion in the literature is attributable to the poorly defined supraspecific group and the relationships between the true dicyphine taxa.

Fieber (1858, 1861) described the genera Dicyphus, Macrolophus, and Cyrtopeltis which have remained the focal genera within the subfamily. However, numerous taxa have been placed in the dicyphines which actually belong to many of the other mirid subfamilies. Poppius (1914) described numerous monotypic genera which he included in the Macrolophini [Dicyphinae], however, as will be discussed later, many of these taxa were unrelated and it is apparent that he did not recognize any meaningful

groupings of genera. Reuter (1910) was also uncertain of the relationships of this group as he placed the ant-like genera Hallodapus Fieber and Systellonotus Fieber within the dicyphines (the former two genera were correctly placed in the Phylinae by Carvalho and Leston (1952)). Knight (1941) in his treatment of Nearctic mirids considered the genus Hyaliodes Reuter as a dicyphine because of the salient similarity of these taxa, however, Carvalho (1952) recognized the later's correct position in the Deraeocorinae. Carvalho (1952) was the first author to treat the dicyphines on a global basis, and later (Carvalho, 1955) provided a key to the world genera, and finally (Carvalho, 1958) a catalogue of the known species. However, he did not have all the available material and he included many non-dicyphine taxa within his group. His classification has not been seriously questioned, although Schuh (1976) suggested that Poppius' Ethiopian genera were in serious need of study and may not be dicyphines. In this study, genera described by Flor (1860), Distant (1904), Poppius (1914), Knight (1935), and Hsiao (1944) have been removed from the dicyphines, and the subfamily is now composed of sixteen genera (see Synopsis of the Subfamily).

Much controversy has remained over the definitions, interrelationships, and nomenclatorial status of the true dicyphine genera. Of particular concern is the so-called

"Cyrtopeltis" complex. Reuter (1909) first synonymized Engytatus Reuter with Cyrtopeltis Fieber, however, he later regarded them as separate genera (Reuter, 1910). Poppius (1913) then placed Gallobellicus Distant in synonymy with Dicyphus Fieber. Horvath (1922) stated that Gallobellicus crassicornis Distant was not a member of Dicyphus, but either a Cyrtopeltis or an Engytatus. Knight (1922) considered that the latter two genera were congeneric. China (1938) further clarified some of the confusion over these genera and Dicyphus. Usinger (1946) was the first to clearly recognize the dilemma, that students of the dicyphines continually changed the generic placement of species with no apparent reason, only to restore them to their original status. He suggested that the male genitalia provided a sound basis for a generic classification, and concluded that there were three genera in this complex: Cyrtopeltis, Engytatus, and Gallobellicus.

China and Carvalho (1952) further recognized the complexity of the situation, however they concluded that it was difficult to make logical use of the male genitalia and to separate females. Thus they synonymized Engytatus and Nesidocoris Kirkaldy (= Gallobellicus) with Cyrtopeltis, and recognized each of them as subgenera, and described three new subgenera: Tupiocoris, Singhalesia, and Usingerella. Their classification was

entirely based on the male genitalia with no mention of any other characters. These actions are seemingly incongruous with their original statements in the same paper. They erected new groups, regarded the synonymized taxa as distinct, only altering their ranking, and provided no means to separate the females. Further, the key they provided to separate the Cyrtopeltis complex from Macrolophus and Dicyphus does not provide reliable identifications. Taxonomic studies after China and Carvalho's (1952) treatment accepted their generic classification (Odhiambo, 1961; Wagner, 1971; Linnavouri, 1975). However, the entire post-1952 literature has only been regional in scope. McGavin (1982) perceived some of the problems by recognizing that some of the Nearctic and Palearctic species of Dicyphus were not congeneric. However he was not aware of the fauna of the entire Western Hemisphere, and Tupiocoris is the proper designation for the included species, rhododendri (Dolling), of his genus Neodicyphus.

BIOLOGY

Relatively little is known about the biology of members of this subfamily beyond their peculiar association with glandular or toxic plants. Information is limited to studies of certain economic pests such as the tomato suck-fly, Engytatus modestus (Distant) (see Tanada and Holdaway, 1954). In my observations of

species belonging to the genera, Dicyphus, Tupiocoris, Usingerella, and Macrolophus, and from the literature (Quaintance, 1898; Tanada and Holdaway, 1954; Cobben, 1968; Wheeler et al., 1979) it appears that many of the taxa are oligophagous. Cobben (1968) has indicated that one species Dicyphus (Idolocoris) pallicornis (Meyer-Dur) is exclusively phytophagous, whereas Russell (1953) and China (1953) suggest that Setocoris species, which are only associated with insectivorous plants, are primarily predacious, feeding on entrapped, transient insects.

Tanada and Holdaway (1954) report that E. modestus feeds mostly on vascular tissue, although secondary feeding occurs in the cortex, endodermis, pericycle, and pith. Kullenberg (1947) reported that Dicyphus (Dicyphus) constrictus (Boheman) feeds on the exudates from the glandular trichomes of Salvia sp. (Labiatae).

The majority of dicyphines are most commonly associated with plants in the families Solanaceae, Compositae, Rosaceae, Labiatae, Scrophulariaceae, Caryophyllaceae, Gesneriaceae, and Geraniaceae. As yet no dicyphines are recorded from gymnosperms or monocots, although a few species are known from ferns (Wheeler et al., 1979). No other mirid group has this restricted association with sticky plants on a broad taxonomic scale, however a very similar pattern of association is

found in the world Berytidae (Wheeler and Schaefer, 1982). The latter group is chiefly found on glandular plants, in almost the same plant families as the dicyphines, and many berytid taxa are oligophagous. This adaptive convergence in life history traits between these groups raises the question whether a coevolutionary pattern exists. In my study however, I found no apparent correlation between plant family and dicyphine (generic level) phylogenies, and it is more probable that these associations are ecologically determined. Moreover, Metcalfe and Chalk (1950) report that the trichomes are common in many angiosperms and show no phylogenetic restriction. At the dicyphine species level, however, it is quite possible that coevolution occurs. For example the species of Setocoris are found on closely related Drosera species. There is no clear indication in any other dicyphine genus that these patterns involve more than a pair of sister species.

Levin (1973, 1976) has demonstrated that plant glandular trichomes are an important plant defense against phytophagous insects, either as a physical barrier, and/or a chemical barrier (trichomes exude secondary compounds). I have observed that the herbivore and predator loads on these "dicyphine" plants is very low, which may indicate that food is not a limiting factor and high levels of mortality are not attributable

to predation. This may explain why dicyphine taxa, up to three species, often coexist on the same host plant without any noticeable partitioning of resources nor any significant temporal separation (personal field observations; Seidenstucker, 1967). Further, these associations are characterized by a strong correlation between trichome presence (temporally variable in plants like Ribes species) and active life cycle and development. There is some degree of host specificity, although some species, such as Dicyphus (Uhlerella) hesperus, are known from as many as ten different hosts.

SUBFAMILY DICYPHINAE REUTER *

*

Idolocoridae Douglas and Scott 1865: 31.

Dicypharia Reuter 1883: 408.

Campyloneuraria Kirkaldy 1902a: 138.

Campyloneurini Kirkaldy 1906: 129.

Macrolophini Kirkaldy 1906: 371.

Macrolophina Reuter 1910: 108.

Macrolopharia Poppius 1911: 29.

Dicyphinae Oshanin 1912: 70.

Dicyphina Schuh 1976: 35.

Type genus: Dicyphus Fieber 1858: 326.

* Nomenclature: According to Article 23 (d)(i) of the most recent International Code of Zoological Nomenclature (1964), if two or more family-groups are synonymized then

the valid name is the oldest family-group name (not the oldest generic name). In this case Idolocoridae is the senior name, however, this name has not been used in the primary zoological literature until 1955 (China and Miller, 1955), which makes the name a nomen oblitum (Article 23(b)), and in such instances the code stipulates the following: 1) a nomen oblitum is not to be used unless the commission so directs (Article 23(b)(i)). 2) a nomen oblitum is referred to the commission. I have for this reason retained the junior family-group name, Dicyphinae, because it is the name in current usage (Article 80), until the situation can be brought to the attention of the commission.

DIAGNOSIS: The body form is elongate, or elongate-ovoid, and most species are fragile with moderately long to long appendages. Base color varies from pale to black, and if pale there are often contrasting markings which are usually red, brown, or fuscous. The setation is always simple, linear, and erect to adpressed.

The head is most often vertical and transverse (figs. 1, 2), although sometimes elongate, and the eyes are protrudent laterally with the posterior margin excavate when viewed from the side. The antennae are linear without modifications, with regularly distributed setae, and the apical third of the penultimate segment and apical segment with adpressed micro-setae.

The pronotum is distinguished by a narrow collar, calli which are varyingly distinct, and a large disc which may be broadly convex.

The mesepimeron is small, most often narrow, anteriorly recurved, and narrowly connected to the basalare. The mesepimeric spiracle is small, and is always bordered by evaporative bodies which extend onto the depressed postalare (see figs. 33, 222).

The metaepisternum is subtriangular and is most often distinguished by a well developed scent efferent system (fig. 222), sometimes secondarily absent, which is subdivided into a mesal, depressed osteole, a suboval to narrow, setate peritremal disc, and evaporative areas.

The legs are most often linear and long, with the following features: the coxae are contiguous; the femora are linear, and the middle and hind femora have variable trichobothria (3-6 mesofemoral, 3-8 metafemoral) which have a tuberculate bothrium and poorly defined trichoma; the tibiae are linear, the front tibiae have a disto-ventral tibial comb, all have rows of spinelets, and the middle and hind tibiae usually have erect, stout spines; the tarsus is linear, not incrassate apically, with the basal segment minute, and the penultimate segment at least 1.5x longer than the apical segment; the pretarsus is variable, claws either strongly recurved (fig. 250), or almost linear (fig. 247) which are cleft basally, the

pseudopulvilli are leaf-like, attached ventrally to the claws adjacent to the unguitractor plate, and the parempodia are setiform.

The hemelytra are often flimsy, and usually partly hyaline, the corial fracture is usually narrow, and there are usually two membrane cells, although the minor cell may be minute or secondarily absent. Sometimes non-sex brachyptery or semibrachyptery occurs, and one instance of aptery is known.

The hindwings are characterized by the absence of a second anal vein, the first anal vein is most often long, extending to the postcubital wing margin, though it may be shortened, and a hamus is never present.

The male genitalia are greatly asymmetrical with the right clasper minute. The pygophore is greatly variable with the genital aperture either dorsal (fig. 260), terminal (fig. 268), or greatly dissected and asymmetrical (fig. 264). The left clasper is most often V-shaped and variable in size and shape. The vesica is membranous, sac-like, and often armed with tuberculations or spiculi. The ducutus seminalis is narrow, long, flexible, and the secondary gonopore is obscure and diffuse. The phallosome is small, strap-like, and most often adnate to the vesica.

The female genitalia are variable with the posterior wall usually simplified and membranous, and the bursa

copulatrix has a pair of sclerotized rings which are most often separate, suboval to subelliptical, and divergent caudally.

Monophylecity and Ranking of the Dicyphinae:

It is beyond the scope of this work to discuss in detail, and analyze the intrafamilial relationships of the Miridae, however with this present investigation of intergeneric variation of the Dicyphinae I am able to suggest characters that allude to the monophylecity of this group, comment on the appropriate suprageneric ranking, and suggest possible character sources that may clarify the present polemics over intrafamilial relationships.

The Dicyphinae are comprised of sixteen genera and 179 species, and can be considered a monophyletic group on the basis of the following character states: 1) male genitalia greatly asymmetrical, with right clasper almost obsolete. 2) diploid chromosome number 48 (Leston, 1957; Southwood and Leston, 1959). 3) testis follicle number 1 (Leston, 1961; Akingbohunge, 1983). 4) osteole a depressed cuticular region. 5) peritremal disc setate, not raised or modified. 6) claws with basal pore.

In preliminary investigations of other mirid taxa, not one of the above character states is present, and these attributes are considered apomorphic for the mirids which supports my contention that the dicyphines are

monophyletic. Moreover, this group is exclusively associated with glandular or toxic plants and this is a unique life history trait for the Miridae.

Previous authors such as Carvalho (1958), Leston ((1961), Wagner and Weber (1964), Knight (1941, 1968), Wagner (1971), Schuh (1976) have all considered the dicyphines as a distinct group, however there is considerable conjecture as to the appropriate ranking and possible sister-group relationships. Carvalho and Leston (1952) first proposed that the dicyphines were a tribe of the subfamily Phylinae on the basis of the similar pulvilli. Schuh (1976) has subsequently shown that the dicyphine pretarsal structure is unlike that of phylines, and the presence of pseudopulvilli suggests a strong relationship between the monalonine Bryocorinae and the Dicyphinae (he also provided correlative evidence for the femoral trichobothria and egg structure). Others have considered the dicyphines as a subfamily (Knight, 1968; Wagner, 1971) although they have not suggested any possible sister-group relationships. Leston (1961) suggested that the dicyphines were a subfamily and distinct from the Phylinae on the basis of reduced testis follicle number and a high diploid chromosome number, and were possibly related to the Deraeocorinae on the basis of the male and female genitalia. Kelton (1959) followed the classification of Carvalho (1958) but regarded the

dicyphine male genitalia as similar to that found in the Cylapinae. Akingbohunge (1983), in investigating a number of attributes and testis follicle numbers of Nearctic mirids, concluded that Schuh's (1976) classification was more appropriate.

I concur with Schuh (1976) that the pretarsal structure indicates a close relationship between the monalonine Bryocorinae and dicyphines, however, there is considerable intergeneric variation in this character. For example, the genus Campyloneura has a pretarsus structure that is very similar to that found in ecritotarsine Bryocorinae. Schmitz (1970) was aware of this and it formed the basis of his diagnosis of the Dicyphinae which included the genus Rhodocoris Schmitz (which Schuh (1976) moved to the ecritotarsines).

I consider it more reasonable to rank the dicyphines as a subfamily for the following reasons: 1) there is adequate information from character analysis to conclude that the dicyphines are monophyletic. 2) the monalonines and dicyphines have numerous features which distinguish them, and these characters are considered as phylogenetically significant (see next section). 4) the subfamily Bryocorinae is in my opinion polyphyletic and it is more reasonable, both nomenclatorially and systematically, to define the suprageneric groups rigidly before possible sister-group relationships are considered

in constructing a classification. 5) the intrafamilial classification of the Miridae is almost exclusively based on pretarsal structure however I have observed that this attribute is variable at the generic level and is probably subject to homoplasy.

New character source for the familial classification of the Miridae:

I have placed great emphasis in this study on the thoracic pleura which have not been used before in the higher classification of the Miridae.

I have used this character in conjunction with the pretarsal characters for identifying suprageneric groups in the Miridae. I have made numerous observations of many mirid taxa and the thoracic pleura appear to show significant differences that are consistent. I describe below the basic morphology for each distinct type for the convenience of the user of this paper. To date five different types can be described, which are as follows:

- 1) Mesepimeric spiracle, internal, intersegmental; metaepisternum scent efferent system well developed, with peritremal disc raised and U-shaped (Cylapinae, Mirinae, Deraeocorini [Deraeocorinae], Bryocorini [Bryocorinae]), or produced into a tube (Hyalodini [Deraeocorinae]).
- 2) Mesepimeric spiracle, internal, intersegmental, metaepisternum scent efferent system reduced, with a

minute osteole, tongue-shaped peritremal disc extending along posterior margin of segment, and evaporative areas absent (Eccritotarsini [Bryocorinae]).

3) Mesepimeric spiracle external, bordered by evaporative bodies; metaepisternum scent efferent system well developed, osteole small, peritremal disc raised, evaporative areas present (Phylinae).

4) Mesepimeric spiracle external, bordered by evaporative areas; metaepisternum scent efferent system well developed, osteole depressed, peritremal disc not raised, evaporative areas present (Dicyphinae).

5) Mesepimeric spiracle external, elongate, narrow slit, opening bordered by dense arrangement of setae, without evaporative areas (Monalonini and Odoniellini [Bryocorinae], or efferent system present (Felisacus, a monalonine Bryocorinae).

At present it is difficult to evaluate the significance of this character for the classification of the Miridae and Cimicomorpha. More information regarding the distribution of certain character states and the possible transformation series is needed. I have used this feature in this classification with reference to my limited observations of Nearctic mirids and tropical bryocorines.

SYNOPSIS OF SUBFAMILY DICYPHINAE REUTER

Included genera of the subfamily Dicyphinae:

Campylonenuropsis Poppius (14 species)

Campyloneura Fieber (2)

Chius Distant (1)

Cyrtopeltis Fieber, Restored status (7)

Dicyphus Fieber = Abibalus Distant, New synonymy =

Bucobia Poppius, New synonymy (47)

D. (Brachyceraea) Fieber (15)

D. (Dicyphus) Fieber (14)

D. (Idolocoris). Douglas and Scott (8)

D. (Mesodicyphus) Wagner (4)

D. (Uhlerella) Cassis, New subgenus (6)

Engytatus Reuter, Restored status (26)

Glarisia Cassis, New genus (2)

Macrolophus Fieber = Macrolophidea Poppius, New
synonymy (25)

Nesidocoris Kirkaldy, Restored status (23)

Setocoris China and Carvalho (3)

Singhalesia China and Carvalho, New status (5)

Tupiocoris China and Carvalho, New status = Leptomiris

Carvalho and Becker, New synonymy = Neodicyphus McGavin,
New synonymy (17)

Usingerella China and Carvalho, New status (2)

Genera of uncertain position retained in the subfamily

Dicyphinae:

Dicyphopsis Poppius (2)

Habrocoris Wagner (1)

Isoproba Osborn and Drake (1)

GENERA REMOVED FROM THE SUBFAMILY DICYPHININAE:

Angerianus Distant (2)

Apollodotidea Hsiao, see Stethoconus Flor

Cychrocapsus Poppius (1)

Hildebrantiella Poppius (1)

Hyalosmella Poppius (1)

Onconotellus Knight (1)

Orthotylidea Poppius (1)

Pseudocamptobrochis Poppius (1)

Stethoconus Flor = Apollodotidea Hsiao, New synonymy (5)

Teratocapsus Poppius (1)

KEY TO GENERA OF SUBFAMILY DICYPHINAE

This key does not include the genera Dicyphopsis, Habrocoris, and Isoproba. From couplet 4 onward males are required in the operation of this key.

1. Metaepisternum with evaporative areas covering almost entire segment (figs. 36, 225, 226, and 227), at least beyond lateral level of mesepimeric spiracle; claws of pretarsus cleft basally (figs. 45, 46, 244, and 247); genital aperture of male dorsal in orientation, with shaft of left clasper contiguous with the ventral margin of the genital aperture (figs. 118, 258, 259, and 260).....
 Dicyphus Fieber (Holarctic, Ethiopian), p. 64.

- Metaepisternum either without scent efferent system (e.g. fig. 34), or moderately developed, with evaporative areas extending, at maximum, to the lateral level of the mesepimeric spiracle (e.g. fig. 222); claws not cleft as above (e.g. fig. 250), although sometimes with basal tooth (e.g. fig. 251); pygophore either with terminal genital aperture (fig. 265), or with a ventral pygophoral process (e.g. fig. 262).....
 2

2. Dorsum most often with stout spines, if not then restricted to femora and tibiae; exclusively associated with insectivorous plants.....
 Setocoris China and Carvalho (Australia), p. 137.
- Dorsum without erect spines, often tibiae with stout spines, but femora without spines.....
 3
3. Lorum enlarged, raised, strongly convex (fig. 4); pretarsus highly modified (fig. 243), claws minute, with pulvilli huge, and claw setae present.....
 Campyloneura Fieber (Palearctic), p. 49.
- Lorum flat to weakly convex, never raised (e.g. fig. 2), pretarsus with pseudopulvilli, never enveloping claws (e.g. fig. 244).....
 4
4. Males with a large, ventral pygophoral process (figs. 113, 262, 264, and 271).....5
- Pygophore of males without ventral process (e.g. fig. 265), at most, ventral margin of genital aperture with small tubercle(s) (e.g. fig. 124)...
 8

5. Hemelytra with only one membrane cell (fig. 109);
left clasper U-shaped (fig. 161).....
.....Usingerella China and Carvalho
(Nearctic), p. 160.

- Hemelytra with two membrane cells; left clasper
V-shaped (fig. 146).....6

6. Left clasper of male huge (fig. 166); pygophore
with dorsodextral tubercle (fig. 264); vesica with
interconnected, sclerotized tubercles.....
.....Nesidocoris Kirkaldy
(circumtropical), p. 128.

- Left clasper of male small (e.g. fig. 146);
pygophore without dorsodextral tubercle; vesica
without interconnected tubercles, either without
sclerotizations, or with sparsely distributed
tubercles.....7

7. Head strongly vertical, eyes usually large,
extending to bucculae (fig. 18); pygophoral
process tapered towards apex (fig. 262), often
bifurcate; vesica of male with subbasal,
sclerotized plate (fig. 183).....
.....Engytatus Reuter (circumtropical),
p. 101.

- Head elongate, eyes never extend to bucculae (fig. 8); pygophoral process globose (fig. 118), never bifurcate; vesica without subbasal, sclerotized plate (fig. 170).....
.....Cyrtopeltis Fieber (Palearctic, Oriental), p. 58.
- 8. Metaepisternum scent efferent system absent (figs. 34, 239).....9
- Metaepisternum scent efferent system present (e.g. fig. 222).....10
- 9. Dorsum highly polished, if pallid, then without two fuscous spots on the posterior margin of the pronotum; postocular margins of vertex convergent toward collar (fig. 27); antennae inserted near midheight of eyes (fig. 28).....
.....Tupiocoris China and Carvalho (Western hemisphere), p. 148.
- Dorsum pallid, not highly polished, posterior margin of the pronotum with two fuscous spots (fig. 5); antennae inserted near base of eyes (fig. 6).....
.....Chius Distant (Central America), p. 55.

10. Males with ventrad process on the 8th abdominal segment (fig. 257).....
.....Campyloneuropsis Poppius
(in part, Neotropical), p. 42.
- Males without ventrad process on 8th abdominal segment fig. 263).....11
11. Ventral margin of genital aperture of males with a suboval, excavate process, and dorsal margin with a pointed tubercle (fig. 263); rostrum extending to base of mesocoxae.....
.....Glarisia Cassis, new genus
(western North America), p. 112.
- Ventral margin of genital aperture of males without excavate process, although sometimes with small, internal tubercle (fig. 124).....
.....12
12. Head elongate (fig. 22), sometimes transverse, but postocular margins of vertex always strongly convex and parallel (fig. 21).....
.....Macrolphus Fieber
(Palearctic, Ethiopian, Nearctic, Neotropical), p. 117.
- Head vertical and transverse (e.g. fig. 1), postocular margins of vertex convergent towards collar (e.g. fig. 2).....3

13. Dorsal margin of pygophore of males with stout bristles (fig. 270); shaft of left clasper S-shaped (fig. 158); vesica simple, modified into a narrow tube (fig. 195, 273), bursa copulatrix of females with separate sclerotized rings (fig. 218).....Singhalesia China and Carvalho (Ethiopian, Oriental, Australian, Oceanic), p. 34.
- Dorsal margin of pygophore without stout bristles (fig. 111); shaft of left clasper linear (fig. 129); vesica sac-like, with numerous spiculi (fig. 168); bursa copulatrix of females with sclerotized rings connected (figs. 202, 204).....
.....Campyloneuropsis Poppius (in part, Old World), p. 42.

TAXONOMY OF THE GENERA OF DICYPHINAE:

Genus Campyloneuropsis Poppius

Figures: 1, 2, 33, 42, 48, 49, 78, 79,
80, 111, 112, 128, 129, 130, 168, 169,
202, 203, 204, and 257.

Campyloneuropsis Poppius 1914: 8 (type species:

Campyloneuropsis annulatus Poppius 1914: 10).

DIAGNOSIS: This genus is very similar to Singhalesia China and Carvalho, and is most easily distinguished by features of the male and female genitalia. The left clasper of the male is V-shaped (fig. 128), with the shaft linear to inwardly recurved. The vesica is multilobed with numerous, apical spiculi, and also, sometimes with a large, falcate spiculum (fig. 168). The sclerotized rings of the bursa copulatrix of the female, are small, lateral in orientation, and are connected by a sclerotized process (figs. 203, 204, and 205).

DESCRIPTION: macropterous; length, males 1.70-4.00, females 1.75-4.20; yellow to testaceous, always with apex of cuneus red to brown, often with fuscous or red markings on head and appendages; rugulose; covered with fine, suberect setae.

Head: (figs. 1, 2) strongly vertical, transverse; frons weakly produced in front of eyes, pale, sometimes

with obscure, red fascia; vertex small, width subequal to length of first antennal segment, postocular margins weakly convex, convergent; clypeus small, barely visible from above, often darker than rest of head.

Eyes: very large, often extending to bucculae (fig. 2), sometimes only to base of lorum; lateral margins excavate; separated from pronotum by thickness of collar; facets very large; red, fusco-red, or fuscous.

Antennae: inserted below, or at midheight of eye; I broad, small, usually pale, with red or brown, mesal annulation; other segments unicolorously pale, or II banded subbasally; second segment less than the width of pronotum at base.

Pronotum: (figs. 1, 2), broadly trapezoidal, rugulose, lateral margins linear, weakly to moderately divergent; collar narrow, mesally constricted, sometimes with mesal groove; calli indistinct, often mesally defined by deep fold, posteriorly obscure; disc posterior margin weakly excavate, posterior angles rounded broadly.

Scutellum: unicolorous, or dark mesally with lateral angles pale.

Thoracic pleura: (figs. 33, 222), mesepimeron broad, subquadrate, spiracle small to moderate in size, subovoid, evaporative areas border spiracle, extend onto lateral margins of weakly depressed postalare;

metaepisternum small, with small, mesal osteole, peritremal disc adjacent to posterior margin of segment, evaporative areas cover about 1/3 of the segment, evaporativae bodies oval in shape, remainder of segment with regular arrangement of microsetae; metaepimeron broad, often bicolored, yellow to testaceous with subapical red to brown marking.

Legs: femora, metafemora often weakly incrassate, fore, and middle, femora small; trichobothria, 3-4 mesofemoral (fig. 49), 4-5 metafemoral (fig. 48); tibiae small, with two rows of spinelets, meso-, and meta-, tibiae with dorsal and lateral spines; tarsus, small, second segment barely longer than apical segment; pretarsus (fig. 42), claws strongly recurved, pseudopulvilli broad, subequal in length to claws.

Hemelytra: (figs. 78, 79, and 80), embolium narrow, corial fracture broad; cuneus broad, in Neotropical species inner margin sinuate (fig. 80); corial fracture and apex of cuneus marked with red or brown; two membrane cells, minor cell small.

Hindwings: (fig. 80) R vein recurved toward costal margin; 1A short, weakly sinuate.

Male genitalia: in Neotropical species segment 8 with a sinistroventral tubercle (fig. 257); pygophore weakly dissected (fig. 111, 257); genital aperture terminal (fig. 112), ventral margin with inner tubercle;

left clasper V-shaped (fig. 128), shaft inwardly recurved (fig. 129), lobe well developed, somewhat elongate; right clasper (fig. 130) linear, articulated near phallosome (fig. 112); vesica multilobed (fig. 168), with a number of small to large, apical spiculi, and often with large, falcate spiculum; ductus seminalis narrow, moderate in length; phallosome strap-like (fig. 169), narrow, dissected apically.

Female genitalia: bursa copulatrix small, sclerotized rings small (fig. 202, 204), lateral in orientation (fig. 203) connected by oval sclerotized processes, Neotropical species with internal teeth on sclerotized processes (fig. 204).

INCLUDED SPECIES, HOST PLANTS, AND DISTRIBUTION:

Note: that the symbol, +, indicates that specimens of that species have been examined.

annulata Poppius 1914: 10. + = virgator Linnavouri 1975:

14. New synonymy. +

Host plant: unknown.

Distribution: west Africa, Ceylon.

cincticornis (Stal) 1860: 52. New combination,

[Cyrtopeltis (Tupiocoris)]. +

Host plant: unknown.

Distribution: Brazil.

cornuta (Odhiambo) 1961: 18. New combination,

[Cyrtopeltis (Singhalesia)].

Host plant: Conyza steudelli Sch. Bip. (Compositae).

Distribution: Uganda.

fagoniae (Linnavouri) 1975: 13. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: Fagoniae arabica (Zygophyllaceae)

Distribution: Sudan.

falciger (Linnavouri) 1975: 13. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: unknown.

Distribution: Sudan.

hyalina (Carvalho) 1947: 16. New combination,

[Cyrtopeltis (Tupiocoris)]. +

Host plant: unknown.

Distribution: Brazil.

impicta (Linnavouri) 1961: 2. New combination,

[Cyrtopeltis]. +

Host plant: unknown.

Distribution: Israel.

infumata (Carvalho) 1947: 16. New combination,

[Cyrtopeltis (Tupiocoris)]. +

Host plant: Nicotiana tabacum L. (Solanaceae).

Distribution: Brazil.

longula (Poppius) 1914: 14. New combination,

[Dicyphus]. +

Host plant: unknown.

Distribution: east, and west Africa.

nigroculata (Carvalho) 1947: 15. New combination.

[Cyrtopeltis (Tupiocoris)]. +

Host plant: Cassia cathartica L. (Leguminosae).

Distribution: Brazil.

pavoniae (Linnavouri) 1975: 14. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: Pavonia glechomaefolia Rich. (Malvaceae).

Distribution: Ethiopia.

pochalla (Linnavouri) 1975: 14. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: unknown.

Distribution: Sudan.

tacsa (Odhiambo) 1961: 16. New combination, [Cyrtopeltis

(Singhalesia)]. +

Host plant: Gynandropsis pentaphylla DC.

(Cleomaceae).

Distribution: Uganda, Kenya.

rubroornata (Poppius) 1914: 15., New combination,

[Dicyphus]. +

Host plant: unknown.

Distribution: east Africa.

SPECIES REMOVED FROM THE GENUS:

seorsus Van Duzee, see Engytatus Reuter

REMARKS: This genus was originally described as a monobasic genus by Poppius (1914), and subsequently Van Duzee (1934) described seorsus in this genus. The identity of this genus has not been clearly defined previously because Poppius' genus description and diagnosis were too brief. Furthermore, the type material of the type species, annulata was not labelled with any such indication. I have located this material and have made lectotype and syntypical designations. The genotype, annulata, is here recognized as a senior synonym of virgator Linnavouri.

The genus is now broadly defined to include numerous species from Africa that are very similar to annulata. Additionally, three species from South America that were previously placed in the subgenus Tupiocoris of the genus Cyrtopeltis have been placed in Campyloneuropsis on the basis of male and female genitalia. Two species, longula and rubroornata, are removed from Dicyphus and placed in

this genus, however, these combinations need further investigation as both species were described from only female specimens.

This genus is very similar to Singhalesia, however, the attributes of the male and female genitalia are considered distinct enough to warrant generic separation.

The genus, as now defined, has a Gondwanan distribution with some Laurasian elements (see map 1). The host plant associations are not apparently phylogenetically significant as the associations are with unrelated and non-repeated plant families. There is no biological information recorded for any of the species in the genus.

Genus Campyloneura Fieber

Figures: 3, 4, 52, 53, 81, 82, 205, 223, 224, and 243.

Campyloneura Fieber 1860: 67 (Type species: Capsus virgula Herrich-Schaeffer 1835: 268, type by monotypy).

Camptoneura Fieber 1858: 309 (name preoccupied by Camptoneura Maequart (Diptera))

DIAGNOSIS: The species in this genus are uniquely characterized by the enlarged, dorsally projecting lorum (fig. 4), and the eyes are almost contiguous with the pronotal collar when viewed from above (fig. 3). Also, the metafemora are greatly elongate, and are almost twice

as long as the middle femora. The pretarsus is characterized by short, stout, strongly recurved claws, with the base of the claws with claw setae (fig. 243), and huge, highly convoluted pulvilli, that surround the claws.

DESCRIPTION: Female. Elongate-ovid, appendages long, macropterous; length 3.50-4.75; pallid with fuscous, and red markings; uniformly covered with long, pale setae.

Head: (figs. 3, 4), broader than long, suboval, fuscous; frons evenly rounded in front of eyes; vertex rounded, wide, postocular margins minute, strongly convergent; clypeus small, not visible from above; lorum small, greatly expanded, directed dorsally, posterior margin not exceeding level of antennal insertions; bucculae enlarged.

Eyes: large, posteroventrad angle greatly excavate; fusco-red to fuscous; facets moderate in size; removed from collar by less than thickness of first antennal segment.

Antennae: inserted well below midheight of eyes; first segment constricted basally, longer than width of the vertex; II at least 1.7x greater than width of posterior margin of pronotum.

Rostrum: extend to apices of metacoxae.

Pronotum: (fig. 3, 4): trapezoidal, distinctly tripartite, lateral margins almost linear; collar entire, not mesally constricted, longer than thickness of first antennal segment, whitish, with lateral, reddish infusion; calli distinct as weakly raised areas, not delimited mesally or posteriorly by deep groove; disc, posterior angles evenly rounded, posterior margin moderately excavate, testaceous with whitish infusion.

Thoracic pleura: (fig. 223), mesepimeron subquadrate, broadly convex, weakly recurved anteriorly, inner margin indistinct, almost linear, posterior margin highly polished, devoid of setae, spiracle large, suboval, somewhat removed from posterior margin of mesepimeron, evaporative areas not produced into crowns, but into depressed cups, with internal, ribbed substructure (fig. 224), and restricted to immediate regions of spiracle, postalare depressed, with evaporative areas extending to posterolateral margin; metaepisternum (fig. 223), scent efferent system well developed, osteole large, narrow, mesal, peritremal disc suboval, weakly depressed, evaporative areas extending to mesepimeric spiracle, evaporative bodies elongate, widely spaced, remainder of segment with regular arrangement of microsetae; metaepimeron narrow, weakly depressed.

Legs: femora linear, hind femora almost twice as long as mesofemora, pallid to testaceous; femoral trichobothria, 5 mesofemoral (fig. 53), 6 metafemoral (fig. 52); tibiae linear, pallid, with suberect setae, middle and hind tibiae with erect spines; tarsi small, weakly incrassate toward apex, all segments subequal in length; pretarsus distinctive (fig. 243), claws small, recurved, stout, with basal claw setae, claws enveloped by huge, convoluted pilvilli.

Hemelytra: (fig. 81), always macropterous; clavus coriaceous, testaceous with fuscous to black, reticulate markings; embolium dark; exocorium hyaline, endocorium hyaline to coriaceous; cuneus broad, bicolored; two distinct membrane cells.

Hindwings: (fig. 82), R vein linear, parallel to costal margin; 1A long, extending to PCu margin; veins heavily pigmented.

Female genitalia: (fig. 205), sclerotized rings separate, divergent caudally, posterior margin linear.

Males. not examined, see Remarks section.

INCLUDED SPECIES, HOST PLANTS, AND DISTRIBUTION:

virgula virgula Herrich-Schaeffer 1836: 5. +

Host plants: Fraxinus sp. (Oleaceae), Tilia sp. (Tiliaceae), Alnus sp. (Betulaceae), and Quercus sp. (Fagaceae). Lattin and Stonedahl (1984) report

numerous other hosts for this species in the western United States where it is an established, introduced species.

Distribution: Europe, North Africa, introduced in to western United States (see Downes, 1947).

virgula marita Wagner 1968: 46.

Host plants: Pistacia lentiscus L. (Pistaciaceae), Phillyrea angustifolia L. (Oleaceae), and Quercus sp. (Fagaceae).

Distribution: Middle Asia, Tunisia, and Algeria.

decorata Kiritschenko 1931: 104.

Host plant: unknown.

Distribution: south-central U.S.S.R (Pamir).

REMARKS: I have not seen any males of the two species in this genus. Only females of the predominately thelytokous subspecies, virgula virgula Herrich-Schaeffer, were available for examination. Wagner and Weber (1964), and Wagner (1971) report that the males of this taxon are exceedingly rare, and that the male genitalia are greatly reduced. Wagner (1971) states that the aedeagus is involuted, and suggests that copulation would be improbable. Wagner (1971) described the genitalia of virgula marita, and notes that the pygophore is trapezoidal with an evenly rounded genital aperture, and a simple vesica with a slender spiculum.

Even though only one of the three taxa in this genus has been investigated the identity of this group is not in question. The morphological distinctness of the head, metafemora, thoracic pleura, and pretarsus, together with the unique biology and host plant associations are sufficient to regard this group as a genus.

There are two included species, of which virgula is divided into two subspecies. There is some question as to the identity of decorata, which is only known from the original description. Kerzhner and Yaczewski (1967) refer to this genus as monotypic, and do not refer to decorata. Also, Wagner (1968) does not refer to this species even though he refers to specimens from Middle Asia, which is the locality of decorata.

This genus has a Palearctic distribution (see map 2), and the subspecies virgula virgula is an introduced taxon in the western United States (Downes, 1957; Lattin and Stonedahl, 1984).

Biological information is restricted to virgula virgula. It is reported to be predacious, feeding on red spider mites, psocopteran eggs and larvae, and aphids (Southwood and Leston, 1959). Masee (1954) reported this species feeding on honeydew. Lattin and Stonedahl (1984) found them in association with the aphid, Illinoia (Masonaphis) lambersi (MacGillivray), on rhododendron, and indicated that they were commonly associated with

aphids on other host plants. The subspecies virgula marita is found on similar host plants and since these associations are atypical for the dicyphines it is conceivable that it is also predacious and has a similar biology to the typical subspecies.

Genus Chius Distant

Figures: 5, 6, 34, 44, 52, 53, 83, 84,
116, 117, 134, 135, 136, 172, 173, and 206.

Chius Distant 1884: 297 (type species: Chius maculatus Distant 1884: 297).

DIAGNOSIS: This genus is distinguished by the elongate head (fig. 6), the parallel postocular margins of the vertex (fig. 5), the antennae inserted near the ventral margin of the eye, and the absence of the metaepisternum scent efferent system (fig. 34). The latter attribute distinguishes it from Macrolophus species which have a well developed scent efferent system (e.g fig. 234).

DESCRIPTION: Macropterous, elongate; length, males 3.75-4.00, females 3.80-4.00; yellow, with 8-10 fuscous spots on the dorsum; sparsely covered with pale, suberect setae.

Head: (figs. 5, 6), elongate, about as broad as long; frons strongly produced in front of eyes, evenly rounded, yellow; vertex broad, weakly convex, postocular

margins parallel, weakly convex, most often with fuscous markings; clypeus moderately produced, visible from above, somewhat truncate dorsally, yellow; jugum large; bucculae moderate in size.

Eyes: very small, strongly protrudent; ventral margin barely reaches jugum (fig. 6); fuscous.

Antennae: inserted near ventral margin of eye (fig. 6), long; I greater in length than vertex width, yellow, with apical, fuscous annulation; II longer than the width of pronotum at base, yellow, with fuscous, basal annulation; III yellow with apical, fuscous annulation; IV yellow.

Rostrum: extending to apices of metacoxae.

Pronotum: (figs. 5, 6) trapezoidal; lateral margins linear, moderately divergent; collar narrow, strongly constricted mesally, yellow; calli flattened, obscure, weakly defined mesally and posteriorly, yellow; disc weakly flanged posteriorly, posterior margin excavate, sinuate weakly, yellow, with two basal, fuscous spots (fig. 6); propleuron, moderately expanded, visible from above.

Scutellum: anterior 1/3 yellow, remainder fuscous, apex rounded broadly.

Thoracic pleura: (fig. 34), mesepimeron broad, spiracle large, oval, bordered by evaporative areas; postalare, weakly depressed, with evaporative areas on

lateral margins; metaepisternum without scent efferent system.

Legs: femora linear, testaceous, uniformly covered with pale, suberect setae; trichobothria, 4 mesofemoral (fig. 53) and 5 metafemoral (fig. 52); tibiae moderately sized, testaceous, uniformly covered with erect, pale setae, no spines present; tarsus long, II 1.5x longer than III; pretarsus (fig. 44) small, claws almost linear, with broad, basal tooth, pseudopulvilli large, leaf-like.

Hemelytra: (fig. 83) embolium narrow, corial fracture and cuneus broad; two membrane cells, minor cell small; yellow with brown to fuscous markings at apex of clavus, above corial fracture, and apex of cuneus.

Hindwings: (fig. 84) R vein parallel to costal margin; 1A short.

Male genitalia: pygophore (fig. 116), genital aperture terminal, ventral margin impressed, weakly expanded (fig. 117), dorsal margin evenly rounded, with an internal, sinistral tubercle; left clasper (fig. 135) V-shaped, shaft strongly recurved when viewed internally; right clasper small, narrow, linear (fig. 136); vesica (fig. 172) sac-like, unilobed, with internal, sclerotized channel, obscurely connected to long ductus seminalis; phallosome (fig. 173) weakly sclerotized, dissected apically.

Female genitalia: (fig. 206), bursa copulatrix large, sclerotized, rings separate, divergent caudally.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

maculatus Distant 1884: 297. +

Host plant: unknown.

Distribution: Guatemala, and south-west Mexico.

REMARKS: This monotypic genus may eventually be synonymized with Macrolophus, however, such action is deferred pending a worldwide revision of the latter (now being conducted by T. J. Henry, USNM and myself).

It is separated from the latter because of the absence of a scent efferent system and spines on the tibiae.

The one included species is known from northern Guatemala, and south-west Mexico (see Map 3), and there is no host plant or biological information reported for this species.

Genus Cyrtopeltis Fieber. Restored status.

Figures: 7, 8, 35, 43, 113, 114, 115,
131, 132, 133, 170, and 171.

Cyrtopeltis Fieber 1860: 76 (Type species: Cyrtopeltis geniculata Fieber 1861: 323).

Cyrtopeltis (Cyrtopeltis) China and Carvalho
1952: 158.

DIAGNOSIS; This genus is most easily diagnosed by the globose, pygophoral process, and the dissected dorsal surface of the pygophore (figs. 113, 114). The pygophoral process is similar to that in Engytatus species, however, in the latter the eyes extend to the bucculae. Also, the head is more elongate in the former (cf. fig. 7 to 17), and is somewhat similar to Macrolophus taxa. The left clasper shaft is extremely broad (fig. 131), the male vesica is characterized by tuberculations (fig. 170), and the ductus seminalis terminates apically as a sclerotized, cup-like process (fig. 170).

DESCRIPTION: macropterous; elongate to elongate-ovoid; length, males 1.85-5.60, females 2.05-5.00; flavescent to yellow, sometimes with fuscous markings on dorsum and appendages; sparsely covered with short, pale, suberect setae.

Head: (figs. 7, 8), elongate; frons strongly produced in front of eyes, often with light brown markings; vertex broadly convex, sometimes marked brown mesally, postocular margins weakly sinuate, convergent towards collar; clypeus broad, strongly produced in front of frons.

Eyes: small to moderate in size, not protrudent, extending to lorum when viewed from side.

Antennae: inserted at midheight of eyes; I small, subequal to vertex width, sometimes with brown

annulation; II subequal in length to width of pronotum at base, sometimes with basal annulation.

Rostrum: extending to apices of mesocoxae.

Pronotum: (fig. 7, 8), trapezoidal, lateral margins linear, moderately divergent; collar small, weakly constricted mesally, shiny; calli large, subequal to disc length, poorly defined mesally and posteriorly, often marked with brown on each callus; disc, posterior angles strongly rounded, posterior margin weakly excavate, somewhat sinuate; propleuron weakly expanded, barely visible from above.

Thoracic pleura: (fig. 35), mesepimeron long, spiracle small, bordered by evaporative areas, extending onto depressed postalare; metaepisternum large, without scent efferent system. Metaepimeron narrow.

Legs: femora fusiform, yellow to testaceous, sometimes with brown infusions apically, uniformly covered with small, stout, suberect setae; trichobothria, 3 mesofemoral and 4 metafemoral; tibiae linear, testaceous, sometimes with basal, brown annulation, with stout, dark spines, uniformly covered with pale to brown, setae, sometimes with irregular arrangement of spinelets; tarsi long, penultimate segment at least 2x longer than the apical segment; pretarsus (fig. 43) minute, claws small, strong, with basal thickening, weakly recurved, pseudopulvilli broad, subequal to claw length.

Hemelytra: unicolorous, testaceous, rarely with an enbrowment at corial fracture; membrane hyaline, minor membrane cell small.

Hindwings: not examined.

Male genitalia: pygophore (fig. 113, 114) with a distinct pygophoral process, apically oriented to left (fig. 115), dorsal margin strongly dissected (fig. 113), with separate, internal, sclerotized cup (fig. 115); left clasper (figs. 131, 132) lobe well developed, somewhat elongate, shaft extremely broad, heavily sclerotized (fig. 131), apically constricted, when viewed internally, notched at apex (fig. 132), remainder linear; right clasper (fig. 133) articulated on dextroventral corner of genital aperture (fig. 114), linear, notched apically; vesica (fig. 170) large, multilobed, with small tuberculations; ductus seminalis long terminating apically in sclerotized cup; phallosome (fig. 171) narrow, expanded basally, dissected apically.

Female genitalia not investigated.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

callosa Odhiambo 1961: 14. [Cyrtopeltis (Cyrtopletis)].

Host plants: gourd leaf (?) (Cucurbitaceae), Sida schimperi (Malvaceae).

Distribution: Uganda.

canariensis (Lindberg) 1936: 36. [Cyrtopeltis (Cyrtopeltis)]. +

Host plant: Cistus vaginatus L. (Cistaceae).

Distribution: Canary Islands.

geniculata Fieber 1861: 323. Restored combination, [Cyrtopeltis (Cyrtopeltis)].

Host plant: Ononis natrix L. (Leguminosae).

Distribution: Mediterranean (Hsiao (1942) reported that this species is found in Mongolia, however, this may be an erroneous identification, and that information is not included in this distributional record).

khalafi Seidenstucker 1964: 327.

Host plant: unknown.

Distribution: Pakistan.

kochi Wagner 1961: 315.

Host plant: unknown.

Distribution: Egypt.

pygmaea Wagner 1956: 1. +

Host plant: Trichodesma africanum (Boraginaceae).

Distribution: Egypt, Sudan.

taxali Seidenstucker 1972: 84.

Host plant: unknown.

Distribution: Pakistan.

Unfortunately the above generic description is based on observations of only two of the included species. The present generic description is supplemented from the original description of the species, and the diagnoses of Wagner and Weber (1964), Wagner (1971), and China and Carvalho (1952). Despite the paucity of material, the generic identity is not in doubt on the basis of the male genitalia, distinct head, and pretarsus structure.

China and Carvalho (1952) decided to place a number of taxa that they deemed related in the genus Cyrtopeltis, under six subgeneric categories.

With the use of new character sources, and a more thorough investigation of the male genitalia, I have elevated all the subgeneric categories to full generic status, although altering their conception and taxic content. The actions of the previous authors was done to render some nomenclatorial and taxonomic stability, however, their decisions were based on a small sample of species, and based chiefly on the male genitalia.

The genus is distributed only in the Palearctic region (map 4). The host plant associations are poorly known, although the available information indicates no phylogenetic significance. Biological information is lacking, although Wagner (1971) reports that geniculata is univoltine and the egg is the overwintering stage. He also states that canariensis overwinters as an adult (Wagner, 1971).

Genus Dicyphus Fieber

Figures: see under subgeneric categories.

Dicyphus Fieber 1858: 326 (as subgenus, Wagner 1951a: 8.

Type species: Capsus pallidus Herrich-Schaeffer 1836: 51, type fixed by Kirkaldy 1906: 129).

Brachyceraea Fieber 1858: 327 (as subgenus, Wagner

1951a: 1. Type species: Gerris annulatus Wolff 1804: 162, type fixed by Kirkaldy, 1906: 129).

Idolocoris Douglas and Scott 1865: 374 (as subgenus,

Wagner 1951a: 6. Type species: Capsus pallicornis Meyer-Dur 1843: 110, type fixed by Kirkaldy 1906: 129).

Mesodicyphus Wagner 1951a: 7 (as subgenus. Type species:

Dicyphus testaceus Reuter 1879: 204).

Abibalus Distant 1909: 521, New synonymy. (Type species:

Abibalus regulus Distant 1909: 521).

Bucobia Poppius 1914: 8, New synonymy. (Type species: Bucobia regulus Poppius: 1914: 8).

DIAGNOSIS: This genus is diagnosed by the distinct, tripartite pronotum (figs. 9, 11, 13, and 15), and the metaepisternum scent efferent system with a large depressed osteole, and evaporative areas almost covering the entire segment (e.g. fig. 225). The genital aperture of the male is dorsal in orientation, with the pygophore either deeply dissected (fig. 118), or with the genital aperture restricted to the posterodorsad angle (figs. 259, 260, and 261). The shaft of the left clasper is contiguous with the ventral margin of the genital aperture (e.g. fig. 118). The pretarsus is distinctive with the claws cleft basally (figs. 45, 46, 244, and 247), and linear, and the pseudopulvilli and parempodia only half the length of the claws.

DESCRIPTION: macropterous, semibrachypterous, or brachypterous; length, males 2.75-6.50, females 2.50-6.50; pallid to black, variously marked with fuscous, testaceous, reddish to ochraceous markings; sparsely covered with short to long, pale to dark, erect to semierect setae.

Head: elongate to vertical; frons variously produced in front of eyes, sometimes broadly, or otherwise strongly in middle, anteriorly either truncate or

rounded, when viewed from side, either concolorous or produced into two posteriorly converging, longitudinal markings; vertex with a mesal, weak depression, postocular margins long, weakly convergent, often marked differently to mesal region of vertex.

Eyes: large, strongly rounded, protrudent, often posteriorly excavate when viewed laterally; red to black; facets small.

Antennae: inserted at about midheight of eyes, variable in length of segments, if body elongate then first segment greater in length than the width of the vertex, or if body broad then I shorter or equal to the vertex width in length; often banded.

Rostrum: variable in length extending between apices of mesocoxae and 4th abdominal segment.

Pronotum: trapezoidal; collar broad, often constricted, shiny to coriaceous, often with very long, erect setae, sometimes indistinctly separated from xiphus, when viewed laterally; calli distinct, inflated, smaller in length than disc, unless brachypterous or semibrachypterous, various types, either subquadrate, mesally confluent, separated by fine, linear groove, or oval, raised, with either a distinct or incomplete, transverse, posterior furrow; disc large, often flanged upward, posterior angles strongly rounded, posterior margin usually deeply excavate, unless hemelytra

shortened, then margin linear to weakly emarginate; propleuron projected laterally, distinctly visible from above.

Thoracic pleura: mesepimeron broad, highly modified, recurved anteriorly, attached broadly to basalare, spiracle small, oval surrounded by extensive evaporative areas, postalare broad, depressed, posterior half with evaporative areas; metaepisternum with well developed scent efferent system, osteole large, expanded apically, peritremal disc shiny to indistinct, either short, subtriangular, extending to level of the mesepimeric spiracle, or long, narrow, recurved, extending to near metaepimeron, evaporative areas extensive, covering almost entire segment, or at least beyond mesepimeric spiracle; metaepimeron small, often shiny.

Legs: femora linear, testaceous to yellow, often marked with one or two rows of brown to fuscous spots, often restricted to apical or basal half of segment, uniformly covered with stout, pallid to fuscous, suberect setae; trichobothria, 4-6 mesofemoral, and 5-7 metafemoral; tibiae linear, moderately long to very long when body elongate, testaceous, rarely with dark markings, if so restricted to apical 1/3, armed with small to large, stout spines, except in Nearctic species, always with irregularly arranged spinelets; tarsi long, II at least 1.5x longer than apical segment, testaceous,

often III fuscous; pretarsus, claws strongly cleft at base, remainder strongly linear, except for weakly recurved tip, pseudopulvilli small, expanded apically, pseudopulvilli and parempodia only half length of claws.

Hemelytra variously developed, most species macropterous, often with non-sex brachyptery, or semibrachyptery; clavus coriaceous, often testaceous, with fuscous markings; exocorium often hyaline, endocorium variously marked; cuneus large, most often elongate; membrane hyaline to pale brown, major cell and minor cell large, delimiting vein terminating mesally on cuneus, veins often infused with brown or red.

Hindwings: R vein always moderately recurved; 1A variable, either short or extending to PCu margin.

Male genitalia: pygophore either deeply dissected, or genital aperture restricted to posterodorsad angle, genital aperture always dorsal in orientation, ventral margin produced into long, posteriorly projecting lip, or posterodextral directed lip, dorsal margin evenly rounded, entire, laterosinistral margin sinuate at articulation of left clasper; left clasper L-shaped, lobe small, usually subquadrate, armed with long, stout setae, shaft evenly recurved, long to very long, apex of shaft often expanded laterally, outer margin of shaft always contiguous with ventral margin of genital aperture, terminating near, or beyond right clasper;

right clasper small, linear, articulated in ventrodextral angle; vesica membranous, multilobed, often armed with 1-2 large spiculi, or with many small spiculi, or one large and many small spiculi, or with internal, sclerotized channels, base of vesica always with a sclerotized ring, ductus seminalis small, terminating indistinctly; phallosome broad, dissected apically.

Female genitalia: bursa copulatrix large, sclerotized rings separate, variable in shape, and divergence toward caudal end, sometimes with sclerotized teeth.

NEW GENERIC SYNONYMIES:

Abibalus Distant 1909: 521.

The monotypic genus Abibalus Distant is placed in synonymy with Dicyphus on the basis of the similar pretarsus structure, femoral trichobothria numbers and position, and the metaepisternum scent efferent system. The species, regulus is tentatively placed in the subgenus Idolocoris, on the basis of its salient similarity to other species in this taxon. However, since this species is only known from one female specimen, this placement within the subgenus may need revision due to the importance of the male genitalia in this classification.

Bucobia Poppius 1914: 8.

The genus Bucobia Poppius is synonymized with Dicyphus, and is also placed in the subgenus Idolocoris

on the basis of the male genitalia which is similar to that of pallicornis (Meyer-Dur), although the vesica of the former has no spiculi.

REMARKS: The identity of this genus is clear on the basis of numerous synapomorphies of the male genitalia, metaepisternum scent efferent system, and the pretarsus structure. The subgeneric categories of Wagner (1951) are retained, although the diagnosis and species of Idolocoris is altered slightly. It may be necessary to further revise the subgeneric classification because of the wide interspecific variation. To date I have not examined any species of the subgenus Mesodicyphus, and only a few species of the subgenus Brachyceraea were available for investigation. For this reason I have deferred any major taxonomic changes pending a worldwide revision of the genus. I have described a new subgenus, Uhlerella, to include all endemic, Nearctic species, which share numerous apomorphies of the male genitalia, and the scent efferent system.

The genus is previously recorded from only the Northern Hemisphere, however one new species remains to be described from South Africa. The genus appears to be restricted to temperate regions, and is most probably a Laurasian group (see maps 5-9). The biogeography and host associations are discussed further in each subgeneric category.

KEY TO THE SUBGENERA OF THE GENUS DICYPHUS FIEBER:

1. Body ovoid, appendages small; first antennal segment small, equal to or less than the vertex width; calli oval, greatly raised, variable in distinctness.....
.....2
- Body elongate to elongate-ovoid, appendages moderate to long in size; first antennal segment always longer than the width of the head; calli subquadrate.....3
3. Calli oval, marked posteriorly by deep, transverse groove; vesica of male with one large, and numerous small spiculi.....
.....Brachyceraea Fieber (west and central Palearctic), p. 72.
- Calli oval, indistinctly separated from disc; vesica of male without spiculi.....
.....Mesodicyphus Wagner (central Palearctic), p. 94.
3. Pygophore of male deeply dissected, ventral margin of genital aperture produced into a broad posteriorly projecting lip (fig. 118); species elongate.....Dicyphus Fieber (west Palearctic), p. 79.

- Pygophore of male not deeply dissected, genital aperture restricted to posterodorsad angle (fig. 259); species elongate to elongate-ovoid.....
.....4

- 4. Osteolar peritremal disc extending to near metaepimeron, beyond mesepimeric spiracle (fig. 227); pygophore with internal sclerotized bar connecting above left and right clasper articulations (fig. 121).....Uhlerella Cassis, new genus (Nearctic), p.

Osteolar peritremal disc subtriangular, not extending beyond mesepimeric spiracle (fig. 226); pygophore without internal sclerotized bar.....
.....Idolocoris Douglas and Scott (Palearctic), p. 88.

Subgenus Brachyceraea Fieber

Figures: 9, 10, 46, 54, 55, 85, 86,
137, 138, 139, 174, 175, 176, 225,
and 258.

Brachyceraea Fieber 1858: 327 (as subgenus,
Wagner 1951a: 1. Type species: Gerris annulatus Wolff
1804: 162 (type fixed by Kirkaldy 1906: 129).

DIAGNOSIS: The species in this subgenus are always broad,
and have a rugulose to coriaceous texture. The pygophore

(fig. 258) is deeply dissected, and dorsal in orientation, and the vesica (figs. 174, 176), and left clasper (figs. 137, 139) are variable. The calli are oval, raised, small (fig. 10), and the head is transverse (fig. 9), and vertical (fig. 10).

DESCRIPTION: macropterous; elongate-ovoid to ovoid, appendages small, length, males 2.50-4.25, females 2.60-4.50; costal margins convex; base color variable, testaceous to dark, with numerous markings; setation most often long and semierect.

Head: (figs. 9, 10), transverse, vertical; frons weakly produced in front of eyes, if mostly testaceous, then with two dark fascia; vertex, postocular margins small, convergent towards collar, often dark; clypeus moderately produced, often pale mesally, remainder of lateral aspect of head most often dark.

Eyes: large, separated from collar by thickness of first antennal segment, fuscous, facets moderately sized.

Antennae: inserted at midheight of eyes, often banded; I small, subequal in length to vertex width.

Rostrum: extending between apices of middle and hind coxae.

Pronotum: (figs. 9, 10), trapezoidal, lateral margins moderately divergent; collar broad, mesally constricted, testaceous, sometimes with dark markings; calli oval, separated by wide depression mesally, often polished,

posterior margin distinct; disc weakly raised, posterior margin linear to weakly excavate; propleuron moderately expanded laterally, visible from above.

Thoracic pleura: (fig. 225), mesepimeron elongate, posterior margin angulate, inner margin linear, spiracle minute, evaporative areas cover 1/2 of segment, postalare depressed, lateral margin with evaporative areas; metaepisternum, scent efferent system well developed, osteole broad, peritremal disc ovoid, short, evaporative areas cover most of segment, sublateral areas highly polished, anterolaterad angle with dense arrangement of microsetae; metaepimeron narrow, strongly reflexed.

Legs: femora linear, somewhat expanded dorsoventrally, testaceous, often with rows of dark spots; trichobothria, 3 mesofemoral (fig. 55) and 4 metafemoral (fig. 54); tibiae with stout, dark spines; pretarsus (fig. 46) claws moderately cleft, almost linear apically.

Hemelytra: (fig. 85), macropterous, coriaceous, testaceous; embolium broad; corial fracture broad, often dark; cuneus broad, often dark at apex; two membrane cells, minor cell moderate in size.

Hindwings: (fig. 86), R vein recurved; 1A extends to PCu margin.

Male genitalia: pygophore (fig. 258) deeply dissected, dorsal in orientation; left clasper variable, lobe either subtriangular, large, and shaft gradually tapered towards apex (fig. 137), or lobe small, rounded, and shaft expanded at apex (fig. 139); right clasper (fig. 138) small, linear, sclerotized along entire length; vesica variable, either with numerous small spiculi (fig. 174), and sometimes with large spiculum, or sac-like, without spiculi (fig. 176), always with basal, sclerotized, U-shaped process; phallosome (fig. 175), moderately broad at base, dissected apically.

Female genitalia: bursa copulatrix large, sclerotized rings large, separate, moderately divergent towards caudal end.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

albonasutus Wagner 1951a: 7. +

Host plant: Pulmonaria officinalis L.

(Boraginaceae).

Distribution: Mediterranean, and Asia Minor.

alluadi Vidal 1951: 64. New combination, [Dicyphus

(Dicyphus)]. +

Host plant: unknown.

Distribution: Morocco.

annulatus (Wolff) 1804: 162. +

Host plant: Ononis spinosa L. (Leguminosae).

Distribution: western Europe, and Morocco.

cerruttii Wagner 1946: 133. +

Host plant: Cerastium arvense (Caryophyllaceae).

Distribution: Switzerland, and Italy.

digitalidis Josifov 1958: 271.

Host plant: Digitalis viridiflora Lindl.

(Scrophulariaceae).

Distribution: Bulgaria.

furcifer Muminov 1974: 1439.

Host plant: unknown.

Distribution: Middle Asia (Tadjikistan).

geniculatus (Fieber) 1858: 343.

Host plants: Cucubalus sp. (Caryophyllaceae), and

Salvia sp. (Labiatae).

Distribution: Mediterranean, and eastern Balkans.

globulifer (Fallen) 1829: 124. +

Host plants: Melandryum sp., Lychnis sp.

(Caryophyllaceae), and Salvia sp. (Leguminosae).

Distribution: Europe.

melanocerus Reuter 1901: 175 = montanus Poppius 1912: 11

= mucheii Wagner 1974: 23 (synonymies by Muminov 1974: 1440).

Host plant: unknown.

Distribution: Middle Asia (Turkestan).

ononidis Wagner 1951: 24.

Host plant: Ononis sp. (Leguminosae).

Distribution: south-western Europe.

orientalis Reuter 1879: 203 = physochlaenae Hutchinson

1934: 138 (synonymy by Muminov 1974: 1440). +

Host plant: Physochlaena prealta Hook. (Solanaceae).

Distribution: Turkestan, Northern India.

pauxillus Muminov 1974: 1438.

Host plant: unknown.

Distribution: Middle Asia (Tadjikistan).

seleucus Seidenstucker 1969: 146.

Host plant: unknown.

Distribution: Turkey.

sengge Hutchinson 1934: 139. +

Host plant: unknown.

Distribution: northern India.

thoracicus Reuter 1879: 204.

Host plant: unknown.

Distribution: Turkestan.

SPECIES REMOVED FROM THE SUBGENUS:

montandoni Reuter, see Idolocoris.

REMARKS: This subgenus is almost identical in conception to that proposed by Wagner (1971), although montandoni is placed in D. Idolocoris on the basis of the male genitalia. The pygophore of the males of this taxon is very similar to that found in D. Dicyphus. However, the pronotum and body shape is considerably different and warrants group separation. The aedeagus is somewhat similar to that found in D. Idolocoris, however, the genital aperture of the male of the latter is restricted to the posterodorsal angle.

This subgenus contains sixteen species. Muminov (1974) has proposed three new species synonymies which I have accepted on the basis of his careful morphological work and examination of the male genitalia. One species, alluaudi was placed in this subgenus from D. Dicyphus by Wagner (1971), and from his description its placement is appropriate according to the present subgeneric diagnosis.

The subgenus is chiefly distributed in the southern Palearctic, although it is also recorded from northern

India (Map 5), and is most probably a Laurasian group.

Of the known host plants the highest frequency of associations are with the plant families Caryophyllaceae and Leguminosae, although they are also known from genera in the Solanaceae and Boraginaceae. Very little is known about the biology of this group. Wagner and Weber (1964) and Wagner (1971) report that most of the species are univoltine and overwinter as adults, however, Wagner (1971) indicates that geniculatus hibernates in the egg stage. Butler (1923) states that globulifer is found in both damp, shady woods, and open hedge habitats, and the adults are gregarious and abundant. Butler (1923) also reports that annulatus is found in sandy places in coastal locales, whereas the species, digitalidis, is recorded from higher altitudes between 1300-2000 meters (Wagner, 1971). This would suggest that there is no altitudinal zonation distinctive for the subgenus.

Subgenus Dicyphus Fieber. Ssensu stricto.

Figures: 11, 12, 36, 45, 56, 57, 87,
88, 89, 118, 119, 120, 140, 141, 177,
178, and 209

Dicyphus Fieber 326 (as subgenus Wagner 1951: 8.

Type species: same as for genus).

DIAGNOSIS: The species of this subgenus are generally elongate, the left clasper is large (fig. 140), and the

pygophore of the male is deeply dissected (fig. 118), and the vesica always has two large spiculi (fig. 177). Also, the pronotum is always distinctly tripartite with the calli large and subquadrate (fig. 11).

DESCRIPTION: macropterous, sometimes brachypterous; appendages long; length, males 3.25-6.50, females 3.50-6.50; costal margins parallel; most often base color testaceous, with fuscous to light brown markings; setation sparse, long and erect.

Head: (figs. 11, 12) elongate; frons moderately produced in front of eyes, testaceous, often with two dark fascia; vertex often with weak, mesal depression, often dark posteriorly; clypeus moderately to strongly produced; bucculae large.

Eyes: moderately sized, separated from collar by at least length of collar; fuscous, often tinged with red; facets small to moderate in size.

Antennae: inserted at midheight of eyes, often banded; I, long, linear, at least 1.5x longer than vertex width.

Pronotum: (fig. 11, 12), trapezoidal, distinctly tripartite; calli distinct, subquadrate, separated by distinct, mesal and posterior sulci; disc distinctly flanged upward, coriaceous, posterior margin deeply excavate; propleuron strongly expanded laterally, visible from above.

Thoracic pleura: (fig. 36), mesepimeron large, elongate, inner margin weakly sinuate, posterior margin rounded, spiracle moderately sized, posterior 1/2 covered with evaporative areas, postalare weakly depressed, posterior 1/2 and lateral margins with evaporative areas; metaepisternum, osteole large, depressed, expanded at apex, peritremal disc moderately sized, tapered towards apex, not extending beyond mesepimeric spiracle, evaporative areas cover almost entire segment.

Legs: femora linear, tapered towards apex, pale, often with rows of fuscous spots, trichobothria, 4-6 mesofemoral (fig. 57) and 6-7 metafemoral (fig. 56); tibiae with large dark spines; tarsus long; pretarsus large (fig. 45), claws deeply cleft, linear, recurved apically.

Hemelytra: (fig. 87), macropterous, sometimes with non-sex brachyptery (fig. 89), testaceous; costal margins parallel; corial fracture broad, often dark; cuneus elongate, apex dark; two membrane cells, minor cell very large.

Hindwings: (fig. 88), R vein parallel to costal margin; 1A short.

Male genitalia: pygophore (fig. 118, 119) deeply dissected, ventral margin of genital aperture produced into a long, posteriorly projecting lip (fig. 120) with internal, sclerotized cup; left clasper (fig. 140), lobe

subquadrate, shaft elongate, inner margin somewhat sinuate, sometimes apex expanded; right clasper (fig. 141) linear, tapered apically; vesica (fig. 177) multilobed, with basal sclerotized U-shaped ring, and two apical spiculi; phallosome (fig. 178) very broad basally, dissected apically.

Female genitalia: (fig. 208), bursa copulatrix large, sclerotized rings separate, widely divergent.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

alkannae Seidenstucker 1956: 145.

Host plant: Alkanna orientalis L. Boiss.

(Boraginaceae).

Distribution: Turkey.

bolivari bolivari Lindberg 1934: 12.

Host plant: unknown.

Distribution: Canary Islands.

bolivari atlanticus Wagner 1951a: 29.

Host plant: Epilobium hirsutum L. (Onagraceae).

Distribution: western Mediterranean.

constrictus (Boheman) 1852: 79. +

Host plant: Melandryum sp. (Caryophyllaceae),

Stachys sp., and Salvia sp. (Labiatae).

Distribution: Mediterranean, and Turkey.

eckerlerti Wagner 1965: 59.

Host plants: Epilobium hirsutum L. (Onagraceae), and

Cirsium sp. (Compositae).

Distribution: eastern Mediterranean.

escalerai Lindberg 1934: 11.

Host plant: unknown.

Distribution: Mediterranean.

flavoviridis Tamanini 1949: 2.

Host plant: Salvia glutinosa L. (Labiatae).

Distribution: Italy.

hyalinipennis (Burmeister) 1835: 268. +

Host plants: Atropa belladonna L. (Solanaceae),

Senecio viscosa L. (Compositae), Ononis natrix L.

(Leguminosae), and Epilobium sp. (Onagraceae).

Distribution: Europe.

lindbergi Wagner 1951a: 17.

Host plant: Hyoscyamus albus L., and H.

aureus L. (Solanaceae).

Distribution: Palearctic.

maroccanus Wagner 1951a: 19.

Host plant: Digitalis atlantica L.

(Scrophulariaceae).

Distribution: Palearctic

pallidus (Herrich-Schaeffer) 1836: 51. +

Host plant: Stachys sylvatica L. (Labiatae).

Distribution: Europe, and North Africa.

rubicundis Blote 1929: 163.

Host plant: unknown.

Distribution: Canary Islands.

stachydis stachydis Reuter 1883: 421. +

Host plants: Stachys sylvatica L., Galeopsis sp.

(Labiatae), Circaea sp. (Onagraceae), and

Digitalis sp. (Scrophulariaceae).

Distribution: Europe.

stachydis wagneri Tamanini 1955: 14.

Host plant: unknown.

Distribution: Mediterranean.

tamaninii Wagner 1951a: 16. +

Host plant: Hyoscyamus niger L. (Solanaceae).

Distribution: Mediterranean.

tamaricis Puton 1886: 19.

Host plant: unknown.

Distribution: North Africa.

SPECIES REMOVED FROM THE SUBGENUS:

agilis Uhler, see Tupiocoris.

alluadi Vidal, see Brachyceraea.

brachypterus Knight, see Tupiocoris.

californicus Stal, see Tupiocoris.

crudus Van Duzee, see Macrolophus.

cucurbitaceus Spinola, see Tupiocoris.

diffRACTUS Van Duzee, see Macrolophus.

disclusus Van Duzee, see Tupiocoris notatus (Distant),
new synonymy.

elongatus Van Duzee, see Tupiocoris.

epilobii Reuter, see Dicyphus (Idolocris).

errans Wolff, see Dicyphus (Idolocris).

famelicus Uhler, see Dicyphus (Uhlerella).

gracilentus Parshley, see Dicyphus (Uhlerella).

hesperus Knight, see Dicyphus (Uhlerella).

longulus Poppius, see Campyloneuropsis.

melanocerus Reuter, see Dicyphus (Brachyceraea).

montanus Poppius, see Dicyphus (Brachyceraea).

nigrifrons Reuter, see Dicyphus (Idolocris).

orientalis Reuter, see Dicyphus (Brachyceraea).

pallicornis Meyer-Dur, see Dicyphus Idolocris.

physochlaenae Hutchinson, see Dicyphus (Brachyceraea)

orientalis Reuter (synonymy by Muminov).

rivalis Knight, see Macrolophus.

rubroornatus Poppius, see Campyloneuropsis.

rufescens Van Duzee, see Tupiocoris.

sengge Hutchinson, see Dicyphus (Brachyceraea).

tinctus Knight, see Tupiocoris.

usingeri Knight, see Macrolophus.

vestitus Uhler, see Dicyphus (Uhlerella).

REMARKS: The number of species in this subgenus is considerably different to that previously proposed by Carvalho (1958). The subgenus now contains 15 species, two of which, bolivari and stachydis, are subdivided into two subspecies. Twenty nine species have been removed to other taxa, fourteen of which are placed in three other genera. McGavin (1982) recognized that many of the Nearctic species of Dicyphus were not congeneric with the Palearctic species of the genus, and erected a new genus, Neodicyphus, to accommodate these distinct species. Unfortunately, McGavin (1982) and other miridologists working on the dicyphines, have not studied the group on a global basis and the genera have remained with regional definitions which are extended to species in other geographic locales without serious consideration of generic limits. This is particularly a problem in the Western Hemisphere where authors such as Blatchley (1926), Knight (1941, 1968), and Kelton (1980b) provided generic diagnoses and keys that were largely artificial. Thus numerous species that belong to the genus Tupiocoris were previously placed in Dicyphus.

The subgeneric definition presented in this study is similar to that proposed by Wagner (1951, 1971), placing great emphasis on the male genitalia with included emphasis on the thoracic pleura and femoral trichobothria numbers.

The subgenus is chiefly distributed in the western Palearctic, including North Africa and extends into Middle Asia (Map 6).

The species are associated with plant genera in six different families, although most of the species are found in association with the Caryophyllaceae, Boraginaceae, and Labiatae. These plant genera are more characterized by their toxic qualities rather than the presence of glandular trichomes, although constrictus is reported to suck the apices of the glandular trichomes of labiate plants (Kullenberg, 1947). Most of the species are univoltine (Southwood and Leston, 1959; Wagner, 1971) and overwintering occurs in both the adult and egg stages. Southwood and Leston (1959) report that constrictus oviposits on the upper parts of the flowering stems of their host plants where the eggs undergo hibernation. The widespread species, stachydis supposedly overwinters as an adult during which considerable melanism occurs (Southwood and Leston, 1959). Most of the species are recorded as polyphagous (Butler, 1923; Wagner, 1971), although it is probable that zoophagy is a secondary feeding strategy.

Southwood and Leston (1959) also state that the larvae of stachydis are sometimes parasitized by a braconid.

Subgenus Idolocoris Douglas and Scott

Figures: 13, 14, 58, 59, 90, 91, 92,

121, 142, 179, 180, 209, 226, 247,

259, and 272 (Habitus: Dicyphus

(Idolocoris) regulus).

Idolocoris Douglas and Scott 1865: 374 (as subgenus,

Wagner 1951: 6 (Type species: Capsus pallicornis

Meyer-Dur 1843: 110 (type fixed by Kirkclady 1906: 129).

DIAGNOSIS: This is a composite group which is chiefly defined by the weakly dissected pygophore of the male (fig. 259), and is distinguished from Uhlerella by the absence of an internal, sclerotized bar on the pygophore, and the smaller peritremal disc (fig. 226).

DESCRIPTION: macropterous, sometimes non-sex semibrachyptery; costal margins parallel; length, males 3.50-5.00, females 3.50-5.25; base color variable, pale to dark; setation moderate in size, erect to suberect.

Head: (figs. 13, 13): transverse, vertical; frons strongly produced in front of eyes, mesally pointed, often pale, with black to fuscous fascia; vertex broad, postoccular margins convergent, often dark; clypeus

weakly produced, lateral aspect of head variable in color, pale to dark.

Eyes: large, protrudent, fuscous, often tinged with red; facets moderate in size.

Antennae: inserted below midheight of eyes, often banded; I longer than vertex width.

Rostrum: extending between apices of metacoxae and 2nd abdominal segment.

Pronotum: (figs. 13, 14), trapezoidal, lateral margins linear, weakly divergent; collar broad not mesally constricted, often bicolored; calli distinct, subquadrate, raised, often pale mesally; disc moderately to strongly raised, posterior angles strongly rounded, posterior margin strongly excavate; propleuron moderately expanded laterally, visible from above.

Thoracic pleura: (fig. 226), mesepimeron strongly angulate, spiracle minute, oval, evaporative areas extensive, extending onto small, depressed postalare; metaepisternum, osteole large, mesal, peritremal disc small, subtriangular, setate, evaporative areas almost extending to metaepimeron, evaporative bodies suboval; metaepimeron narrow.

Legs: femora linear, testaceous, often with dark markings; trichobothria, 4-6 mesofemoral (fig. 59) and 5-7 metafemoral (fig. 58); tibiae linear, hind tibiae with small spines; pretarsus (fig. 247), large,

claws cleft basally.

Hemelytra: (fig. 90), macropterous, testaceous with variable, dark markings; corial fracture broad, often dark; cuneus elongate, apex dark; two membrane cells, minor cell large; sometimes species with brachypterous morphotypes (fig. 92).

Hindwings: (fig. 91), R vein strongly recurved; 1A short.

Male genitalia: pygophore (fig. 259) weakly dissected, genital aperture dorsal; left clasper (fig. 142) shaft moderately sized, apex expanded, sometimes outer margin serrate; right clasper (fig. 143) small, linear, heavily sclerotized; vesica (fig. 179) multilobed with 2 spiculi, or with internal, sclerotized channels, heavily sclerotized basally; phallosome (fig. 181) dissected apically, lateral margins overlapping.

Female genitalia: (fig. 209) sclerotized rings large, weakly divergent posteriorly, suboval.

INCLUDED SPECIES HOST PLANT(S), AND DISTRIBUTION:

annulifer Lindberg 1927: 23. [Dicyphus (Dicyphus)]. +

Host plant: unknown.

Distribution: Eastern Palearctic (Amur).

errans (Wolff) 1804: 161. [Dicyphus (Dicyphus)]. +

Host plants: Geranium sp. (Geraniaceae), Stachys,

Salvia sp. (Labiatae), Cucubalus sp.

(Caryophyllaceae), and Ononis sp. (Leguminosae).

Distribution: south-eastern Europe, and Turkey.

epilobii (Reuter) 1883: 52. [Dicyphus (Dicyphus)]. +

Host plants: Epilobium hirsutum L. (Onagraceae),

and Cucubalus sp. (Caryophyllaceae).

Distribution: western Palearctic.

gracilis (Poppius) 1914: 8. New combination, [Bucobia]. +

Host plant: unknown.

Distribution: east Africa.

montandoni Reuter 1888: 62. [Dicyphus (Brachyceraea)].

Host plant: unknown.

Distribution: eastern Europe.

nigrifrons Reuter 1906: 61. +

Host plant: unknown.

Distribution: eastern Palearctic (Szechwan).

pallicornis (Meyer-Dur) 1843: 110. +

Host plant: Digitalis purpurea L.

(Scrophulariaceae).

Distribution Europe (introduced into western North America).

regulus (Distant) 1909: 521. New combination,

[Abibalus]. +

Host plant: unknown.

Distribution: northern India.

REMARKS: Douglas and Scott (1865) described the genus Idolocoris which was synonymized with Dicyphus by Poppius (1911). Wagner (1951) subsequently described the former as a subgenus of Dicyphus with only one included species, pallicornis. Carvalho (1958) did not recognize Wagner's action and included pallicornis in D. Dicyphus. Subsequently, Wagner and Weber (1964) retained Idolocoris as a subgenus distinguishing it from Dicyphus sensu stricto by the short setation. Wagner (1971) then intimated that Idolocoris may be a synonym of the typical subgenus but kept it as a separate taxon. In this classification, I regard Idolocoris as a distinct subgenus on the basis of the small genital aperture of the male, which is more similar to D. Uhlerella. Indeed the genital character offers the only diagnostic feature and there may be further need for revision. I have included eight species in this taxon, including the new combinations of the species formerly placed in Abibalus and Bucobia.

This group is broadly distributed in the Palearctic and extends into central Africa which is the southern

limit for the subgenus. The species, pallicornis is introduced into the western United States (Downes, 1957), as is the host plant Digitalis purpurea. Both are significantly increasing their range, and I have recorded both from Humboldt County, California, and are common along roadsides and in disturbed habitats.

The host plant associations for this subgenus are poorly known. The type species, pallicornis, is apparently host specific, whereas epilobii and errans are polyphagous, particularly the latter. There appears to be no phylogenetic significance to the plant family associations. Th western European species are reportedly bivoltine (Butler, 1923; Southwood and Leston, 1959; Wagner, 1971). Butler (1923) states that the three latter species overwinter in the egg stage. Cobben (1968) records that pallicornis hibernates in all life stages in the Netherlands, but none of them exhibit a true diapause. Cobben (1978) also states that pallicornis is entirely phytophagous, and records that in an unpublished student report this species did not feed on bruised drosophilid flies which is a suitable food for many semi-carnivorous bugs.

Subgenus Mesodicyphus Wagner

Mesodicyphus Wagner 1951: 7 (Type species: Dicyphus testaceus Reuter 1879: 204).

DIAGNOSIS: Body broad with short appendages. The head is transverse, and pentagonal, and the vertex is wider than the length of the first antennal segment. The eyes are separated from the collar by a thickness of the first antennal segment. The calli are oval, and indistinctly defined posteriorly. The male genitalia is characterized by a vesica with one large spiculum, and the shaft of the left clasper is small.

The above diagnosis is adapted from Wagner (1951; 1970) as I have not seen any of the species included in this subgenus. There are four included species that are distributed in the Mediterranean and Middle Asia (map 8).

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

linnavouri Wagner 1967: 116.

Host plant: Silene succulenta Forsk.

(Caryophyllaceae).

Distribution: Israel.

martinoi Josifov 1958: 273.

Host plant: unknown.

Distribution: eastern Europe (Balkans).

sedilotti Puton 1886: 20.

Host plant: Silene succulenta Forsk.

(Caryophyllaceae).

Distribution: North Africa (Tunisia, and Egypt).

testaceus Reuter 1879: 204.

Host plant unknown.

Distribution: Middle Asia (Turkey).

Subgenus Uhlerella Cassis. New subgenus.

Figures: 15, 16, 60, 61, 93, 94, 95,
121, 144, 145, 181, 182, 227, 228,
244, 245, 246, 260, 261, and 273 (figure
273, Habitus of D. (Uhlerella)
paddocki Knight).

Type species: Idolocoris famelicus Uhler 1878: 413.

Eytomology: This species is named after P. R. Uhler who described two Nearctic species of Dicyphus belonging to this subgenus.

DIAGNOSIS: The species of this subgenus are characterized by an elongate peritremal disc (fig. 227), and the hind tibiae have no spines. Also, the pygophore of the male has an internal, sclerotized bar (fig. 121), and the vesica of the male has no spiculi (fig. 181).

DESCRIPTION: elongate to elongate-ovoid, appendages long; macropterous, sometimes semibrachypterous; testaceous to fuscous base color, sometimes with ochraceous to red markings; setation, sparse to long, and erect.

Head: (fig. 15, 16) elongate to weakly pentagonal; frons weakly to moderately produced in front of eyes, testaceous to dark, if pale then with two dark fascia; vertex, postocular margins linear, convergent towards collar, often marked with fuscous or red, sometimes dark basally; clypeus strongly produced, clearly visible from above.

Eyes: small to moderately sized, separated from collar by at least 1/2 dorsal length of eye; fuscous, fuscured or reddish; facets moderately sized.

Antennae: inserted just above, or at midheight of eyes, most often banded; I longer than vertex width.

Rostrum: extending between apices of middle and hind coxae.

Pronotum: (figs. 15, 16), trapezoidal, lateral margins moderately divergent; calli subquadrate, confluent mesally, separated by fine, linear groove, sometimes more widely separated anteriorly, posterior margin distinct, sometimes excavate mesally; disc flanged, posterior angles broadly rounded, posterior margin deeply excavate; propleuron expanded laterally, visible from above.

Thoracic pleura: (fig. 227), mesepimeron broad, spiracle small, posterior 1/3 of segment covered with evaporative areas, extending onto postalare; metaepisternum, osteole broad, depressed, peritremal disc elongate, recurved apically, extending to lateral margin of segment, narrow towards apex, evaporative areas covering almost entire segment, evaporative bodies elongate (fig. 228); metaepimeron narrow, weakly reflexed.

Legs: femora linear, testaceous, sometimes with rows of fuscous spots; trichobothria, 5-6 mesofemoral (Fig. 61) and 6-7 metafemoral (fig. 60); tibiae moderately to large in size, without spines; tarsus long; pretarsus (figs. 244, 245, and 246), claws cleft, linear apically, unguitractor plate reduced (fig. 246), retracted into apical, tarsal segment, pseudopulvilli small, broad apically.

Hemelytra: (figs. 93, 95) macropterous, sometimes with non-sex semibrachyptery (fig. 95); embolium narrow; clavus usually clothed with elongate fuscous markings; corium variously marked; corial fracture broad, fuscous; cuneus elongate, apex fuscous; two membrane cells, minor cell large.

Hindwings: (fig. 94), R vein reduced, somewhat parallel to costal margin, strongly recurved at tip; 1A short.

Male genitalia: pygophore (figs. 121, 260, and 261) not deeply dissected, genital aperture restricted to posterodorsad angle, with internal sclerotized bar (fig. 121); left clasper (fig. 144), shaft contiguous with ventral margin, shaft linear, expanded apically, extending beyond right clasper; right clasper (fig. 145) linear, tapered towards apex; vesica (fig. 181) sac-like, basally sclerotized into U-shaped process, with internal sclerotized channels; phallosome (fig. 182), broad basally, dissected apically.

Female genitalia: (fig. 209), sclerotized rings separate, elongate, inner margins almost parallel anteriorly, moderately divergent posteriorly.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

discrepans Knight 1923: 476. [Dicyphus (Dicyphus)]. +

Host plants: Horkelia sp., Aster sp. (Compositae), Scrophularia californica Cham. & Schlecht, Castilleja sp. (Scrophulariaceae), Rosa sp., Rubus sp., Ranunculus sp. (Rosaceae), and Stachys sp. (Labiatae).
Distribution: North America.

famelicus (Uhler) 1878: 413. [Dicyphus (Dicyphus)]. +

Host plant Rubus odoratus (Rosaceae).
Distribution: north-eastern North America.

gracilentus Parshley 1923: 21. [Dicyphus (Dicyphus)]. +

Host plant: Polymnia canadensis L. (Compositae).

Distribution: north-eastern United States.

hesperus Knight 1943: 56. [Dicyphus (Dicyphus)]. +

Host plants: Verbascum thapsus L. (Scrophulariaceae),

Rubus strigosus Michx. (Rosaceae), Stachys rigida

Nutt. ex. Benth., S. albens Gray (Labiatae),

Arctostaphylos sp. (Ericaceae), Phacelia distans

Benth. (Hydrophyllaceae), Ribes sp. (Gesneriaceae),

and tomato (Solanaceae).

Distribution: U.S.A., and Canada, chiefly western.

paddocki Knight 1968: 73. [Dicyphus]. +

Host plant: Solanum sp. (Solanaceae).

Distribution: U.S.A., central to southern, coastal California.

vestitus Uhler 1895: 46. [Dicyphus (Dicyphus)]. +

Host plant: unknown.

Distribution: north-central, and western U.S.A.

REMARKS: This new subgenus is erected on the basis of numerous apomorphies of the male genitalia and the thoracic pleura. The species are grossly similar to to D. (Dicyphus) species, although the male genitalia is more similar to that found in D. (Idolocoris) taxa.

There are six included species, and two new species remain to be described. They are exclusively distributed in the Western Hemisphere, with all the species found in North America, and hesperus extending into southern Baja California (Map 9).

Very little biological information exists for the species. The two most ubiquitous species, discrepans and hesperus, are polyphagous and are found on numerous, unrelated host plants, whereas the north-eastern United species, famelicus and gracilentus, are host plant specific. There appears to be no restriction to certain host plant families, although like the other subgenera of Dicyphus, the species are often associated with labiate plants.

I have observed that both discrepans and hesperus are bivoltine, and the latter hibernates in the adult stage and appears to be exclusively phytophagous. Kelton (1982) reports that the latter two species and famelicus overwinter as adults in Canada, and all lay eggs in the spring. He also states that discrepans is predacious on aphids.

Genus Engytaus Reuter. Restored status.

Figures: 17, 18, 37, 63, 96, 97, 146,
147, 148, 183, 184, 211, 229, 230,
248, and 262

Engytatus Reuter 1876: 82 (Type species: Engytatus geniculatus Reuter 1876: 82 (= modestus Distant, valid name of type species is modestus, as the former name was placed in homonymy with geniculata Fieber, when China and Carvalho (1952) placed Engytatus in synonymy with Cyrtopeltis Fieber).

Neoproba Distant 1884: 270 (synonymy by Carvalho 1955: 222).

Cyrtopeltis (Engytatus) China and Carvalho 1952: 159
(type species

DIAGNOSIS: This genus is most easily diagnosed by the ventral, pygophoral process of the male (fig. 262), which is most often bifurcate. Other distinguishing features of the male genitalia include the broad shaft of the left clasper (fig. 146), and the non-tuberculate, sac-like vesica, which has a subbasal, sclerotized plate (fig. 183). The head is characterized by very large eyes which extend to the bucculae (fig. 18), and in this regard, and in other salient features, the genus is very similar to Nesidocoris Kirkaldy. The females of these two genera are not separable, except for the genitalic differences (cf. figs. 211 and 212, to fig. 216).

DESCRIPTION: macropterous; elongate to elongate-ovoid; costal margins parallel to weakly convex; length, males 2.75-4.75, females 2.75-5.20; yellow, testaceous or ochraceous base color, sometimes with fuscous markings, rarely base color dark; densely covered with pale, rarely dark, suberect setae.

Head: (figs. 17, 18) transverse, strongly vertical; frons weakly produced in front of eyes, broadly rounded; vertex small, postocular margins minute, convergent; clypeus moderately produced; lateral aspect of head often reduced.

Eyes: greatly enlarged, extending to bucculae, lateral margins excavate (fig. 18), often almost contiguous with collar, fuscous to fusco-red, often tinged with red; facets large.

Antennae: inserted at midheight of eyes, or just below; most often unicolorous, either yellow or testaceous, sometimes banded; I variable in length, either subequal to or greater than vertex width.

Rostrum: extending between apices of metacoxae and third abdominal segment, except for one species, lysmachiae in which rostrum terminates at apices of forecoxae.

Pronotum: (figs. 17, 18), trapezoidal, lateral margins widely divergent; collar small, sometimes constricted mesally, narrow laterally; calli obscure,

recognized as weakly raised areas, sometimes more strongly defined by weak depressions, mesally and posteriorly; disc flat, posterior margin weakly excavate; propleuron variable in lateral expansions, usually not visible from above.

Thoracic pleura: (figs. 37 , 229), mesepimeron elongate, broadly recurved anteriorly, spiracle oval, with associated evaporative areas, extending onto weakly depressed postalare; metaepisternum variable, scent efferent system either absent (fig. 229), or moderately developed (fig. 37), osteole small, weakly depressed, peritremal disc small, adjacent to posterior margin of segment, tapered towards apex, evaporative areas cover about 1/3 of segment; metaepimeron moderately broad.

Legs: femora linear, sometimes hind femora expanded dorsoventrally, testaceous, sometimes with rows of brown spots, uniformly covered with pale to dark, suberect setae, and ventral surface with elongate, trichomae-like, pale setae; femoral trichobothria variable, mesofemora with 2-5 (e.g. fig. 63), metafemora with 3-5 (e.g. fig. 62); tibiae linear, testaceous, often with basal, fuscous markings, middle and hind tibiae with large, dark spines, regular rows of dark spinelets; tarsi long, penultimate segment at least 2x length of apical segment; pretarsus (fig. 248) small, claws with small basal projection, remainder strongly recurved, parempodia

small, pseudopulvilli large, laterally recurved, unguitractor plate reduced.

Hemelytra: (fig. 96), always macropterous, mostly unicolorous, sometimes with dark markings on corial fracture and apex of cuneus; always with two membrane cells, minor cell small to minute.

Hindwings: (fig. 97) R vein recurved; 1A extending to PCu margin.

Male genitalia: pygophore (fig. 262) highly modified, ventral surface produced into pygophoral process, either bifurcate, of which each arm can be hooked, or posterior arm can be further subdivided; left clasper (figs. 146, 147) V-shaped, lobe broad, dorsal margin often sinuate, with moderately long setae, shaft greatly broadened, narrowed, and heavily sclerotized, apex often notched; right clasper (fig. 263) small, linear, variable in position; vesica simple, unilobed with no tuberculations or spiculi, always with a subbasal, sclerotized plate (fig. 183); phallosome (fig. 184) narrow to moderately broad at base, dissected apically (fig. 184).

Female genitalia: bursa copulatrix huge, narrow, subquadrate (fig. 212), lateral margins convergent posteriorly; sclerotized rings small, subelliptical, parallel (fig. 211, 212).

INCLUDED SPECIES, HOST PLANTS(S), AND DISTRIBUTION:

acuminatus (Knight) 1938: 176. New combination,

[Cyrtopeltis]. +

Host plants: Cyrtandra sp. (Gesneriaceae), Vaccinium sp. (Ericaceae), Sclerotheca sp. (Campanulaceae), and Cyathea sp. (Cyathaceae).

Distribution: Marquesas Is. (Uapou I.).

affinis (Gagne) 1968: 175. New combination, [Cyrtopeltis

(Engytatus)]. +

Host plant: Scalesia affinis (Kuschel) (Composiate).

Distribution: Galapagos Is. (Santa Cruz I.).

andinus (Carvalho and Becker) 1958: 335.

New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: unknown.

Distribution: Brazil.

aridus (Gagne) 1968: 176. New combination, [Cyrtopeltis

(Engytaus)]. +

Host plant: Scalesia sp. (Compositae).

Distribution: Galapagos Is. (Santa Cruz I.).

aristidesi (Carvalho) 1975: 456. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: unknown.

Distribution: Brazil.

confusus (Perkins) 1911: 729. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Cyrtandra cordifolia (Kuschel)

(Gesneriaceae).

Distribution: Hawaiian Is. (Oahu I.).

cyrtandrae (Gagne) 1968: 41. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Cyrtandra sp. (Gesneriaceae).

Distribution: Hawaiian Is. (Oahu I.).

floreanae (Gagne) 1968: 176. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Scalesia sp. (Compositae).

Distribution: Galapagos Is. (Floreana I.).

gummiferae (Gagne) 1968: 172. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Scalesia gummiferae (Kuschel)

(Compositae).

Distribution: Galapagos Is. (Isabela I.).

hawaiianensis (Kirkaldy) 1902b: 138. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plants: Daubatia sp., Raillardia menziesii

Gray, Raillardia sp. (Compositae).

Distribution: Hawaiian Is. (Maui I., Molokai I.).

helleri (Gagne) 1968: 174. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Scalesia sp. (Compositae).

Distribution: Galapagos Is. (Barrington I.).

itatiaianus (Carvalho) 1980: 437. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: unknown.

Distribution: Brazil.

lysmachiae (Carvalho and Usinger) 1960: 252. New

combination. [Cyrtopeltis (Engytatus)]. +

Host plant: Lysmachia sp. (Primulaceae)

Distribution: Hawaiian Is. (Kauai I.)

marquesanus (Knight) 1938: 173. New combination,

[Cyrtopeltis]. +

Host plants: Metrosideros collina (Myrtaceae),

Weimannia parviflora, Weimannia sp. (Cunoniaceae),

Cyrtandra sp. (Gesneriaceae), Paspalum conjugatum

Berg. (Gramineae), Freycinetia sp. (Pandanaeae),

Cyathea sp. (Cyathaceae).

Distribution: Marquesas Is. (Nukuhiva I., Hivaoa I.,

Fatuhiva I., Uapou I., and Uahuka I.).

minutus (Knight) 1938: 176. New combination,

[Cyrtopeltis]. +

Host plant: Weinmannia sp. (Cunoniaceae).

Distribution: Marquesas Is. (Hivaoa I., Nukuhiva I.)

modestus (Distant) 1893: 447. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plants: Solanum sp., Solanum sisymbriifolium

(Solanaceae), Jatropha gossypifolia L.

(Euphorbiaceae) Heterotheca grandiflora Nutt.

(Compositae), Merremia aegyptia (L.) Urban

(Convolvulaceae), Gynandropsis pentaphylla DC.

(Cleomaceae), Lagenaria sp. (Cucurbitaceae),

Bougainvillea sp. (Nyctaginaceae),

Distribution: South America, Central America, and
south-western United States, and islands in Pacific
Basin.

nicotianae (Koningsberger) 1903: 32. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Nicotiana sp. (Solanaceae).

Distribution: Pacific Basin (Australia, Fiji, Guam,
Java, New Caledonia, New Guinea, and Cook Is.).

perplexa (Gagne) 1968: 40. New combination, [Cyrtopeltis

(Engytatus)]. +

Host plant: Raillardia sp. (Compositae).

Distribution: Hawaiian Is. (Maui I.).

phyllostegiae (Carvalho and Usinger) 1960: 251. New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: Phyllostegia hirsuta Benth. (Labiatae).

Distribution: Hawaiian Is. (Oahu I.).

quitoensis (Carvalho and Gomes) 1968: 535. New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: unknown.

Distribution: Ecuador.

rubescens: (Distant) 1884: 270. New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: unknown

Distribution: Mexico

seorsus (Van Duzee) 1934: 325. New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: unknown.

Distribution: Marquesas Is (Havaoa I.).

sidae (Gagne) 1968: 40. New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: Sida sp. (Malvaceae).

Distribution: Hawaiian Is. (Maui I.).

similaris (Carvalho) 1947: 18. New combination, [Cyrtopeltis (Engytatus)]. +

Host plant: unknown.

Distribution: Brazil.

terminalis (Gagne) 1968: 42. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Cyrtandra sp. (Gesneriaceae).

Distribution: Hawaiian Is. (Oahu I.).

tuberculatus (Knight) 1938: 175. New combination,

[Cyrtopeltis]. +

Host plants: Scaevola sp. (Camapanulaceae), Tectaria

sp. (Aspidiaceae), Freycinetia sp. (Pandanaaceae),

Piper latifolium (Piperaceae), Paspalum latifolium

(Graminae), ferns.

Distribution: Marquesas Is. (Hivaoa I.).

varians (Distant) 1884: 271. New combination,

[Cyrtopeltis (Engytatus)]. +

Host plant: Nicotiana tabacum L. (Solanaceae).

Distribution: Guatemala.

REMARKS: Reuter (1876) originally described Engytatus as a monotypic genus, then he synonymized it with Cyrtopeltis (Reuter, 1909), and finally regarded them as separate genera. China and Carvalho (1952) erected the former as a subgenus of Cyrtopeltis. However, I regard these groups as distinct, and in many respects Engytatus is more similar to Nesidocoris (it also has a similar distribution pattern). Subsequent to China and Carvalho's subgeneric designation many new species have been added to this taxon, particularly from the Pacific Basin island

archipelagos (Carvalho and Gagne, 1968; Gagne, 1968).

Carvalho (1958) considered four species described by Knight (1938) from the Marquesas Islands as of uncertain position within Cyrtopeltis. I conclude that their placement in Engytatus is without doubt, despite that the pygophoral process is not bifurcate (the vesica and left clasper features are similar to Neotropical species). The species, seorsus was described by Van Duzee (1934) in Campyloneuropsis, however, it clearly belongs to Engytatus on the basis of the male genitalia (although the head structure is somewhat atypical).

The greatest species diversity of this genus is in the Hawaiian, Galapagos, and Marquesas Islands, where all the species are endemic. There are also numerous species in the Neotropical region, and four species remain to be described from South Africa, which represents the first Engytatus species recognized from the Ethiopian region. The genus can be considered to have a tropicopolitan distribution (Map 10), represented by 26 species. I have completed a study of this genus and 16 species remain to be described.

The host plant associations for this genus are very broad, and many of the species are known from numerous host plants (although the Hawaiian Island species are predominantly host specific). Most of the associations are with plants in the families Compositae, Solanaceae,

and Gesneriaceae, although there are numerous atypical associations with families such as the Cyathaceae, Goodeniaceae, and Primulaceae.

The biology of this genus is very poorly known, however, a large amount of information is known for the economically important pest, the suck-fly, Engytatus modestus, which has at times been considered a major problem in tobacco plantations. Tanada and Holdaway (1954) in an important study of this species indicated the following points of interest: 1) larvae and adults feed, and cause lesions, 2) bugs prefer mature lesions and have a tendency to return and feed on formerly created lesions, 3) feeding is mainly on the flowers and young shoots, 4) vascular tissue is the major site of feeding, although the cortex, endodermis, pericycle, and pith are also feed on.

Glarisia Cassis. New genus.

Figures: 9, 20, 64, 65, 98, 99, 122,
149, 150, 151, 185, 86, 213, 231,
232, 233, 249, and 263.

Type species: Cyrtopeltis melanocephalus Reuter 1909: 63.

Eytomology: Glaris, Greek, meaning chisel, suffix "-ia", Greek, meaning pertaining to.

DIAGNOSIS: This genus is distinguished by the large chisel-shaped process on the ventral margin of the genital aperture (fig. 263) of the male. Also, the sinistrodorsal margin of the genital aperture is produced into an apically pointed process. Further, the ventral margin of the phallosome has a number of processes (fig. 186). The rostrum is short, extending to between the apices of the mesocoxae and the middle trochanters. The tibiae have no spines or spinelets.

DESCRIPTION: elongate to elongate-ovoid; macropterous, costal margins weakly convex; length, males 3.25-3.85, females, 3.25-4.00; ochraceous to testaceous, sometimes with dark markings; moderately setae, with short, pale, suberect setae.

Head: (figs. 19, 20), moderately transverse, vertical; frons moderately produced in front of eyes, more so mesally, often dark, sometimes pallid; vertex broad, strongly convex, postocular margins convergent, most often dark; clypeus moderately produced, visible from above; lateral aspect of head mostly concolorous with dorsal aspect of head; sometimes lorum and part of bucculae pallid.

Eyes: moderately large, extending to lorum; removed from collar by at least length of collar; facets moderately sized; fuscous.

Antennae: inserted at midheight of eyes, most often banded; I subequal to or greater than vertex width, testaceous to yellow with mesal, fuscous band; II length variable, relative to posterior width of pronotum, testaceous, sometimes with basal, fuscous band; setation often erect on apical segments.

Rostrum: extending between apices of mesocoxae and middle trochanters; last segment entirely fuscous, or only at tip.

Pronotum: (figs. 19, 20), trapezoidal, lateral margins weakly sinuate, strongly divergent; collar small, yellow to testaceous, constricted mesally, sometimes with small sulcus; calli somewhat distinct, moderately raised, posterior and mesal sutures obscure, fuscous, yellow to testaceous mesally, with small, stout, pale setae; disc, posterior margin deeply excavate, weakly sinuate.

Thoracic pleura: (figs. 231, 232), mesepimeron narrow, inner margin excavate, obscure basally, spiracle large, evaporative areas restricted to spiracle; postalare small, depressed; metaepisternum, scent efferent system well developed, osteole small, strongly depressed, peritremal disc moderately large, adjacent to posterior margin of segment, tapered towards apex, evaporative areas cover about 1/3 of segment, evaporative bodies moderately separated (fig. 233); metaepimeron moderately broad.

Legs: femora linear, hind femora sometimes arched basally, testaceous, sometimes hind femora with subapical embrownment, with small, stout, pale setae; trichobothria, 3-5 mesofemoral (e.g. fig. 65), 4-5 metafemoral (e.g. fig. 64); tibiae linear, testaceous, rarely with basal, fuscous annulation, devoid of spines or spinelets, with stout, pale setae; tarsi moderate in size, penultimate segment 1.5x to subequal to length of apical segment, testaceous, apex fuscous; pretarsus moderately large, claws strongly recurved (fig. 249), inner margin sometimes sinuate, pseudopulvilli large, outer margin recurved, unguitractor plate well developed.

Hemelytra: (fig. 98), hyaline to thickened, most often ochraceous, with apical fuscous spot on endocorium, sometimes yellow with black markings on endocorium, clavus and apex of cuneus; corial fracture distinctly notched, broad, cuneus small; two membrane cells, minor cell large.

Hindwings: (fig. 99), R vein sometimes sinuate; 1A vein long, extending to PCu margin.

Male genitalia: pygophore (figs. 122, 263) modified, genital aperture terminal, ventral margin of aperture, with large, suboval, mesal process, outer margin concave, coriaceous, sinistrodorsal margin of aperture with large tubercle; left clasper (fig. 14) strongly V-shaped, lobe heavily sclerotized, large, shaft elbowed, inner margin

strongly sinuate (fig. 150), apex of shaft truncate; right clasper (fig. 151) small, linear, membranous basally, apex moderately sclerotized, tip truncate; vesica (fig. 185) sac-like, unilobed, without spiculi; phallosome (fig. 186) with three lateral projections on the ventral surface.

Female genitalia: (fig. 213), bursa copulatrix moderately large, sclerotized rings suboval, divergent towards caudal end, rings basally with internal teeth.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

melanocephala (Reuter) 1909: 63. New combination, [Cyrtopeltis (Tupiocoris)].

Host plant: unknown.

Distribution: south-western United States

stitti (knight) 1968: 72. New combination [Dicyphus]. +

Host plant: Martynia parviflora (Woot.) Woot. and Standl. (Martyniaceae).

Distribution: south-western United States.

REMARKS: This genus is described to account for the two unique species, melanocephala, and stitti. They are characterized by a very short rostrum which does not extend beyond the trochanters of the middle legs and the male genitalia are also distinctive with the phallosome with peculiar outgrowths. An undescribed species, which is superficially different to the other two species

shares the same diagnostic character states.

The genus appears to be restricted to the southwestern United States (Map 11), although it may also be represented in north-western Mexico. No biological information is known for this genus, although I have many female specimens which were collected in the early spring which may suggest that the gravid females are the overwintering stage.

Genus Macrolophus Fieber

Figures: 21, 22, 66, 67, 152, 153,
154, 187, 188, 189, 214, 215, 234,
235, 236, 250, 251, 265, and 266.

Macrolophus Fieber 1858: 326 (Type species: Capsus nubilus Herrich-Schaeffer 1835: 135).

Pandama Distant 1884: 271 (type species: praeclara

Distant 1884: 271; synonym by Carvalho 1945: 525).

Pandamus Atkinson 1890: 81 (error pro Pandama Distant).

Pandanus Kirkaldy 1906: 138 (error pro Pandama Distant).

Tylocapsus Van Duzee 1923: 151 (type species lopezi Van

Duzee 1923: 151 synonym by Carvalho 1955: 224).

Macrolophidea Poppius 1914: 8, New synonymy (type species longicornis Poppius 1914: 23).

DIAGNOSIS: This genus is a composite group which has no exclusive synapomorphies uniting the species. Generally, the species are narrow, linear, with the head elongate, and the postocular margins of the vertex strongly convex and parallel (figs. 21, 22). The genital aperture of the male is terminal in position (figs. 265, 266), with the left clasper and vesica highly variable in structure. The genus is superficially similar to Tupiocoris species, but is easily separated from them by the presence of a metaepisternum scent efferent system, and the dorsum is not highly polished.

DESCRIPTION: small to large species; macropterous, rarely semibrachypterous; length, males 2.35-5.25, females 2.50-5.50; usually yellow, with dark markings on appendages, and head, often with hemelytra spotted, rarely with broad, dark markings; vestiture pale, fine, and suberect to erect.

Head: (figs. 21, 22), elongate, nearly as long as broad; frons strongly produced in front of eyes, sometimes pointed, from side strongly declivous; vertex strongly rounded, postocular margins convex and parallel, almost always marked with a dark band; clypeus strongly pointed in front of frons, distantly removed from eyes.

Eyes: most often very small, not extending ventrally beyond jugum, removed from collar by $2/3$ to full length

of the eye; fuscous to black; facets usually small (in some western South American and Galapagos Islands species the eyes are large, the facets large, and eyes are often red.

Antennae: inserted below midheight of eye; I longer than vertex width, except in broad species, other segments most often long, concolorous with rest of body, sometimes with small, dark bands, or entire first segment dark.

Rostrum: variable in length, extending between apices of the mesocoxae and third abdominal segment.

Pronotum: (figs. 21, 22), trapezoidal, lateral margins linear, moderately divergent; collar narrow, entire, rarely constricted mesally; calli usually indistinct, sometimes defined by weak depressions, more often fused with disc; disc, posterior margin moderately excavate; propleuron weakly expanded laterally, barely visible from above.

Thoracic pleura: (figs. 234, 235, and 236), mesepimeron elongate, narrow, spiracle small, somewhat depressed, with evaporative areas adjacent to spiracle; postalare, moderately depressed, evaporative areas on lateral margins; metaepisternum, scent efferent system weakly to moderately developed, osteole small, narrow, peritremal disc, ovoid with dense arrangement of microsetae; evaporative areas cover about 1/3 of segment,

evaporative bodies subovoid to elongate, often widely separated, remainder of segment with regular arrangement of microsetae; metaepimeron lateral margin recurved, not strongly reflexed.

Legs: femora linear, testaceous, rarely with dark markings, with fine, pale, suberect setae, sometimes also with erect, stout setae on ventral surface; trichobothria, 4-5 mesofemoral (e.g. fig. 67) and 5-7 metafemoral (e.g. fig. 66); tibiae linear, with erect setae, rows of minute spinelets, middle and hind tibiae always armed with erect spines on ventral surface; pretarsus variable, either with long, strongly recurved, narrow claws, with a small, basal projection (fig. 250), or with stout, recurved claws, with a large basal tooth (fig. 256).

Hemelytra: either concolorous with remainder of body, or spotted, or sometimes with broad bands; cuneus elongate to broad; two membrane cells, minor cell often small.

Hindwings: not investigated

Male genitalia: pygophore (figs. 265, 266) weakly dissected, genital aperture terminal, often with ventral margin weakly impressed, never with external tubercles, dorsal margin evenly rounded; left clasper (figs. 152, 153) V-shaped, lobe large, often extending beyond midpoint of ventral margin of genital aperture, shaft

often blade-like, sometimes greatly flattened; right clasper (fig. 154) small, linear; vesica variable, either without tubercles or spiculi, with internal, sclerotized channels, and ductus seminalis short (fig. 187), or with numerous, large, apical spiculi, and small tuberculations, and ductus seminalis terminating near apex of vesica (fig. 189); phallosome (fig. 188) small, apically dissected.

Female genitalia: bursa copulatrix variable (cf. figs. 214 and 215); Palearctic species with small to moderately sized sclerotized rings (fig. 214); Neotropical species with huge bursa copulatrix, sclerotized rings large, separate, inner margins almost adnate to large, mesal, suboval process (fig. 215).

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

aragarsanus Carvalho 1945: 530 +

Host plant: unknown.

Distribution: Brazil.

balcanicus Wagner 1960: 59. +

Host plant: unknown.

Distribution: Balkan Peninsula.

basicornis (Stal) 1860: 52. +

Host plant: unknown.

Distribution: Brazil, Guatemala, and Cuba.

brevicornis Knight 1926: 315. +

Host plant: Physalis sp. (Solanaceae), and Asclepias
(Compositae)

Distribution: north-eastern America.

caliginosus Wagner 1950: 1.

Host plant: Inula viscosa (L). Aiton (Compositae).

Distribution: Mediterrrranean.

costalis Fieber 1858: 342. +

Host plants: Cistus sp. (Cistaceae), Sarothamnus sp.
(Leguminosae), Cirsium sp., Carduus sp. (Compositae),
tobacco, and tomato (Solanaceae).

Distribution: Europe.

crudus (Van Duzee) 1916: 240. New combination, [Dicyphus
(Dicyphus)]. +

Host plant: unknown.

Distribution: California.

cuiabanus Carvalho 1945: 529. +

Host plant: unknown.

Distribution: Brazil.

diffRACTUS (Van Duzee) 1923: 153. New combination,
[Dicyphus (Dicyphus)]. +

Host plant: unknown.

Distribution: California.

epilobii Putshkov 1978: 853.

Host plant: Epilobium sp. (Onagraceae).

Distribution: U.S.S.R..

glauescens Fieber 1858: 341

Host plant: Echinops sp. (Compositae).

Distribution: Czechoslovakia, Hungary, and Yugoslavia.

innotatus Carvalho 1968: 167. +

Host plant: unknown.

Distribution: Galapagos Is. (Santa Cruz I., San Cristobal I.).

ethiopus (Poppius) 1914: 8. New combination,

[Macrolophidea]. The name ethiopus is proposed for this species which is placed in homonymy with

longicornis Knight (Macrolophus). +

lopezi (Van Duzee) 1923: 51. +

Host plant: Eucnide cordata (Loasaceae).

Distribution: lower California.

melanotoma (Costa) 1852: 269 (Carvalho (1958) has

recognized this species as a synonym of nubilus

Reuter, however, Wagner (1971) retains this as a

valid species, and since he was more familiar with

the Palearctic material I have followed his actions).

Host plant: unknown.

Distribution: Spain.

mimuli (Knight) 1968: 75. +

Host plant: Mimulus cardinalis Dougl. ex. Benth.
(Scrophulariaceae).

Distribution: western North America.

nubilus nubilus (Herrich-Schaeffer) 1804: 135. +

Host plants: Stachys sylvatica L. (Labiatae),
Pulmonaria sp. (Boraginaceae), and Cucubalus sp.
(Caryophyllaceae).

Distribution: western Europe.

nubilus geranii Josifov 1961: 87.

Host plant: Geranium macrorrhizum L. (Geraniaceae).

Distribution: Bulgaria.

praeclarus (Distant) 1884: 271. +

Host plant: unknown.

Distribution: Brazil, Paraguay, Mexico, Puerto Rico,
and Cuba.

punctatus Carvalho 1968: 168. +

Host plant: unknown.

Distribution: Galapagos Is. (Santa Cruz I.).

rivalis (Knight) 1943: 54. New combination, [Dicyphus
(Dicyphus)]. +

Host plant: Rubus strigosus Michx. (Rosaceae).

Distribution: western North America.

rubi Woodroffe 1957: 125.

Host plant: Rubus sp. (Rosaceae).

Distribution: England.

saileri Carvalho 1947: 107. +

Host plant: unknown.

Distribution: Mexico.

separatus (Uhler) 1894: 194. +

Host plants: Gerardia pedicularia

(Scrophulariaceae), Polymnia sp. (Compositae).

Distribution: North America, Jamaica, and Grenada.

tenuicornis Blatchley 1926: 913. +

Host plants: Polymnia canadensis L. (Compositae),

Dennstaedtia punctilobula (Michx) (Polypodiaceae).

Distribution: eastern North America.

usingeri (Knight) 1943: 55. New combination, [Dicyphus
(Dicyphus)]. +

Host plant: Chamaebatiaria foliosa (Rosaceae).

Distribution: western North America.

NEW GENERIC SYNONYMY: Macrolophidea Poppius 1914: 8.

This genus was described and has remained a monotypic taxon since Poppius (1914) first described only included species, longicornis. There is no doubt that it is closely related to the typical species, nubilus s. s., having similar male genitalia and salient features.

REMARKS: Macrolophus is the most unresolved genus of the, Dicyphinae, and as it is defined here, it probably is a polyphyletic taxon. This genus has always been considered as being distinct (Carvalho, 1945; China and Carvalho, 1952; Knight, 1941; Wagner, 1971), however, there has never been a clear diagnosis of this genus, and usually the species are included in this genus on the basis of having small eyes. This feature is artificial and shows considerable interspecific variation. I have defined the group also on head character states, i. e. the postocular margins of the vertex are parallel, and the head is generally elongate. I consider these features and the present diagnosis as unsatisfactory, however, a global revision of the genus is in progress (with T. J. Henry, USNM) and I have deferred any taxonomic changes until more information is available. The species in the Western Hemisphere do not appear to be congeneric with the Palearctic species.. The Neotropical species, cuibanus, basicornis, innotatus, and punctatus, seem to form a distinct assemblage of species, and on the basis

of the female genitalia (fig. 215) these species show some affinities with Campyloneuropsis species. In the Nearctic, the species are greatly variable and no species groups can be recognized and requires considerable study.

The genus as defined in this work is distributed in the Ethiopian, Neotropical, and Nearctic regions (Map 12).

At present there is little information about the host plant associations, and other biological information is restricted to certain Palearctic species, and a somewhat detailed study of the Nearctic species, tenuicornis (Wheeler et al, 1979). The latter species is associated with hayscented fern, on which it completes its full development, is bivoltine, and overwinters in the egg stage. The larvae and adults feed indiscriminately on the fern, and also feed on fern aphids in the process of molting (Wheeler et al, 1979). Cobben (1968) and Wagner (1971) report that many species in this genus overwinter in either the larval or egg stages, and nubilus is found to have a constant diapause in the fifth larval instar (Cobben, 1968).

Genus Nesidocoris Kirkaldy. Restored Status.

Figures: 23, 24, 68, 69, 100, 101, 161,
162, 190, 191, 216, 237, 238, 252, and 264.

Nesidocoris Kirkaldy 1902: 247 (type species: Nesidocoris
volucer Kirkaldy 1902: 247).

Gallobelicus Distant 1904: 477 (type species:
crassicornis Distant 1904: 477; synonymy by Reuter
1910: 166).

Cyrtopeltis (Nesidocoris) China and Carvalho
1952: 159.

DIAGNOSIS: This genus is primarily defined by the male genitalia. The pygophore is deeply dissected, with a narrow pygophoral process, and the dorsodextral angle of the genital aperture is produced into a narrow, elongate tubercle (fig. 264). The left clasper is greatly enlarged (fig. 161), and is produced below the ventral margin of the genital aperture (fig. 264). Further, the vesica is uniquely characterized by sclerotized, interconnected, triangular tubercles (fig. 190).

DESCRIPTION: macropterous; costal margins linear; length, males 2.35-5.00, females 2.45-5.00; base color yellow, testaceous or ochraceous, often with fuscous markings; regularly covered with fine, pale to dark, suberect setae.

Head: (figs. 23, 24), transverse, strongly vertical; frons weakly produced in front of eyes, mostly pale, sometimes dark with lateral regions pale; vertex usually small, width less than length of first antennal segment, most often pale, sometimes with posterior margins fuscous; clypeus weakly produced, often marked with fuscous, at least ventrally; remainder of lateral aspect of head similarly colored to dorsal aspect of head.

Eyes: large, extending to bucculae (fig. 24), almost contiguous with collar; lateral margins excavate; fuscous; facets large.

Antennae: inserted at, or above midheight of eyes (fig. 24); segments variable in length, most often banded, sometimes unicolorous; II variable in length relative to posterior width of pronotum.

Rostrum: extending between apices of metacoxae and second abdominal segment.

Pronotum: (figs. 23, 24), trapezoidal, lateral margins linear, and widely divergent; collar narrow, often constricted mesally, usually pale; calli indistinctly marked, somewhat raised, usually yellow to testaceous; disc weakly flanged, posterior angles broadly rounded, posterior margin weakly excavate.

Scutellum: evenly rounded, apex strongly pointed; unicolorously pale, or mesally dark.

Thoracic pleura: (fig. 237), broad and elongate, inner margin almost linear, spiracle elongate-ovoid to oval, bordered by evaporative areas; postalare moderately depressed, with evaporative areas on lateral margins; metaepisternum, scent efferent system moderately developed, osteole small, mesal in position, peritremal disc subovoid, extending along posterior margin of segment, evaporative areas not extending beyond mesepimeric spiracle, cover from $1/3$ to $1/2$ of segment, evaporative bodies oval (fig. 238), remainder of segment with regular arrangement of microsetae.

Legs: femora linear, sometimes expanded weakly dorso-ventrally, fore-, and meso-, femora usually $2/3$ length of metafemora, testaceous without dark markings, rarely with brown infusions, often clothed with dark, suberect setae; trichobothria, 2-4 mesofemoral (e.g. fig. 69) and 3-5 mesofemoral (e.g. fig. 69); tibiae linear, with rows of minute spinelets, with large, stout spines on dorsal and lateral surfaces of middle and hind tibiae; tarsus small, penultimate segment $1.5\times$ longer than apical segment, often fuscous at apex; pretarsus (fig. 252) moderately sized, unguitractor plate strongly developed, claws weakly recurved, pseudopulvilli large, leaf-like.

Hemelytra: (fig. 100), macropterous, costal margins weakly recurved; embolium narrow; corial fracture broad, often dark; cuneus moderately elongate; two membrane

cells, minor cell sometimes small.

Hindwings (fig. 101) R vein recurved; Cu vein weakly declivious; 1A long, extending to wing margin.

Male genitalia: pygophore (fig. 264) deeply dissected, genital aperture highly asymmetrical, more so on sinistral margin, ventral margin produced into a narrow, pygophoral process, dorsodextral margin always with a strongly produced tubercle; left clasper (fig. 166) extremely large, strongly V-shaped, lobe linear, small, projected below ventral margin of pygophore (fig. 264); right clasper (fig. 167) linear, tapered toward apex; vesica (fig. 190) multilobed, with strong sclerotized, interconnected tuberculations, ductus seminalis extending to near apex of vesica; phallosome (fig. 191) dissected apically.

Female genitalia: bursa copulatrix (fig. 216) moderately sized, sclerotized rings U-shaped, separate, narrowed and divergent caudally.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

atricornis (Distant) 1913: 180. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Seychelles.

brunneicollis brunneicollis (Linnavouri) 1975: 12.

New combination [Cyrtopeltis (Nesidocoris)]. +

Host plant: Echinops sp. (Compositae).

Distribution: Ethiopia.

brunneicollis alkannae (Linnavouri) 1975: 12. New

combination, [Cyrtopeltis (Nesidocoris)]. +

Host plant: Alkanna orientalis (L). Boiss
(Boraginaceae).

Distribution: Yemen.

callani (Odhambo) 1961: 9. New combination, [Cyrtopeltis

(Nesidocoris)]. +

Host plants: Gynandropsis pentaphylla DC.

(Cleomaceae), Nicotiana sp., and tomato (Solanaceae).

Distribution: Uganda.

caesar (Ballard) 1927: 67. New combination, [Cyrtopeltis

(Nesidocoris)]. +

Host plant: unknown.

Distribution: southern India.

cruentata (Ballard) 1927: 67. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: southern India.

diluta (Odhiambo) 1961: 7. New combination, [Cyrtopeltis
(Nesidocoris)]. +

Host plants: Aeschynomene americana, A. shimperi, A.
Rich., Cajanus sp. (Leguminosae), Conyza steudelli
Sch. Bip. (Compositae).

Distribution: Uganda.

flavoviridis (Linnavouri) 1975: 17. New combination,
[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Ethiopia.

florida (Odhiambo) 1961: 5. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plants: Aeschynomene americana, A. shimperi
(Leguminosae), Gynandropsis sp. (Cleomaceae), and
Chenopodium sp. (Chenopodiaceae).

Distribution: Uganda, Kenya.

kristenseni (Poppius) 1914: 20. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Eritrea, Yemen.

leontion (Linnavouri) 1974: 5. New combination.

[Cyrtopeltis]. +

Host plant: unknown.

Distribution: Nigeria.

longicornis (Linnavouri) 1975: 13. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Equatoria.

macifei (Poppius) 1914: 18. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Nigeria.

montivaga (Linnavouri) 1975: 12. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Sudan.

nigricornis (Linnavouri) 1974: 5. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Nigeria.

pallens (Poppius) 1914: 18. New combination, [Cyrtopeltis

(Nesidocoris)]. +

Host plant: unknown.

Distribution: east Africa.

plebejus (Poppius) 1914: 61. New combination,

[Cyrtopeltis (Nesidocoris)].

Host plant: unknown.

Distribution: Formosa.

poppiusi (Carvalho) 1958: 188. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Formosa.

pulchricornis (Poppius) 1914: 164. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Java.

scutellaris (Poppius) 1914: 18. New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Nyassa.

tabaci (Froggatt) 1920: 715. New combination,

[Cyrtopeltis (Nesidocoris)].

Host plants: Nicotiana sp. (Solanaceae).

Distribution: Australia.

tenuis (Reuter) 1895: 139 = ebaeus Odhiambo 1961: 12

(synonymy by Linnavouri 1975: 16). New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: Nicotiana sp. (Solanaceae), and

Gynandropsis sp. (Cleomaceae).

Distribution: cosmopolitan.

volucer volucer Kirkaldy 1902: 247 (removed from synonymy with tenuis by Lindberg 1958: 100). Restored combination, [Cyrtopletis (Nesidocoris)].

Host plant: Nicotiana sp. (Solanaceae).

Distribution: Island of Reunion (Indian Ocean).

volucer persimilis (Poppius) 1910: 52. New combination, [Cyrtopeltis (Nesidocoris)]. +

Host plant: Nicotiana sp. (Solanaceae), and

Gynandropsis sp. (Cleomaceae).

Distribution: Africa.

SPECIES REMOVED FROM THE GENUS:

obscuricornis Poppius, see Singhalesia

REMARKS: This genus is restored to its original generic ranking. Contrary to the judgement of China and Carvalho (1952), I regard this taxon as very distinctive on the basis of the male genitalia. The areas of highest taxic diversity are in the Ethiopian and Oriental regions, although similarly to Engytatus it has a circumtropical distribution (Map 13) (the Neotropical representatives may be introductions from the Ethiopian region).

The genus is composed of 23 species for which there is little host and biological information. It is apparent that most species are recorded from solanaceous plants. It is probable that this group, like Engytatus, is oligophagous. Odhiambo (1961) reports that volucer

persimilis and callani feed on the eggs of the tobacco slug, Lema bilineata (Germar).

Genus Setocoris China and Carvalho

Figures: 25, 26, 38, 39, 4, 47, 70, 71,
102, 103, 104, 123, 124, 155, 156, 157,
192, 193, 194, and 217.

Setocoris China and Carvalho 1958: 205 (type species:
Setocoris bybliphilus China and Carvalho 1951: 222).

DIAGNOSIS: This genus is distinguished by the regular arrangement of large, stout spines on the body, and/or the legs (fig. 41). The head is vertical (fig. 26), and the pronotum is subquadrate (fig. 25) to elongate-trapezoidal. The metaepisternum scent efferent system is absent (fig. 38), and the pretarsus is very large (fig. 47), whereas as the tarsus is small with the penultimate segment subequal to the third. The hemelytron is characterized by only one membrane cell (fig. 102), and the type species is apterous.

DESCRIPTION: apterous, micropterous, or macropterous; elongate, elongate-ovoid, or ovoid; length, males 2.35-4.00, females 2.50-4.20; often strongly convex; brillaintly colored, either testaceous to yellow, often with red, fuscous and white markings, or mostly red, uniformly covered with erect, dark spines or bristle-

like, suberect setae.

Head: (fig. 25, 26), vertical, transverse; frons strongly produced in front of eyes in most instances, testaceous, sometimes with or fuscous markings; vertex wide, convex, testaceous, sometimes fuscous basally, postocular margins sinuate, strongly convergent towards collar; clypeus variably produced, not visible from above; lorum and jugum very small.

Eyes: oval, small, in some species substylate, ventral margin not extending ventrally beyond jugum; reddish.

Antennae: inserted nearer to jugum than eye, at midheight of eyes, banded, with large, erect, stout setae; I subequal in length to vertex width, margins sinuate; II variable in length relative to posterior width of pronotum; III and IV, also clothed with fine, adpressed microsetae.

Rostrum: extending between apices of middle and hind coxae.

Pronotum: (fig. 25, 26), subquadrate to elongate-trapezoidal, lateral margins either linear or weakly excavate; collar small, sometimes indistinctly separated from calli; calli absent to very weakly developed; posterior margin linear to weakly excavate; testaceous to yellow, with fuscous markings, sometimes with narrow, basad, black band.

Thoracic pleura: (figs. 38, 39), mesepimeron either reduced in apterous species (fig. 38), or fully developed (fig. 39), spiracle small, oval, bounded by evaporative areas; postalare small, weakly depressed, evaporative areas extending on lateral margins; metaepisternum, scent efferent system absent, posterior margin linear to weakly excavate.

Legs: femora (fig. 41) greatly enlarged, fusiform, with large, erect, dark spines, and sometimes with irregular distribution of fine, erect, pale setae, pale to testaceous, with base of each seta with brown or red spot, sometimes with subbasal enbrowmment; tibiae similar color and vestiture to femora, foretibiae with enlarged tibial comb; tarsus small, weakly incrassate, weakly arched, penultimate segment subequal in length to third; pretarsus (fig. 247) large, claws strongly recurved, with basal tooth, pseudopulvilli broad.

Hemelytra: apterous, reduced to subquadrate, thickened lobe, with stout spines (fig. 104), micropterous, or macropterous (fig. 102); variously marked, base color testaceous to yellow, with black, white, and red markings; covered with either, large, erect, dark spines, or suberect, bristle-like setae.

Hindwings: (fig. 103), caesura not sinuate, R vein linear; PCu vein, and 1A extending to PCu margin.

Male genitalia: pygophore (fig. 123, 124) weakly dissected, genital aperture terminal, sometimes with tubercles on ventral or dorsosinistral margins; left clasper variable, either Y-shaped (fig. 155), or V-shaped (fig. 156), apex of shaft recurved; right clasper linear (fig. 57); vesica either, unilobed without sclerotizations (fig. 192), or with internal, sclerotized channels (fig. 193), ductus seminalis variable, always extending to near apex of vesica; phallosome (fig. 193) 194) broad, dissected apically.

Female genitalia: (fig. 217), bursa copulatrix large, sclerotized rings separate, large, U-shaped, anteriorly almost contiguous, laterally broadened, divergent toward caudal end.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

bybliphilus China and Carvalho 1951: 222. +

Host plant: Byblis gigantea Lindl. (Byblidiaceae)

Distribution: south-western Australia

droserae China 1953: 3. New combination, [Cyrtopeltis (Cyrtopeltis)]. +

Host plants: Drosera pallida Lindl, D. erythrorrhiza Lindl. (Droseraceae).

Distribution: south-western Australia.

russelli (China) 1953: 6. New combination, [Cyrtopeltis
(Cyrtopeltis)]. +

Host plants: Drosera pallida, D. erythrorrhiza
(Droseraceae).

Distribution: south-western Australia.

REMARKS: This genus is endemic to Australia (see map 14), and three new species remain to be described, two of which are collected from Queensland which extends the distribution of the genus to eastern Australia. The species, russelli and droserae, are placed in this genus on the basis of the presence of spines on the body, one membrane cell in the hemelytra, and the pretarsus and tarsus structure. The type species, bybliphilus, is somewhat atypical morphologically. Both sexes are apterous, and there are a number of autapomorphies of the body and pronotum that are associated with this condition. Further, the male aedeagus and left clasper for this species is unique, although the pygophore is of the type found in the congeners. On the basis of the latter, and other morphological attributes, and similar host associations, I regard the identity of the genus as unquestionable, despite the peculiarity of the type species.

China's (1953) original generic placement for russelli and droserae in Cyrtopeltis (Cyrtopeltis), was conceived on the basis of such characters as: a terminal

genital aperture, reduced phallotheca, and absence of a minor membrane cell in the hemelytra. However, the taxa of Cyrtopeltis have a deeply dissected pygophore, with a pygophoral process, and the hemelytra has two membrane cells. The shape of the phallotheca described by China (1953) is more diagnostic for the whole subfamily, and cannot be considered to be of generic worth.

The species of this genus are exclusively associated with insectivorous plants in the genera Drosera (Droseraceae) and Byblis (Byblidiaceae). China (1953) indicated a possible evolutionary scenario for the acquisition of a predatory habit for russelli and droserae. Russell (1953) listed detailed observations for these species, and suggested that the species were carnivorous, and feed on entrapped, transient insects. The residents were observed to move freely over the plant surface, although preferring the less mucilaginous, abaxial leaf surfaces. Russell (1953) further suggested that the bright red markings of the bugs may serve as a camouflage, mimetic device, as the plants also have red pigmentation. This may serve as an effective crypsis against visual predators such as birds. Russell (1953) rarely observed probing of plant material by these species. However, there may be some reason to suspect that these species are oligophagous. J. A. Slater (personal communication) has sent me specimens of an

undescribed species from south-western Australia, and has indicated that population densities for this species were very high, which may suggest that phytophagy is a possible feeding strategy. Russell (1953) reported similarly high population densities for the species he investigated.

Genus Singhalesia China and Carvalho. New status

Figures: 29, 30, 40, 72, 73, 105, 106, 125,
126, 158, 159, 160, 195, 196, 218, 255,
and 270.

Cyrtopeltis (Singhalesia) China and Carvalho

1952: 159 type species: Engytatus indicus Poppius 1913: 246).

DIAGNOSIS: This genus is distinguished by features of the male genitalia. The dorsal margin of the dorsal margin of the genital aperture of the male is clothed with stout, erect setae (fig. 125, 270), and the left clasper is S-shaped (fig. 126, 158). Also, the vesica is reduced to a narrow, conical tube (fig. 195) Saliently these taxa are very similar to Campyloneuropsis species, however the males are readily distinguished, and the females of the latter genus have connected sclerotized rings (cf. figs. 203 to 218).

DESCRIPTION: macropterous, elongate-ovoid, coriaceous; length, males 1.95-2.80, females 2.20-3.00; base color yellow to testaceous, or entirely fuscous, with pale appendages, if pale, often with fuscous and red markings; covered with stout, suberect setae.

Head: (figs. 29, 30), strongly vertical, transverse; frons weakly produced in front of eyes, pale, sometimes with darker markings; vertex small, width subequal to length of first antennal segment, postocular margins convergent, often dark; clypeus small, barely visible from above.

Eyes: large, terminating below lorum, not reaching bucculae, separated from collar by at least thickness of collar; facets large; fuscous, often with red infusion.

Antennae: inserted below midheight of eyes, often banded, unicolorous; I broad, small, often with mesal, red or fuscous band; II subequal or smaller than width of pronotum at base.

Pronotum: (fig. 29, 30), trapezoidal, lateral margins widely divergent; collar weakly defined, mesal and posterior impressions sometimes with fuscous; disc flat, about twice calli length, posterior margin linear to weakly excavate, posterior angles broad, often darker; propleuron not expanded laterally, not visible from above.

Scutellum: lateral angles pale, mesally dark.

Thoracic pleura: (fig. 40), mesepimeron broad, inner margin almost linear, spiracle small, bordered by evaporative areas, not extending to base of segment; postalare rounded, depressed lateral margins with evaporative areas; metaepisternum, scent efferent system present, moderately developed, osteole small, narrow, peritremal disc small, parallel and adjacent to posterior margin of segment, evaporative areas cover about 1/3 of segment; metaepimeron moderately broad, often shiny.

Legs: femora fusiform, testaceous, often with subapical, dark band, hind femora weakly incrassate; 4-5 trichobothria, 3-4 mesofemoral (e.g. fig. 73) and 4-5 metafemoral (e.g. 72); tibiae linear, testaceous, often with basal, brown band, with spines, and two rows of spinelets; tarsus small, II subequal in length to III, often fuscous; pretarsus (fig. 255), claws recurved with basal tooth, with a pore, pseudopulvilli broad.

Hemelytra: (fig. 105) testaceous to black, often with coriaceous texture, if pale then corial fracture and apex of cuneus dark; two membrane cells, minor cell minute.

Hindwings: (fig. 106), R vein parallel to costal margin; 1A vein long, extends to PCu margin.

Male genitalia: pygophore (fig. 125, 270) weakly dissected, genital aperture terminal (fig. 126), ventral margin with 1 or 2 tubercles, dorsal margin with large, stout, erect setae (fig. 270); left clasper (figs. 158)

159) lobe broad, dorsal margin expanded, shaft S-shaped, apex directed towards dextral margin of pygophore; right clasper (fig. 160) small, linear; vesica (figs. 195) reduced to a narrow, conical tube; ductus seminalis extends to apex of vesica; phallosome (fig. 196) basally produced into three lobes.

Female genitalia: bursa copulatrix small, sclerotized rings small, separate, oval, weakly divergent posteriorly, separate (fig. 218).

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

diabolus (Linnavouri) 1975: 13. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: Echinops sp. (Compositae).

Distribution: Ethiopia.

indicus (Poppius) 1913: 246. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: unknown.

Distribution: Sri Lanka.

obscuricornis (Poppius) 1915: 62 New combination,

[Cyrtopeltis (Nesidocoris)]. +

Host plant: unknown.

Distribution: Sri Lanka, Formosa, New Guinea, north-eastern Australia, and Solomon Is.

tenuissima Lindberg 1958: 163. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plants: Aeschynomene americana (Leguminosae),

and Sterculia setigera Del. (Sterculiaceae).

Distribution: Canary Islands.

turcica Siedenstucker 1958:126. New combination,

[Cyrtopeltis (Singhalesia)]. +

Host plant: Nicotiana sp., and Hyoscyamus muticus L.

(Solanaceae).

Distribution: Israel.

REMARKS: This genus is very similar to Campyloneuropsis, but is considered different on the basis of the male and female genitalia. China and Carvalho (1952) originally described this taxon as a subgenus of the genus Cyrtopeltis, however, it is quite different from the latter.

This genus has five species which all have very similar male genitalia and are most easily separated on the basis of color, some morphometric features, and subtle differences in the male genitalia.

The group is distributed in the Palearctic, Ethiopian, Oriental, Australasian, and Oceanic regions (Map 15). Three new species remain to be described from South Africa. There is no biological information for this genus.

Genus Tupiocoris China and Carvalho. New combination.

Figures: 27, 28, 74, 75, 107, 108, 163,
164, 165, 197, 198, 199, 219, 220, 239,
240, 241, 253, 254, 267, 268, 269, and 274
(Habitus Tupiocoris californicus
Stal, Figure 274).

Cyrtopeltis (Tupiocoris) China and Carvalho

1952: 159 (type species: Neoproba notata Distant 1893:
432, type fixed by China and Carvalho 1952: 162).

Leptomiris Carvalho and Becker 1957: 199, New
synonymy (type species: mexicanus Carvalho and Becker
1977: 200).

Neodicyphus McGavin 1982: 79, New synonymy (type species:
Dicyphus rhododendri Dolling 1972: 241).

DIAGNOSIS: None of the species have a metaepisternum
scent efferent system (figs. 239, 241), and the genital
aperture of the males is terminal in orientation (fig.
127, 267, and 268). In most species the left clasper of
the male is V-shaped (fig. 163), and the vesica is
reduced to a single lobe with one apical spiculum (fig.
199), or in the type species, with four apical spiculi
(fig. 197). Most species are slender, and fragile (fig.
275), with the costal margins parallel (fig. 107), and
the hemelyton is at least, partly hyaline, but often with
fuscous or red markings. The eyes are usually prominent,

but never reach the bucculae (fig. 28). The pretarsus is characterized by evenly recurved claws (figs. 253, 254).

DESCRIPTION: usually macropterous, rarely brachypterous, fragile, small to large species; length, males 2.25-5.25, females 2.05-5.25; base color most often fuscous to black, with yellow markings, rarely ochraceous to yellow; uniformly covered with short, suberect setae.

Head: (figs. 27, 28), vertical, transverse; frons weakly produced in front of eyes, fuscous unless body is pale, then yellow to pale brown; vertex evenly rounded, fuscous often with two yellow markings adjacent to eyes, postocular margins narrowly or strongly convergent; clypeus weakly to moderately produced in front of frons barely visible from above or not seen; lateral aspect of head mostly fuscous to brown; bucculae small.

Eyes: most often moderate in size, rounded or posterior margin weakly excavate; ventral margin never extends to bucculae, sometimes near base of lorum; fuscous often with reddish tinge, rarely with silver infusion.

Antennae: inserted near midheight of eyes, variable in length, sometimes banded, often apical segment yellow, remainder dark; length of second segment variable, relative to width of pronotum at base.

Rostrum: extending between apices of the middle and hind coxae.

Pronotum: (figs. 27, 28), trapezoidal, with lateral margins always widely divergent; collar narrow, mesally constricted, sometimes with mesal, obscure sulcus, most often yellow; calli most often indistinctly marked, but always raised, separated by weak, mesal, dissected, posterior groove, most often fuscous to brown, sometimes yellow mesally, or entire calli region pale; disc, posterior angles broadly rounded, posterior margin linear to weakly excavate, pale to dark.

Scutellum: broadly convex, often with apex strongly pointed, fuscous, often with lateral angles yellow.

Thoracic pleura: (figs. 239, 240, and 241), mesepimeron long, narrow, strongly recurved anteriorly, spiracle small (fig. 240), oval, bordered by evaporative areas (in larvae spiracle without evaporative areas (fig. 241)); postalare subtriangular, weakly depressed with evaporative areas on lateral margins; metaepisternum, with no scent efferent system, segment with regular arrangement of microrsetae.

Metabasisternum: most often with elongate, posteromesad process, although in type species broader.

Legs: femora linear, sparsely covered with fine, pale setae, testaceous, often with rows of fuscous to brown spots or markings; trichobothria, 3-4 mesofemoral (fig. 75) and 3-5 metafemoral (fig. 74); tibiae usually long, with erect spines on middle and hind tibiae;

tarsus long, penultimate segment at least 1.5x longer than apical segment; pretarsus (fig. 253, 254) small to moderate in size, claws evenly rounded, with base projecting ventrally, base with a small pore, and pseudopulvilli broad.

Hemelytra: (fig. 107), variable in development, usually macropterous with some sexual dimorphism, often with abdomen terminating at the corial fracture in males, one species with non-sex semibrachyptery, two species with brachypterous females, and macropterous males; usually hyaline, with fuscous, and/or red markings, cuneus usually very long, at least 3x longer than broad; always with two membrane cells, minor cell often very small.

Male genitalia: pygophore (figs. 127, 267, 268), and 269), genital aperture terminal, ventral margin with two internal tubercles (fig. 127), sinistrolateral margin sinuate; left clasper (fig. 163) usually V-shaped, sensory lobe broad, with numerous stout setae, shaft viewed internally S-shaped (fig. 164); right clasper (fig. 165) small, linear, sometimes apically recurved, usually membranous for at least basal half; vesica most often reduced to small, membranous lobe, with one small to large, apical spiculum (fig. 199), or multilobed with four apical spiculi (fig. 197); ductus seminalis small, narrow, flexible, not extending beyond base of

phallotheca; phallotheca (fig. 198) small, strap-like, conical, often reduced with small apical dissections.

Female genitalia: for type species, sclerotized rings reduced to two adjacent, sclerotized plates (fig. 219), remainder of species with separate sclerotized rings, divergent posteriorly (fig. 220).

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

agilis (Uhler) 1877: 425. New combination, [Dicyphus

(Dicyphus)] +

Host plant: Ribes sp. (Grossulariaceae).

Distribution: North America.

brachyptera (Knight) 1943: 53. New combination, [Dicyphus

(Dicyphus)]. +

Host plant: Polemonium humile R. & S.

(Polemoniaceae).

Distribution: western North America (Washington State).

californica (Stal) 1859: 259. New combination, [Dicyphus

(Dicyphus)]. +

Host plant: Madia sp. (Compositae).

Distribution: western North America.

chlorogaster (Berg) 1879: 290. New combination,

[Cyrtopeltis (Tupiocoris)]. +

Host plants: Petroselinum sativum L. (Salsa)

(Umbelliferae), and Petunia myctaniflora (Petunia)
(Solanaceae).

Distribution: South America, Central America, and
Mexico.

confusa (Kelton) 1980: 389. New combination, [Dicyphus].

+

Host plants: Lonicera involucrata (Richards)

(Caprifoliaceae), Rhus glabra L. (Anacardiaceae),

Rosa nutkana Presl., Rubus sp. (Rosaceae), and

Viburnum edule (Michx) (Scrophulariaceae).

Distribution: North America.

cucurbitaceus (Spinola) 1852: 196. New combination,

[Dicyphus (Dicyphus)]. Kelton (1980) has

recognized this species as distinct, and rejects its
synonymy with agilis (Uhler) that was proposed by
Carvalho (1947). From the available specimens
Kelton's actions are correct, however, there is some
doubt as to the identity of the Spinola type
material. +

Host plant: Nicotiana tabacum L. (Solanaceae).

Distribution: South America.

diplaci (Knight) 1968: 71. New combination, [Dicyphus]. +

Host plant: Mimulus longifloris (Nutt.) A. L. Grant
(Scrophulariaceae).

Distribution: western North America.

elongata (Van Duzee) 1917: 269. New combination,

[Dicyphus (Dicyphus)]. +

Host plant: Rubus parviflorus Nutt. (Rosaceae).

Distribution: western North America.

notata (Distant) 1893: 432. New combination, [Cyrtopeltis

(Tupiocoris)] = disclusus (Van Duzee) 1923: 152, New
synonymy (the junior synonym was previously placed in
the genus Dicyphus and may account for the lack of
recognition of the identity of these two species.

The two species are the same saliently and in all
aspects of the male genitalia). +

Host plants: Nicotiana trigonophylla L., Solanum sp.
(Solanaceae), Mirabilis sp. (Nyctaginaceae),
Atriplex sp. (Chenopodiaceae).

Distribution: South America, Central America, Mexico,
and south-western U.S.A.

phaceliae (Knight) 1968: 71. New combination, [Dicyphus

(Dicyphus)]. +

Host plant: Phacelia ramosissima Dougl. ex. Lehm
(Hydrophyllaceae).

Distribution: western North America (California).

rhododendri (Dolling) 1972: 241. New combination,

[Neodicyphus]. +

Host plant: Rhododendron sp. (Ericaceae).

Distribution: north-eastern United States.

ribesi (Knight) 1968: 70. New combination, [Dicyphus

(Dicyphus)]. +

Host plant: Ribes sp. (Grossulariaceae).

Distribution: western North America.

rubi (Knight) 1968: 72. New combination, [Dicyphus

(Dicyphus)]. +

Host plant: Rubus strigosus (Rosaceae).

Distribution: North America.

rufescens (Van Duzee) 1917: 268. New combination,

[Dicyphus (Dicyphus)]. +

Host plant: unknown.

Distribution: western North America (California).

similis (Kelton) 1980: 389. New combination, [Dicyphus].

+

Host plants: Geranium viscosissimum Fisch. & Mey.

(Geraniaceae), Rubus idaeus L., Rubus sp. (Rosaceae),

and Aster sp. (Compositae).

Distribution: western North America.

tibialis (Kelton) 1980: 390. New combination, [Dicyphus].

+

Host plants: Geranium viscosissimum F. (Geraniaceae),
and Ribes sp. (Grossulariaceae).

Distribution: western North America.

tinctus (Knight) 1943: 55. New combination, [Dicyphus
(Dicyphus)]. +

Host plant: unknown.

Distribution: western North America.

SPECIES REMOVED FROM THE GENUS TUPIOCORIS:

bakeri (Knight), see Usingerella China and Carvalho

cincticornis Stal, see Campyloneuropsis Poppius

hyalinus (Carvalho), see Campyloneuropsis Poppius

infumatus (Carvalho), see Campyloneuropsis Poppius

melanocephalus Reuter, see Glarisia Cassis, new genus

nigroculatus (Carvalho), see Campyloneuropsis Poppius

NEW GENERIC SYNONYMIES:

Leptomiris Carvalho and Becker 1957: 199

This monotypic genus is synonymized with Tupiocoris. The authors distinguished this species as a separate genus on the basis of wing sexual dimorphism, shape of pronotum and shape of the calli. These are considered autapomorphic character states for this species and are not of generic worth. It is common in the Heteroptera that the pronotum is modified when the wings are shortened. Sex dimorphism of the wings occurs in other Tupiocoris

species, and mexicanus has similar male genitalia to other Tupiocoris species.

Neodicyphus McGavin 1982: 79

This genus is synonymized with Tupiocoris. McGavin (1982) correctly recognized that many Nearctic species of Dicyphus could not be considered congeneric with the Palearctic species assigned to this genus. However, he did not recognize the similarity of the Nearctic species to the Neotropical species that are now all grouped in Tupiocoris.

REMARKS: The subgenus, Tupiocrois, of the genus Cyrtopeltis has been elevated to full generic status, however its conception and taxic content is considerably altered from that conceived by China and Carvalho (1952). Only two species, notata, and chlorogaster, are retained in the genus. Numerous species from the Nearctic that were previously placed in the genus Dicyphus have been placed in this genus, for a total of 17 species. The type species, notata is considerably different from the other species in the genus, particularly in the male and female genitalia, however these differences are considered autapomorphic. Overall, the absence of a scent efferent system, recurved claws, trichobothrial numbers, polished dorsum and narrow phallotheca, provides sufficient synapomorphy to group the species.

This genus is found exclusively in the Western Hemisphere (map 16). In North America, the species are similar morphologically, and cannot be separated by minor differences in the male genitalia, and certain morphometric characters. A number of the species are recorded as being host specific, however, this may be a sampling bias, as I have, in my own collections in the western United States, found additional host records for a number of species. The majority of species are associated with plants in the families Solanaceae, Rosaceae and Gesneriaceae, and in particular with the genus Ribes in western North America. At the specific level there may be significant coevolutionary patterns, and will warrant further analysis.

The biology of the species of this genus is almost unknown, and most information is restricted to the "suck-fly", notata, which was considered a serious pest of tobacco in Florida (Quaintance, 1898; Howard, 1898). Davidson and Lyon (1982) report that this species can periodically cause serious damage in late-planted fields. Quaintance (1898) reported that this species caused considerable damage by sucking the "cell-sap", which resulted in leaf wilting and necrosis. Life history traits recorded by Quaintance (1898) included: complete development in 15 days, voracious feeding, adult preference to shaded areas, and high population

densities. Davidson and Lyon (1982) further report that feeding reduced coloration, weight, and thickness of the cured leaves, and also lower the quality of the tobacco because of specks of excrement on the undersides of the leaves.

Dolling (1972) reported that rhododendri was commonly associated with an aphid, Masonaphis sp., on which they were observed to feed, although adults were present, even in the absence of the aphid later in the summer.

My own observations of Tupiocoris species in western North America suggest that some of these species are oligophagous. In caged experiments development was completed from early instars on both host plant material and animal material. In some instances, individuals were observed feeding on dead individuals of the same species. Further, these species are multivoltine, and in the field, complete development was variable, but usually took about 30 days. Of particular interest is the common association of Tupiocoris species with other dicyphine taxa. For example, T. confusa is consistently associated with Usingerella bakeri and Macrolophus rivalis on the host plant Ribes viscosissimum throughout Oregon and Washington. The species, californica, however is the only dicyphine found on Madia sativa, which has long and densely distributed glandular trichomes. The bug is adept at moving on such a substrate by straddling the

stalks of the trichomae, and not the glandular apex. Also, they are continually engaged in trivial flights to non-host plants, and are also continually preening.

Genus Usingerella China and Carvalho. New status

Figures: 31, 32, 76, 77, 109, 110, 166,
200, 201, 242, 218, 256, and 271.

Cyrtopeltis (Usingerella) China and Carvalho 1952: 165

(type species: Cyrtopeltis simplex Reuter 1909: 63).

DIAGNOSIS: This genus is distinguished by the deeply dissected pygophore of the male (fig. 271). The left clasper is very large (fig. 166), U-shaped, with the sensory lobe linear, and positioned below the ventral margin of the genital aperture. The sclerotized rings of the females are lateral in orientation, and are incomplete anteriorly (fig. 218). The hemelytra are characterized by only one membrane cell (fig. 109). The male genitalia may be confused with that found in Nesidocoris species, however in the latter the left clasper is distinctly V-shaped, and the eyes are much larger, extending to the bucculae (cf. figs. 24 to 32).

DESCRIPTION: macropterous, elongate-ovoid, costal margins weakly convex; length, males 2.85-3.25, females 2.85-3.40; pallid to fuscous, with various testaceous to fuscous markings; densely setate with short, pale to dark, suberect setae.

Head: (figs. 31, 32), transverse, moderately vertical; frons moderately produced in front of eyes often with two dark fascia; clypeus weakly produced, visible from above, pale with fuscous marking ventrally; vertex weakly convex, pale with areas adjacent to collar fuscous.

Eyes: moderately sized, strongly rounded, when viewed from above; removed from collar by at least thickness of first antennal segment; fuscous to fusco-red; facets moderate in size.

Antennae: inserted below midheight of eyes; I small and broad, subequal in length to vertex width; II linear, length less than width of pronotum at base.

Rostrum: extending between apices of the middle and hind coxae.

Pronotum: (figs. 31, 32), trapezoidal; collar broad, weakly constricted mesally; testaceous to black, with suberect setae; calli indistinct, somewhat raised, with incomplete mesal and posterior depressions, testaceous to fuscous, if fuscous sometimes with yellow markings mesally; disc not produced, posterior angles strongly

rounded, posterior margin sinuate, barely excavate;
propleuron weakly expanded laterally, barely visible
from above.

Thoracic pleura: (fig. 242), mesepimeron elongate,
inner margin sinuate, spiracle moderately sized,
depressed, bordered by evaporative areas, extending onto
lateral margins of depressed postalare. Metaepisternum,
with well developed scent efferent system, osteole small,
produced into elongate peritremal disc, broadest at apex,
densely covered with minute setae, evaporative areas
covering about 1/2 of segment, not surpassing mesepimeric
spiracle.

Legs: femora fusiform, expanded dorsoventrally,
covered with erect, pale to dark setae, testaceous
sometimes with dark markings, mesofemora weakly recurved;
trichobothria, 4 mesofemoral (fig. 77) and 5 metafemoral
(fig. 76); tibiae linear, small, with two rows of
spinelets, and erect stout setae, hind tibiae with large,
stout spines on apical 2/3, sometimes pale basally,
mesotibiae about 1.3x greater in length than mesofemora;
tarsi long, testaceous, claws evenly rounded (fig. 256),
with a pore at base, basal ventral projection,
pseudopulvilli broad, leaf-like.

Hemelytra: (fig. 109, testaceous to hyaline, often
with clavus and exocorium fuscous, corial fracture broad,
with only one membrane cell; cuneus small, broad,

sometimes with mesal fuscous spot.

Hindwings: (fig. 110), R vein not parallel with costal margin, strongly recurved, 1A extending to PCu margin.

Male genitalia: pygophore (fig. 271) deeply dissected, genital aperture terminal with a small, ventral pygophoral process, sinistral margin highly modified, narrowly, and deeply dissected at articulation of left clasper, dextral margin entire; left clasper (fig. 161) very large, U-shaped, projected below ventral margin of genital aperture, lobe small, narrow, shaft recurved, apex weakly expanded; right clasper (fig. 162) small, tapered weakly toward apex; vesica (fig. 200) membranous, unilobed, basally sclerotized, with internal sclerotized channels, extending toward apex; ductus seminalis long, terminating obscurely apically; phallosome (fig. 201) narrow, dissected apically.

Female genitalia: (fig. 221), bursa copulatrix small, sclerotized rings small, separate, lateral in orientation, anteriorly obscure, with internal projections posteriorly, with U-shaped process basally, sclerotized at margins of bursa copulatrix.

INCLUDED SPECIES, HOST PLANT(S), AND DISTRIBUTION:

bakeri (Knight) 1943: 58. New combination, [Cyrtopeltis
(Tupiocoris)]. +

Host plants: Ribes viscosissimum (Grossulariaceae)
and Rubus parviflorus (Rosaceae).

Distribution: western North America.

simplex (Reuter) 1909: 63. New combination, [Cyrtopeltis
(Usingerella)]. +

Host plant: Mimulus cardinalis (Scrophulariaceae).

Distribution: western North America (southern
California).

REMARKS: This genus is also elevated from the subgeneric level proposed by China and Carvalho (1952). There are two included species and it is distributed in the western United States, south-western Canada, and Baja California (Map 17). The biology of this group is not known.

GENERA RETAINED IN SUBFAMILY (NOT EXAMINED):

Dicyphopsis Poppius 1914: 11 (type species: nigriceps
Poppius 1914: 11).

This genus was described by Poppius (1914) from one female specimen. Unfortunately this specimen has been completely destroyed (on shipment to me from the Naturhistoriska Riskmuseet, Stockholm, Sweden). Poppius' description gives no indication of any characters that

could be considered of generic worth. Linnavouri (1975) described one species, spectabilis, in this genus recognizing the huge eyes (which are almost holoptic in the male) as a diagnostic feature. I have observed two specimens of this species, and on the basis of the male genitalic characters it is probable that the latter species belongs to Campyloneuropsis, however, I have deferred any taxonomic changes until more specimens are available for examination. The genus is known from east Africa.

Habrocoris Wagner 1951b: 153 (type species: breviceps Wagner 1951b: 153).

This is a monotypic genus which was described by Wagner (1951) from Egypt. I have not seen any specimens of this genus and from his description it could be a synonym of Dicyphus. Again, I have deferred any taxonomic changes until specimens can be examined.

Isoproba Osborn and Drake 1915: 553 (type species: picea Osborn and Drake 1915: 533).

This is a monotypic genus described from Guatemala. The generic description is very short, and the authors comment that the species resembles Parabroba [Orthotylinæ]. Carvalho (1952) placed this genus in the Dicyphini [Dicyphinae], although he gave no reasons to justify this action. I have attempted to locate this

specimen in North American institutions, however, I have not as yet located it. Thus, I leave this genus within the Dicyphinae with considerable reservation.

GENERA REMOVED FROM THE SUBFAMILY DICYPHINAE:

Angerianus Distant 1904: 437.

This genus contains two species, maurus Distant, and fractus Distant, both of which are recorded from India. Distant (1904) placed these taxa in the Division Cylaparia, whereas Reuter (1910) was uncertain of their proper placement, and Carvalho (1952) placed the genus in his tribe Dicyphini (Phylinae). I have examined typical material of both species, and additional material from Nepal. It is apparent that this genus belongs in the subfamily Deraeocorinae, and I tentatively regard it as most closely related to the hyalodines, which is of interest since most of these taxa are New World.

The genus has the following combination of characters: body punctate, cleft claws, parempodia setiform, pulvilli/pseudopulvilli absent, collar present, collar region marked by by posterior, transverse sulcus, head vertical, metaepisternum scent efferent system well developed, with osteole produced into tube-like auricle, mesepimeric spiracle intersegmental, and scutellum raised.

The two included species may be conspecific, however, more male specimens are needed before any synonymy can be proposed with any confidence.

Apollodotidea Hsiao 1944: 395, see Stethoconus Flor.

Cychrocapsus Poppius 1914: 24.

Poppius (1914) described this genus from a single female specimen and placed it in his Division Macrolopharia [Macrolophinae]. Carvalho (1952) retained this genus with the dicyphines (Phylinae: Dicyphini). I have examined the type specimen which is badly damaged, having no head, and only one pretarsus intact. The claws are cleft, and there are no parempodia or pulvilli. On the basis of this and the general body form I have placed this genus in the Deraeocorinae.

Odhiambo (1960) grouped this genus with Petasma Odhiambo (= Bunsua Carvalho), and Hildebrandtiella Poppius as dicyphines with a punctate body. All of these genera are not considered as dicyphines in this classification.

Hildebrandtiella Poppius 1914: 25.

This genus was described by Poppius (1914) in his Division Macrolopharia, and Carvalho (1952) retained them in his tribe Dicyphini [Phylinae]. The only included species, scutellaris is known from one female specimen. This specimen is remarkably similar to Deraeocoris

Kirschbaum species, and keys to this genus in Carvalho's world generic key (Carvalho, 1955). However, because of the lack of material and the probable polyphyletic nature of Deraeocoris (Razafimahatratra, personal communication), I have not synonymized this genus, but have placed it with certainty in the tribe Deraeocorini [Deraeocorinae].

The genus is characterized by cleft claws, a weakly incrassate second antennal segment at the apex, frons strongly produced in front of eyes, and the body is punctate. This genus is known from Madagascar.

Hyalosomella Poppius 1914: 8

This genus was also placed in the Division Macrolopharia by Poppius (1914), and again Carvalho (1952) recognized this as a dicyphine taxon. It was described from one female specimen, and there is only one included specimen from east Africa. This specimen is teneral, and badly damaged, with most legs missing, and the rostrum is broken. The head is collapsed, but it appears to be of an orthotyline type. Only one pretarsus remains, and the leaf-like structures arising from the ventral surface are interpreted to be pulvilli. There is apparently no collar, but the anterior 1/4 of the bug is so collapsed that it is difficult to judge. I place this genus in the Orthotylinae, but with some reservations.

The metaepisternum scent efferent system has a raised auricle process which is never present in the Dicyphinae, and I have thus some confidence in removing from the latter.

Onconotellus Knight 1935: 201

I have not obtained specimens of this genus. Knight (1935) described it from one female specimen from Samoa, and placed it in the Dicyphinae on the basis of the pretarsus structure. It has remained with only one included species, buxtoni. From the description, and the habitus figure it is obviously not a dicyphine. It most probably belongs to the Monalonini (Bryocorinae) on the basis of the vertical head, pronotum structure, and pretarsus structure.

Orthotylidea Poppius 1914: 12

This is another monotypic genus which was described from one female specimen by Poppius (1914). Carvalho (1952) recognized this as a dicyphine. The only included species, lateralis, was described from east Africa. The type specimen is badly damaged with only one leg and no antennal segments. The pretarsus structure, head and pronotum structure, and the absence of a collar enable me to place this genus in the Orthotylinae with confidence.

Pseudocamptobrochis Poppius 1911: 12

Poppius (1911) in describing this genus suggested that it was near Camptobrochis Fieber and Deraeocoris (cited as Stal). Carvalho (1952) placed this genus in the Deraeocorini, and placed it in his key to the Deraeocorini (Carvalho, 1955). Subsequently, Carvalho (1958) placed this genus in the Dicyphini (Phylinae), and recognized that he misplaced this genus in the Deraeocorini. The only included species, pilosus, described from Tasmania (Australia), from one male and female specimens. I have obtained the only known specimen, however, only parts of the antennae and membrane of the hemelytra remain on the card. The antennae are atypical for dicyphines and is very similar to that found in deraeocorines. From only this evidence, and believing that by a lapsus calami, Carvalho (1958) placed it in the wrong subfamily. Indeed I support his original contention that the genus belongs to the Deraeocorini.

Stethoconus Flor 1860: 615 = Apollodotidea Hsiao 1944:

395, New synonymy.

This genus was placed by Reuter (1910) in his Division Macrolopharia, and Carvalho (1952) sustained their position within the dicyphines. Wagner and Weber (1964) also placed them in the dicyphines. Kerzhner and

Yaczewski (1964) removed this genus to the tribe Clivinemini, in the subfamily Deraeocorinae. This action was not recognized by Wagner (1971) who retained them in the subfamily Dicyphinae. Subsequently, Kerzhner (1971) placed the genus again in the Clivinemini, providing a key to two species, and figures to three species, and removed pyri Mett. from synonymy with cyrtopeltis Flor.

It is obvious that this genus is not a dicyphine, and is somewhat similar to Angerianus. It is in my judgement most definitely a deraeocorine, however its affinities with the Clivinemini are in question. This is more due to the artificial tribal classification of the Deraeocorinae.

The genus Apollodotidea Hsiao, which is also placed with the dicyphines (Carvalho, 1952), is placed in synonymy with Stethoconus, and only differs from the latter in the degree that the scutellum is raised. The genus Stethoconus thus contains six species, cyrtopeltis, frappi Carayon, japonicus Schunacher, praefectus Distant, pyri, and ysignata Hsiao. The genus is characterized by similar features to Angerianus, although the mesepimeron and scutellum are strongly raised. The genus is distributed chiefly in Palearctic, although ysignata is known from Borneo.

Teratocapsus Poppius 1911: 10

I have not been able to locate the type material of

this genus, and it is conceivable that it is lost. Poppius (1911) in describing the included species, megacoeloides, from Tasmania referred to its similarity to Megacoelum Fieber (Mirini). I have removed this genus from the Dicyphinae on the basis of the original description, and tentatively place it in the Mirini.

PHYLOGENETIC ANALYSIS OF THE GENERA OF THE DICYPHINAE:

The following cladistic analysis is the first of its type for the Dicyphinae. The genera have been defined as monophyletic groups on a global basis, and with the investigations of new character sources I have suggested intergeneric relationships and consider the importance of certain character transformations.

In phylogenetic analysis, outgroup comparison enables the polarization of character states (Wiley, 1981). As the relationships of the subordinate groups of the Miridae are largely unresolved (see Schuh, 1976), the selection of an outgroup for the dicyphines remains conjectural. In this study I have selected the genus Felisacus Carvalho as the outgroup. This genus was placed by Carvalho (1981) in the tribe Bryocorini (Bryocorinae), however, Schuh (1976) recognized the correct position of this genus with the monalonine Bryocorinae. Unlike all other monalonines the species of this genus have a metaepisternum scent efferent system which I considered to be of analytical importance in this study, as this character is used greatly in my classification of the dicyphines. The characters and character states are summarized in Table 1, and the raw data are presented in Table 2. The most resolved cladogram is provided in Figure 275. Numbers in brackets in the discussion and on the cladogram refer to apomorphies.

TABLE 1: Characters and character states for the genera of the Dicyphinae (see text for discussion).

CR = consistency index; integers (e.g. 0, 1, 2, 3) = character states; * = unordered character states.

TABLE 1:

CHARACTERS	CHARACTER STATES
1. Body.	Shiny (0). Dull (1). CR = 1.00
2. Setation.	Suberect (0). Adpressed (1) Erect (2) CR = 1.00.
3. Setation.	Sparse (0). Dense (1). CR = 1.00.
4. Head.	Transverse (0). Elongate (1). CR = 1.00.
5. Vertex.	Postoccular margins convergent (0). Parallel (1). CR = 1.00.
6. Lorum.	Flat (0). Expanded (1). CR = 1.00.
7. Eyes.	Removed from collar (0). Contiguous with collar (1). CR = 1.00.
8. Eyes. *	Extend to lorum (0). To jugum (1). To bucculae (2). CR = 0.667.
9. Antennae. *	Inserted above midheight of eyes (0). At midheight (1). Base of eye (2). CR = 1.00.
10. Antennal segment 1.	Length greater than vertex width (0). Smaller (1). CR = 0.50.
11. Calli.	Distinct (0). Indistinct (1). Obsolete (2). CR = 1.00.
12. Collar.	Broad (0). Narrow (1). CR = 1.00.
13. Scutellum.	Caudal tip pointed (0). Broadly rounded (1). CR = 1.00.

TABLE 1 (CONTINUED):

14. Mesobasisternum. Rounded (0). Pointed (1).
CR = 1.00.
15. Membrane minor cell. Large (0). Small (1).
CR = 1.00.
16. Postalare. Without evaporative bodies (0).
Present on lateral margins (1).
Cover posterior half of segment (2)
CR = 1.00.
17. Mesepimeron. Evaporative bodies raised (0).
Depressed (1). CR = 1.00.
18. Scent efferent system. * Present (0). Absent (1).
CR = 0.333.
19. Osteole. Mesal (0). Posterior (1). CR = 1.00.
20. Peritremal disc. Narrow (0). Broad (1). CR = 1.00.
21. Metaepisternum. * Evaporative areas extend to
mesepimeric spiracle (0)
Halfway to spiracle (1).
To metaepimeron (2). CR = 0.667.
22. Metaepisternum. Evaporative bodies oval (0).
Elongate (1). CR = 0.500.
23. Metatibiae. Without spines (0). With spines (1).
CR = 0.500.
24. Femora. Spines absent (0). Present (1).
CR = 1.00.
25. Metafemora. Linear (0). Expanded (1). CR = 1.00.

TABLE 1 (CONTINUED):

26. Metafemoral. Trichobothria mostly distal (0).
Mostly proximal (1). CR = 1.00.
27. Tarsi. * Expanded distally (0).
Weakly expanded (1). Linear (2).
CR = 1.00.
28. Pretarsus. With pseudopulvilli (0).
With pulvilli (1). CR = 1.00.
29. Claws. Pore absent (0). Present (1).
CR = 1.00.
30. Claws. * Recurved (0). Linear (1). Strongly
recurved (2). CR = 0.667.
31. Pygophore. * Genital aperture dorsal (0).
Terminal (1). Ventral margin strongly
produced caudally (2). Greatly
modified, dissected (3). CR = 0.667.
32. Pygophore. Dorsal margin with simple setae (0).
With strong, erect bristles (1).
CR = 1.00.
33. Genital aperture. * Dorsal margin entire (0).
Impressed (1).
Dissected (2). CR = 1.00.
34. Pygophore. Dorsodextral tubercle absent (0).
Present (1). CR = 1.00.
35. Genital aperture. Ventral margin with chisel-
like tubercle (1). CR = 1.00.

TABLE 1 (CONTINUED):

36. Genital aperture. Dorsosinistral margin absent
(0). Present (1). CR = 1.00.
37. Vesica Subbasal process absent (0).
Present (1). CR = 1.00.
38. Vesica. * Without tuberculations (0). With
dispersed tuberculations (1).
Tuberculations interdigitized (2).
CR = 1.00.
39. Vesica. Sac-like (0). Tube-like (1).
CR = 1.00.
40. Ductus seminalis. Obscure apically (0). Produced
into sclerotized cup (1).
CR = 1.00.
41. Ductus seminalis. Terminates subbasally in
vesica (0). Subapically (1).
Apically (2). CR = 0.500.
42. Vesica. Without internal channels (0).
With internal channels. CR = 0.333.
43. Phallotheca. Lateral expansions absent (0).
Present (1). CR = 1.00.

TABLE 1 (CONCLUDED):

44. Left clasper. Shaft contiguous with ventral margin of genital aperture (0).
Shaft perpendicular (1). CR = 1.00.
45. Left clasper. Small (0). Large (1). CR = 1.00.
46. Left clasper. V-shaped (0). U-shaped (1). CR = 1.00.
47. Left clasper. Outwardly linear (0).
Inwardly S-shaped (1). CR = 1.00
48. Left clasper. Shaft not greatly flattened (0).
Greatly flattened (1). CR = 0.500.
49. Left clasper. Outer apex entire (0).
Outer apex with serrations (1).
CR = 1.00.
50. Right clasper. Articulation distant from vesica (0).
Articulation adjacent to vesica (1). CR = 1.00.
51. Sclerotized rings. Connected mesally by sclerotized bar (0).
Separate (1). CR = 0.500.
-

TABLE 2: Raw data for the cladistic analysis of the genera of the Dicyphinae.

For character # refer to Table 1 for character descriptor, and the integers referring to character states. The integer 9 indicates missing data.

The following codes are used in this Table for the genera:

FELI.....Feliacus

CAMN.....Campyloneuropsis

CAMY.....Campyloneura

CHIU.....Chius

CYRT.....Cyrtopeltis

DICY.....Dicyphus

ENGY.....Engytatus

GLAR.....Glarisia

MACR.....Macrolophus

NESI.....Nesidocoris

SETO.....Setocoris

SING.....Singhalesia

TUPI.....Tupiocoris

USIN.....Usingerella

Character analysis:

In this analysis the intergeneric relationships are fully resolved. Nine cladograms were produced using the PAUP program, all of which were equally parsimonous and consistent (total length = 89 steps; overall consistency index = 0.760). Five cladograms were calculated that were identical and fully resolved (fig. 275), and this tree topology is used in this discussion (two other types of cladograms were produced that were not fully resolved, in that both grouped Glarisia, Setocoris, and Usingerella from one node, i.e. a trichotomy). The majority of characters were fully homologous (i.e. consistency index = 1.00), and a number of transformation series were established [2, 9, 11, 16, 27, 33, and 38]. A number of features were homoplasious, i.e either character reversals [-20, -22, -26, -29, -31', -42, and -51], or parallelisms [+7, +8, +10, +18, +20, +21, +30, +30', +31'', +41, +42, +45, and +48].

A natural classification of the dicyphines is hypothesized as all the genera are recognized as monophyletic groups on the basis of one or more apomorphies, and no genus is exclusively defined by a homoplasious character.

A basic separation of the genus Dicyphus and the remaining dicyphine genera is strongly indicated. The autapomorphies of Dicyphus are thoracic, pretarsus, and

genital characters [16', 21', 30, and 49]. The claws are linear and deeply cleft basally [30], and the pseudopulvilli and parempodia are small. The basally cleft claws somewhat resembles the condition found in a number of taxa within the Deraeocorinae, but the absence of pseudopulvilli in the latter taxon suggests that there is no reason to regard Dicyphus as a paraphyletic taxon. The extensive evaporative areas on the metaepisternum in Dicyphus ([21'''], covering almost the entire segment), is to my knowledge unique for the entire family Miridae. The sister-group association of Dicyphus with Felisacus is based only on symplesiomorphies such as the dorsal genital aperture (which is invariant in the monalonine Bryocorinae), and the left clasper shaft contiguous with the ventral margin of the genital aperture of the male [44], and its basal position in the cladogram is more an indication of its uniqueness.

The genus Campyloneura also shows a clear separation from the remainder of the dicyphine genera, and its sister-group association with Felisacus + Dicyphus is more due to its distinctness than any synapomorphies, and its grouping with Dicyphus is based chiefly on symplesiomorphies [11, 12, 20, and 29], although both have elongate evaporative bodies on the metaepisternum ([22], cf. figs. 222 and 227; note that this feature is variant in the genus Dicyphus, see figs. 225, 226, and

the coding of this character is based only on the subgenus Dicyphus).

The genus Campyloneura is a distinct monophyletic group on the basis of head [6 and +8], thoracic [17], and pretarsal [28] characters. The evaporative bodies around the mesepimeric spiracle are depressed and not raised which appears to be the consistent state throughout the Cimicomorpha (see Carayon, 1971). The pretarsus structure (fig. 243) is very similar to that in eccritotarsine Bryocorinae (Schmitz, 1970; Schuh, 1976), and this suggests that Campyloneura, on the basis of this character, is a paraphyletic member of the Dicyphinae. I have used pretarsal characters [characters 28-30] in this cladistic analysis and I consider them of critical importance. The intergeneric variation of this feature in the dicyphines (and in other mirid taxa such as the Deraeocorinae, see Razafimahatratra, 1980) indicates that the correct level of universality, of certain components of the pretarsus, is at the generic level and not the subfamilial level as suggested by others (Carvalho, 1952; Carvalho and Leston, 1952; Schuh, 1974, 1976). For example, I regard cleft claws and the presence of pseudopulvilli as characters not of subfamilial worth. The homoplasious pretarsus structure of Campyloneura is not considered sufficient to place this genus in the Eccritotarsini (Bryocorinae). The genus

has a typical dicyphine metaepisternum scent efferent system (the eccritotarsines have a scent efferent system without evaporative areas) and the non-punctate, linear body form, and male genitalic features (Wagner, 1971) are sufficient grounds to retain Campyloneura in the Dicyphinae.

The remainder of the dicyphines, (Campyloneuropsis + Singhalesia + + Macrolophus), are more clearly grouped on the basis of pronotal [11, 12], and pretarsal characters [29]. These genera have a peculiar pore at the base of the claw (e.g. fig. 250) which is apparently absent in Campyloneura, Dicyphus, and Felisacus (Nesidococoris, Engytatus, Campyloneuropsis, and Cyrtopeltis have not been examined). The presence of this pore was first reported for Tupiocoris rhododendri by McGavin (1982), and its function remains unknown.

The sister-taxa grouping of Chius and Macrolophus is based on the synapomorphy of the parallel postocular margins of the vertex [5]. Two other features, the extent of evaporative areas on the metaepisternum [+21] and the internal channels of the vesica [+42], define the group but are homoplasious characters. The latter indicates a possible relationship between this group and the Glarisa + Setocoris + Usingerella group, which is considered monophyletic on the basis of this homoplasious character alone. The genus Chius is retained as a monophyletic

genus on the basis of two autapomorphies, i.e. the antennae inserted at the base of the eyes [9], and the caudal end of the scutellum is broadly rounded [13].

There is good reason to retain the generic status of this genus despite that it is a monotypic taxon, and in this analysis it has more apomorphies than Macrolophus with which I indicated a potential congeneric status. I have avoided this synonymy because of the heterogeneity of Macrolophus which is only defined by one apomorphy, the elongate head [5]. Other miridologists (China and Carvalho, 1952; Wagner, 1971) have stated that Macrolophus is a distinct genus on the basis of its small eyes, but this is not a reliable generic character as it is found in numerous genera (e.g. Tupiocoris and Cyrtopeltis). I have indicated beforehand that Macrolophus is possibly a polyphyletic taxon. It is apparent that a number of Neotropical species (e.g. basicornis and cuibanus) are more closely allied to Campyloneuropsis species than to the typical Macrolophus species, nubilus s. s., and the other closely related Palearctic species. The male (cf. figs. 168, 187, and 189) and female genitalic characters (cf. figs. 202, 214, and 215) seem to provide enough evidence to move these Neotropical species to Campyloneuropsis, however, I have deferred this action pending the completion of an ongoing analysis of Macrolophus. The Nearctic species of

Macrolophus are even more variable, and there may be a need for the description of new genera to accommodate certain species groups.

The monophyletic group, Campyloneuropsis + Singhalesia + + Tupiocoris, is defined by synapomorphies of the vestiture [2], and the metafemoral trichobothria [26]. This arrangement is not considered definite as the above attributes need to be investigated further. The group is also defined by the eyes extending beyond the lorum, however, this character is partially homoplasious ([+8], see Dicyphus, fig. 275).

The sister group relationship of Tupiocoris and Cyrtopeltis is considered conjectural as it is defined by only a homoplasious feature, i.e. the metaepisternum scent efferent system is absent [+18], which has obviously occurred independently in other dicyphine taxa (e.g. Chius and Setocoris). The absence of the scent efferent system may be strongly correlated with taxa that are associated with very "sticky" plants. For example, Tupiocoris is often associated with glandular Ribes species, and Setocoris is only known to be associated with insectivorous plants such as Drosera (the host plant associations of Chius and Cyrtopeltis are poorly known. This would suggest that the monophylecity of the Tupiocoris + Cyrtopeltis group is highly questionable. Furthermore, Cyrtopeltis has obvious affinities with

Engytatus, especially in relation to male genitalic characters [31', 48]. These taxa need to be investigated further to analyze whether the homoplasy of these features, as indicated now, is incorrect. The genus Tupiocoris is monophyletic on the basis of two autapomorphies, the pointed mesobasisternum [4], and the claws which are strongly recurved [+30] which also occurs in Setocoris. There are a number of other features, particularly in the male genitalia, which define Tupiocoris clearly, however, the nominal species, notatus, is considerably different from all the other species in the genus, and these characters were consequently not used in this analysis. The genus Cyrtopeltis is monophyletic on the basis of five autapomorphies, of the vestiture [3], and male genitalia [31', 33, 38', 40, 48]. The ductus seminalis terminates in a sclerotized cup [40] which is a unique feature for the Dicyphinae (in all other dicyphine taxa the ductus seminalis is apically obscure and diffuse).

The group, Campyloneuropsis + Singhalesia....
+Usingerella, is defined by one vestiture character [3], and the obsolete calli [11], and the monophylecity of this group is seemingly well established. The sister-group association of Setocoris and Usingerella is defined by the absence of a minor membrane cell of the hemelytron [15']. I consider this

attribute of questionable value because in a number of genera (e.g. Campyloneuropsis) there is a tendency for progressive loss of the minor cell, and it is often almost fused to the inner cuneal margin and the major membrane vein. This is of importance since the absence of a minor membrane cell is one of the chief defining criteria for the subfamily Bryocorinae. This analysis indicates it is a generic character and is probably a feature that is subject to convergence. The genus Usingerella is defined by features of the male genitalia [+31'', =45, 46], however, only the U-shaped left clasper [46] is an autapomorphy. The genus Setocoris is defined by three autapomorphies of the vestiture [2'], femora [24], and tarsi [27'], and four homoplasious characters [+18, +30', +41, -42]. The tarsi of the species in the genus are somewhat incrassate distally which indicates a possible relationship with the bryocorines. The one new genus in this study, Glarisia, is clearly defined by the autapomorphies of the male genitalia [34, 35, 43] and its recognition as a supraspecific taxon is justified.

The group, Campyloneuropsis +....+ Nesidocoris, is defined by three autapomorphies, i.e. the elongate-oval body shape [1], the eyes extending to the buccule [8'], and the osteole is contiguous with the posterior margin of the metaepisternum, which is a feature that has a similar state in the Eccritotarsini (Bryocorinae). There

are three homoplasious characters [+7, +10, -20] indicating other potential relationships. The sister-group, Engytatus and Nesidocoris, is defined by one autapomorphy (dorsal margin of the genital aperture is not entire, [33']). Furthermore, the male pygophore is deeply dissected [+31]. The genus Nesidocoris is defined only by characters of the male genitalia [36, 38'', +41, +45], and the male vesica is perhaps the most defining character (see fig. 190). The females of this genus and Engytatus are not separable except for certain internal female genitalia characters. However, the apomorphies of Engytatus [-31', 37, +48] are considered sufficient to separate the latter genera and consider them as separate monophyletic genera.

The sister taxa, Campyloneuropsis and Singhalesia, are defined by one autapomorphy, i.e. the metafemora are dorsoventrally expanded [25]. These two genera are recognized as separate, although they are saliently almost identical. The genus Singhalesia is strongly defined by numerous autapomorphies of the male genitalia [32, 39, 41', 47], and Campyloneuropsis is defined by one autapomorphy of the male genitalia [50]. One homoplasious character [-51], the connected sclerotized rings of the females (e.g. fig. 203) is considered homologous to that found in Felisacus, although a more thorough analysis of the female internal genitalia in the dicyphines and

bryocorines is required.

Biogeographic analysis:

Since Croizat et al (1974), there has been considerable discussion about the nature of biogeographic hypotheses and the methods of analysis (Ball, 1975; Nelson and Rosen, 1981; Nelson and Platnick, 1981). In the recent literature, views have been largely polarized into either dispersal (Brundin, 1981), or vicariance (Nelson and Platnick, 1981) paradigms. Very few have considered the importance of both (Ball, 1975), and there has been a tendency for the acceptance of the vicariance approach because of the difficulty in falsifying dispersal hypothesis.

Ball (1975) has aptly designated three phases in biogeography, i.e. descriptive, narrative, and analytical. The analytical phase is the most complex requiring a knowledge of the distribution and phylogeny of distantly related or unrelated taxa (Humphries, 1981). It is beyond the scope of this study to compare the phylogeny and distribution of the dicyphine genera with other organisms. For this reason I have restricted the following biogeographic considerations to a narrative of the possible factors involved in producing the present distribution of dicyphines. I have used the techniques recommended by Morse and White (1979), without making any a. priori assumptions regarding vicariance or dispersal,

but rather, I have analyzed the area relationships (cladistic relationships) relative to the general patterns of area connections (earth history information). I have made no attempt to consider centers of origin or routes of dispersal.

In Figure 276 I have listed the regional areas occupied by each dicyphine genus (also included in Table 3), and the presumed occupied areas of the hypothetical ancestors.

The genera Campyloneuropsis and Singhalesia both have predominately tropical, Gondwana distributions, and are narrowly sympatric in the Ethiopian (east Africa) and Oriental (Ceylon) regions. The sister group association of these genera indicates a probable Gondwana origin. As they are only narrowly sympatric, it is possible that their ancestor was widespread throughout Gondwanaland, and these extant genera are vicariated groups. If so, this would indicate an ancient age for these taxa, at least 100 my BP (Raven, 1979), with the separation of India from Antarctica and Africa.

Campyloneuropsis is chiefly distributed in the Ethiopian (nine species), and the Neotropical (three species) regions. These two species assemblages are quite distinct and morphological studies indicate probable, regional monophyly for each group. If these are vicariated groups, then these are also very old

TABLE 3: Regional distribution of the Dicyphinae genera,
and the outgroup Felisacus.

The following abbreviations for biogeographic
regions are used in the table.

P	Palearctic
N	Nearctic
E	Ethiopian
NE	Neotropical
O	Oriental
A	Austalasian
OC	Oceanic

TABLE 3:

BIOGEOGRAPHIC REGION

GENUS	P	N	E	NE	O	A	OC
<u>Felisacus</u>		X			X	X	
<u>Dicyphus</u>	X	X	X				
<u>Campyloneura</u>	X						
<u>Macrolophus</u>	X	X	X	X			
<u>Chius</u>				X			
<u>Tupiocoris</u>		X		X			
<u>Cyrtopeltis</u>	X		X		X		
<u>Usingerella</u>		X					
<u>Setocoris</u>					X		
<u>Glarisia</u>		X					
<u>Nesidocoris</u>			X	X	X	X	X
<u>Engytatus</u>			X	X		X	X
<u>Singhalesia</u>			X		X	X	X
<u>Campyloneuropsis</u>			X	X			

assemblages, because the separation of Africa and South America is estimated to be between 120 - 140 my BP (Dietz and Holden, 1970; Smith and Briden, 1977), and this separation was great in the Cretaceous (Dietz and Holden, 1970).

The genus Singhalesia contains only five species, two of which occur in Ceylon. There is some difficulty in analyzing the distribution of this genus, as I suspect that some of the species, such as, indicus and obscuricornis, may have been introduced into the Australasian and Oceanic regions (both are known from weedy solanaceous plants). If these distributions are not due to introductions, the track of this genus supports the contention that a warm temperate or subtropical migration pathway existed in Gondwanaland (Raven, 1979). This is supported by the absence of Singhalesia in western and southern Australia. In Map 15 I have shown the distribution of Singhalesia extending to South Africa. This is based on three undescribed species, and suggests that a cool temperate migration route existed via Antarctica. This would require a minimum age of 125 my BP to account for the separation of Africa and Australia (Raven, 1979). This could be tested by searching for Singhalesia species in the more temperate regions of Australia.

The sister group relationship of Engytatus and Nesidocoris seems to be significantly confirmed by morphological studies (fig. 275), and the genera are apparently sympatric in the Ethiopian, Neotropical, Australasian, and Oceanic regions (fig. 276). This sympatry, however, could be based on various species introductions. The distributional limits of Nesidocoris are poorly understood. Only one species, tenuis, is recorded in the Neotropical region, however, this species has been broadly introduced on a global basis (probably cosmopolitan) and as yet its area of endemism cannot be estimated. Furthermore, 65% of the species of Nesidocoris are known from the Ethiopian region (predominately in central-east Africa) and 30% are known from the Oriental region. Conversely, 52% of the species of Engytatus are known from the Pacific Basin, and 41% are endemic to the Neotropical region. Both genera are represented by one species in north-east Australia, however the Engytatus species, nicotianae, is also known from the Pacific Basin, New Guinea, New Caledonia, and Java, and it may be an introduction into Australia. This evidence indicates that these two genera are only narrowly sympatric, and it is possible that they represent vicariated groups (with subsequent dispersal). This complies with a Gondwanaland hypothesis, with the common ancestor of these taxa being distributed broadly in the latter

region. This explanation, however, also requires a very ancient age for these genera.

The common ancestor of the Campyloneuropsis + Singhalesia + Engytatus + Nesidocoris group would necessarily have occupied Gondwanaland if a vicariance hypothesis is proposed (although the ancestors leading to these pairs of sister taxa do not comply with a vicariance explanation as both have been shown to occupy the same areas (fig. 276)).

The genera, Setocoris and Usingerella, are broadly disjunct with the former endemic to Australia and the latter restricted to the western Nearctic. I indicated previously that there is some doubt as to the validity of this sister group relationship, as it based on a homoplasious character state (fig. 275). If we assume that this relationship is correct, then the disjunction of these two genera represents either, a dispersal event, or one of the genera was formerly distributed (or remains undiscovered) in South America. This migration track is quite possible because South America and Australia were connected via Antarctica until the Eocene (48 my BP; Raven, 1979).

The genus Glarisia is known from the western United States, and its relationship with Usingerella is probably correct (fig. 275). The species of this genus are not apparently sympatric, with the former restricted

to the eastern side of the Sierra Nevada Range, and the latter found west of the Sierras (in the southern regions of its distribution). This again would suggest a vicariance explanation.

The genera, Cyrtopeltis and Tupiocoris are placed as sister-groups in the previous analysis, however, their relationship is based on one homoplasious character (fig. 275). The genera are disjunct, with Tupiocoris restricted to the Western Hemisphere, and Cyrtopeltis distributed in the Palearctic, Ethiopian, and Oriental regions. This suggests a Euramerica land connection, with a subsequent track (for Neotropical Tupiocoris species) extending into South and Central America. There was a north temperate connection between the Nearctic and Palearctic regions until the Eocene (Smith and Briden, 1977). This suggests that these genera are also vicariated groups. The genus Tupiocoris is now represented by fourteen species in the Nearctic, and three species in the Neotropical region. However, numerous species remain to be described from the latter region. The Neotropical species form a distinct assemblage (based on the multilobed vesica) and probably show regional monophyly. In the Eocene, South America was more accessible to interchange with North America (Raven, 1979), which roughly correlates with the vicariance of Cyrtopeltis and Tupiocoris.

The common ancestor of the group, Campyloneuropsis + + Tupiocoris, is considered to have a Pangaeic distribution (fig. 276), however, this is difficult to reconcile with the possible origin of the Miridae. Leston (1961) suggests a possible Tertiary origin for the Miridae, although he offered no evidence for his conclusions. Schuh (1976) was only aware of one fossil Miridae, Archaeofulvius Carvalho, which gives a minimum age of 60 million years for the subfamily Cyalpinae (Miridae). There are, however, fifteen described mirid fossil genera, most of which are known from amber (Scudder, 1890; Larsson, 1978). The oldest known mirid fossil genus, Miridoides Becker-Migdisova, dates to the Jurassic (Rohdendorf, 1962), and this would indicate that primitive mirid subfamilies existed at least in the mid-Mesozoic. There is evidence to consider the Dicyphinae as a plesiomorphic mirid subfamily (based on thoracic pleural structure), however, all the species are known from angiosperms, which enter the fossil record in the Barremian stage of the Lower Cretaceous (130 my BP; Cronquist, 1981). This somewhat negates a Pangaeic origin for the Dicyphinae, and the Pangaea distribution of the Campyloneuropsis + + Tupiocoris common ancestor (and the more basal ancestors) cannot, at present, be regarded as vicariant patterns.

The genera, Macrolophus and Chius are sympatric,

however, the former genus is not fully resolved and I refrain from commenting on the distribution of these genera until the taxonomy is more complete.

The basal placement on the cladogram (fig. 276) of the genera, Campyloneuropsis and Dicyphus, is more due to their unique features than to any subsequent synapomorphies between them or with the outgroup, Felisacus. Of interest is the distribution of the subgenera of Dicyphus (Maps 5, 6, 7, 8, 9). Only the Nearctic subgenus, Uhlerella, has a disjunct distribution with the remainder of the Dicyphus taxa (the others are broadly sympatric). Slater (1974) indicated that the eastern Nearctic species of Dicyphus were of Palearctic origin. I believe it is more reasonable to consider that the genus had a Larusian origin (the genus is almost entirely restricted to the Northern Hemisphere).

Host plant association analysis:

In seeking coevolutionary hypotheses, it is necessary to address the extent of phylogenetic interaction between lineages, and how they influence each other's evolution. Mitter and Brooks (1983) suggested a possible analytical method for host associations, using a logic analogous to that used in phylogenetic reconstruction of character evolution. By considering host plant associations as character sources, I have listed these data on the cladogram for the dicyphine genera to analyze

disjunctions and similarities of host plant family associations (fig. 277).

From this preliminary analysis there is no apparent coevolutionary trend. None of the genera, except for the smaller groups (e.g. Glarisia), show any restricted association with a particular plant family, and the majority of genera are known from many, and often, unrelated plant families. In fact, the dicyphines are known from five of six subclasses of dicotylodenous angiosperms (Cronquist's classification, 1981). This further supports the view that coevolution is not prominent in the dicyphines, and their associations are based more on ecological factors.

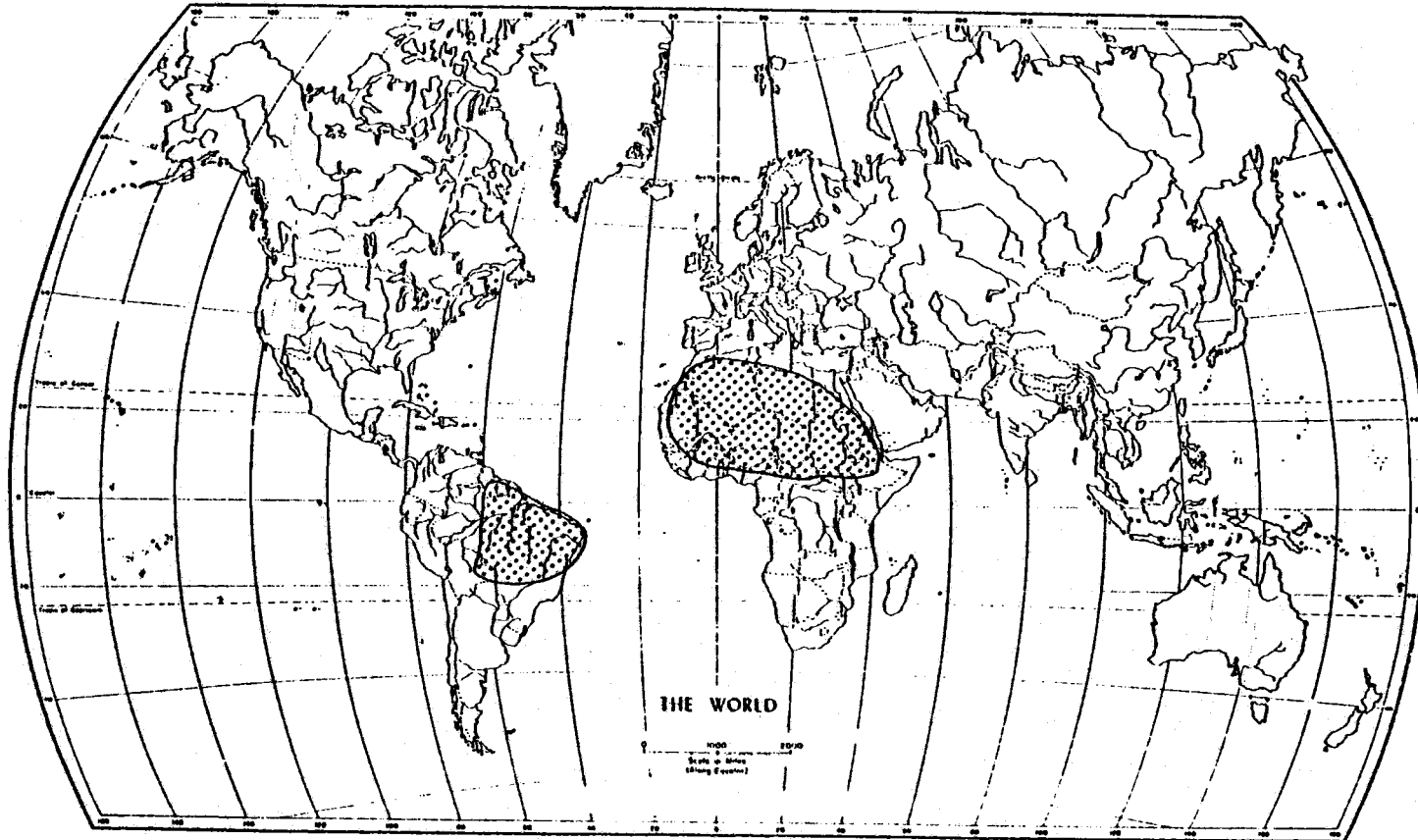
According to Metcalfe and Chalk (1950), the presence of glandular trichomes is not phylogenetically restricted in the angiosperms. Since the majority of dicyphines are associated with trichomate plants, it is more probable that their evolution is linked to the presence of one morphological attribute, i.e. presence of trichomes. As mentioned previously, the herbivore and predator loads on trichomate plants are apparently low, and it is possible that the dicyphines have occupied and successfully exploited an abundant nutrient source which is not easily utilized by other organisms. In a case such as this, the food source is probably not a limiting factor in the evolution of the group.

I consider it profitable to continue coevolutionary studies in the Dicyphinae, however, the species level for both the bug and the host plants, is probably the taxonomic level at which any patterns are present. The previously mentioned examples of Setocoris with its insectivorous host plant associations, and the Tupiocoris species associated with Ribes spp. are evidence enough to continue such studies.

MAP II. 1.

Campyloneuropsis.

1

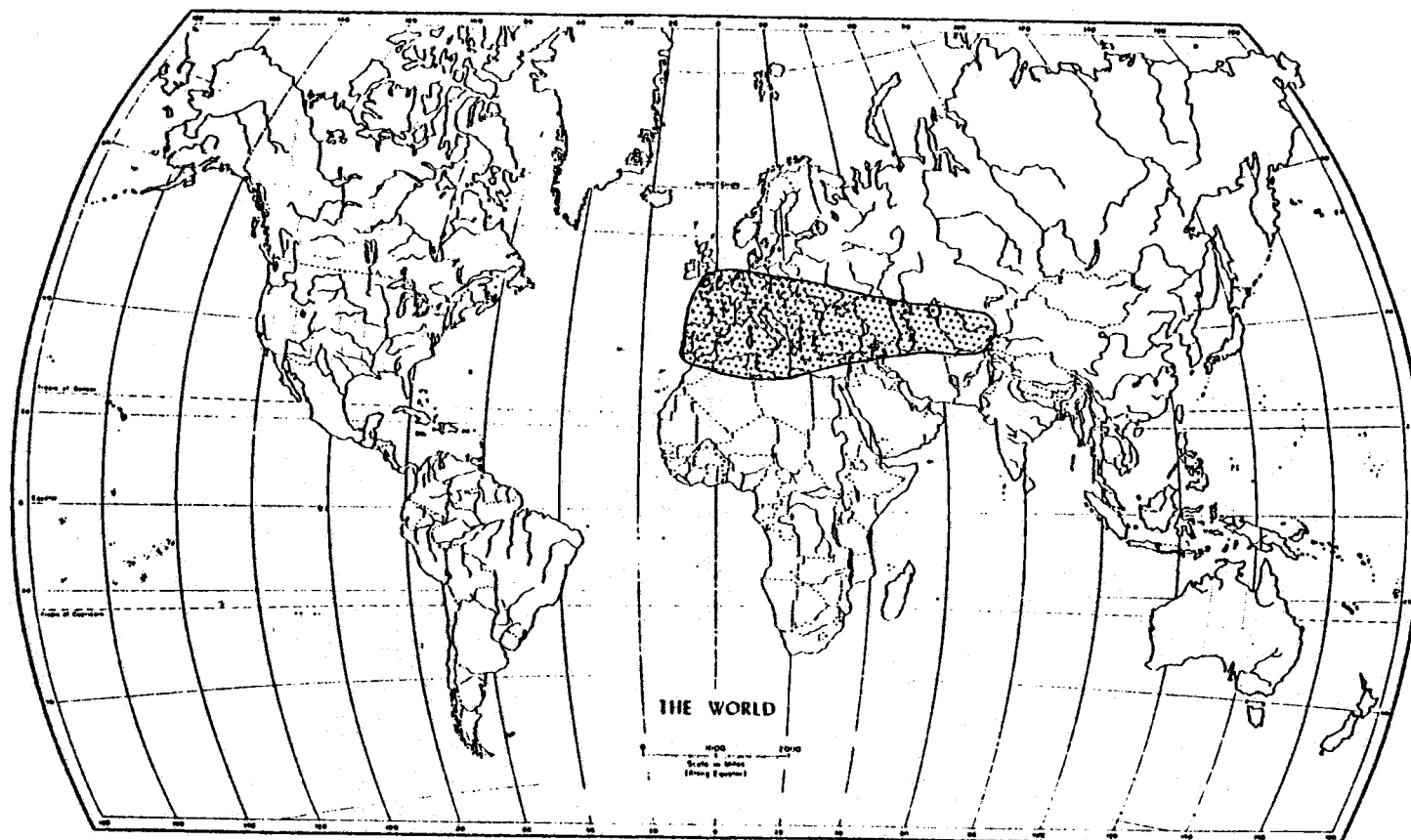


MAP II. 1.

MAP II. 2.

Campyloneura.

2

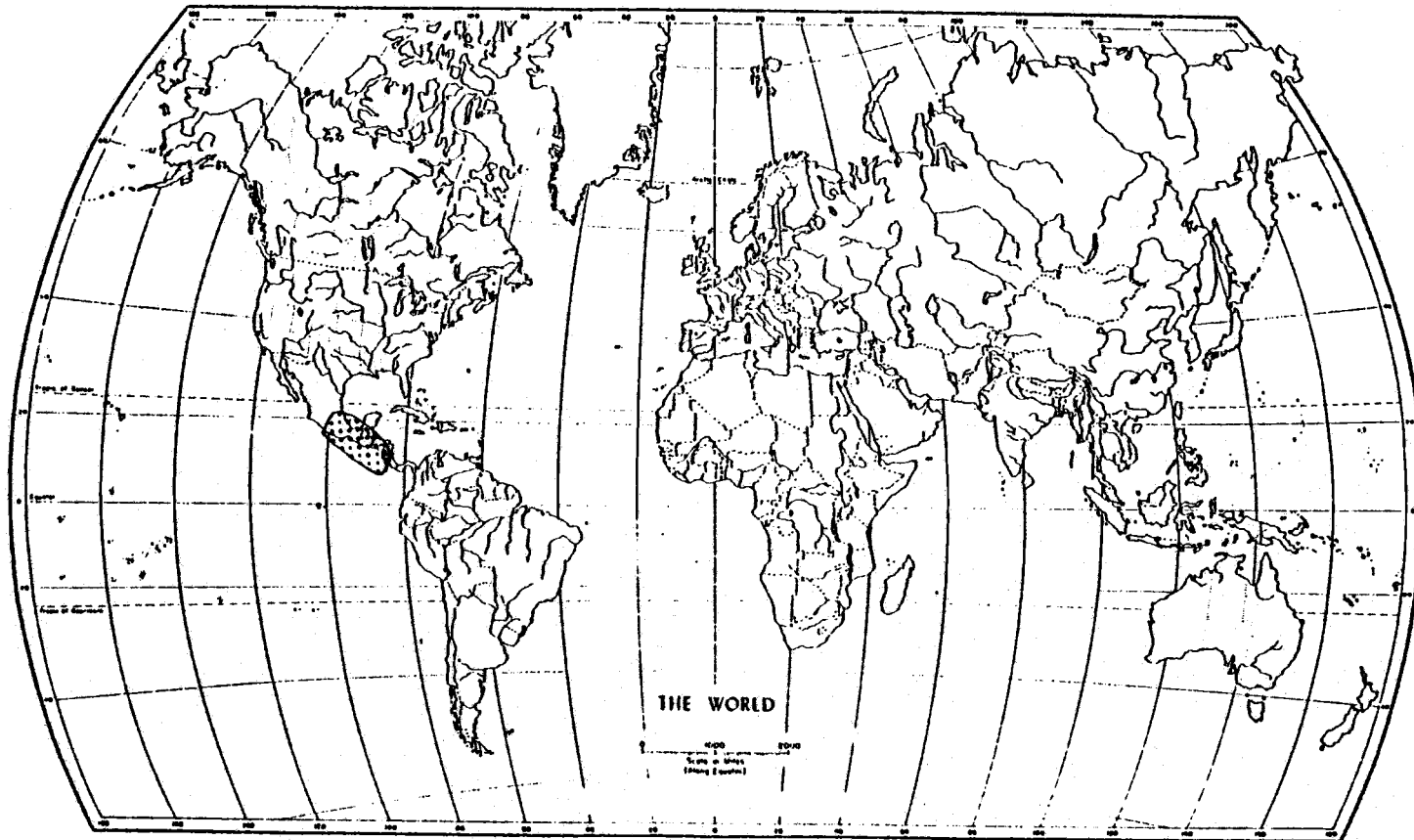


MAP II. 2.

MAP II. 3.

Chius.

3

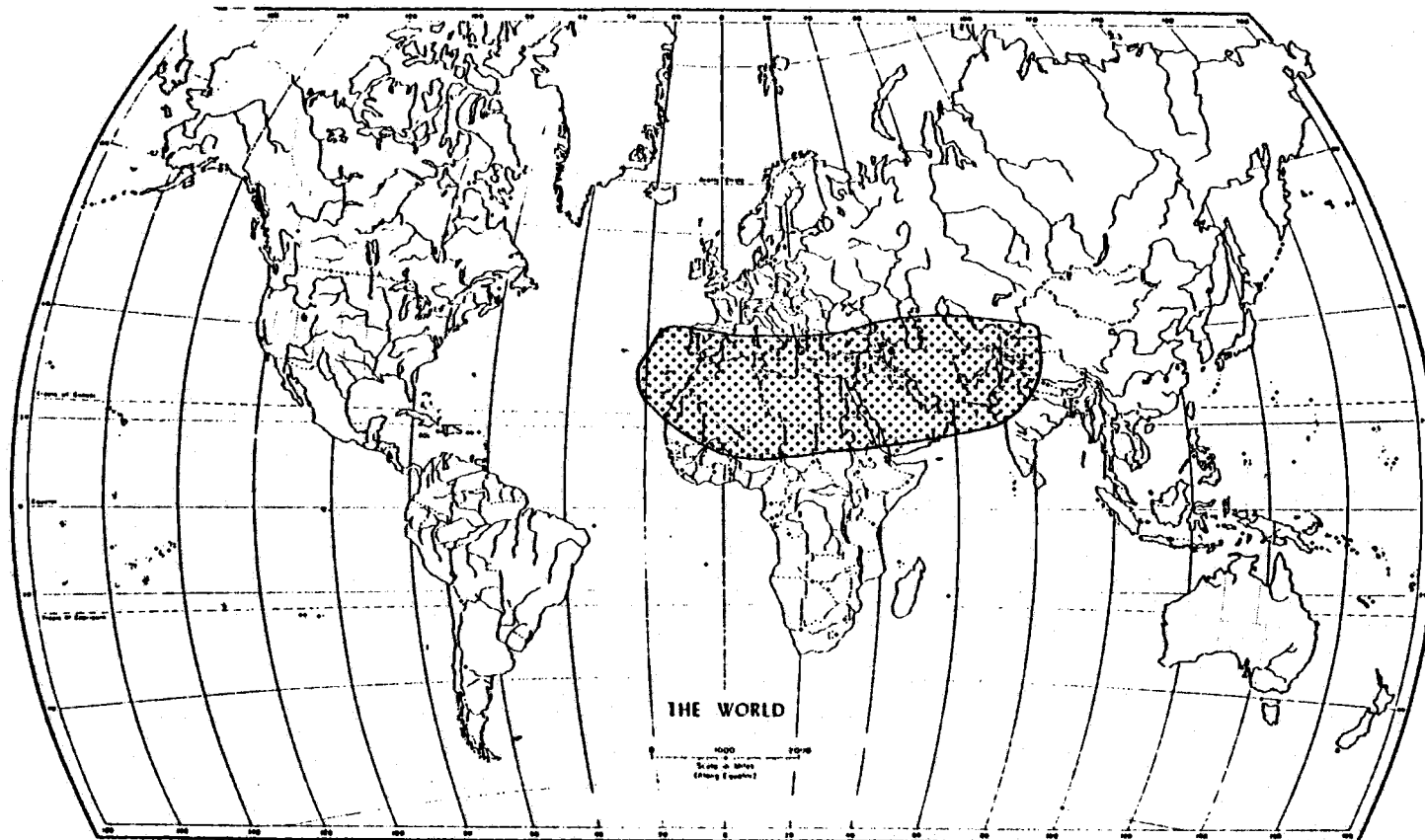


MAP II. 3.

MAP II. 4.

Cyrtopeltis.

4

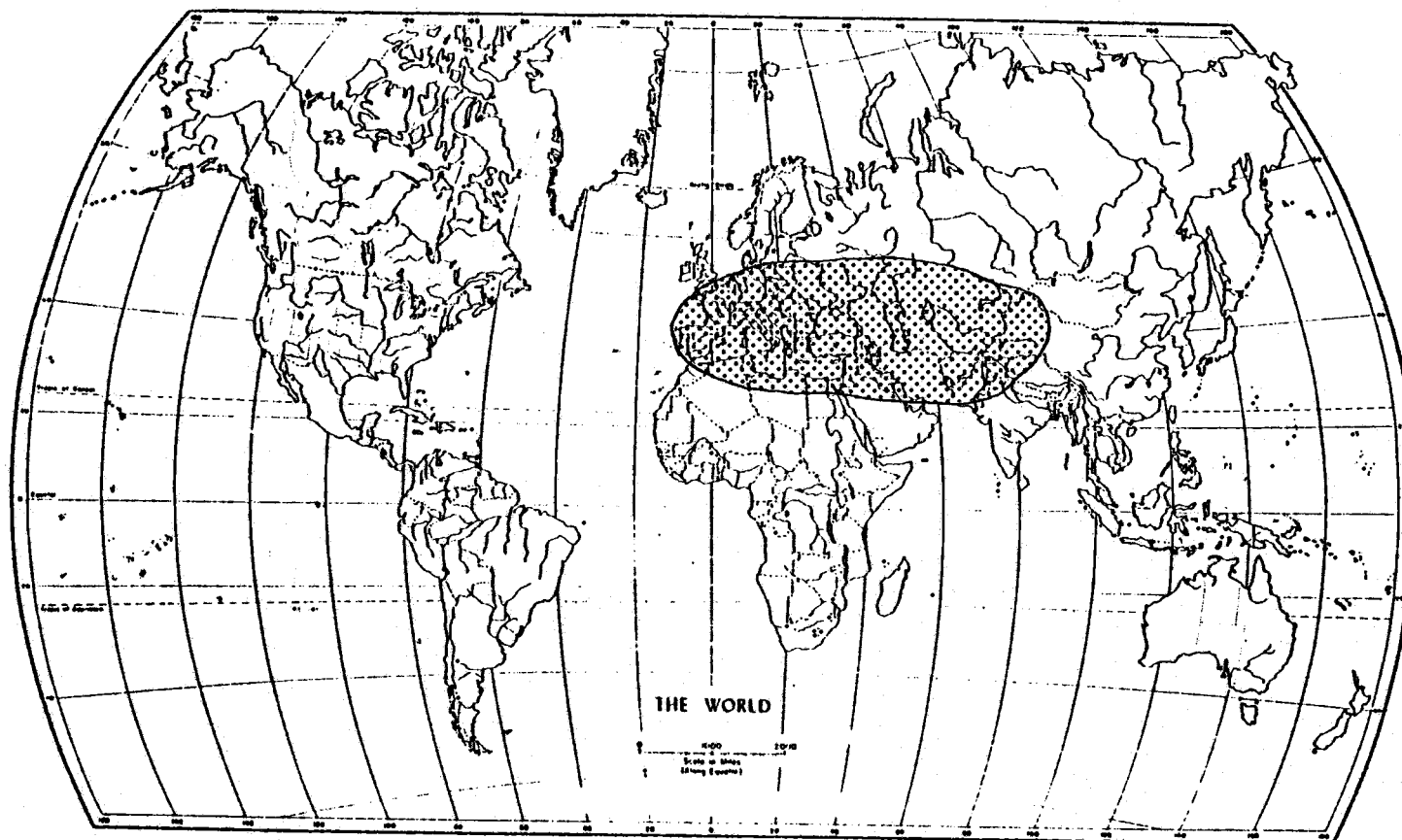


MAP II. 4.

MAP II. 5.

Dicyphus (Brachyceraea).

5

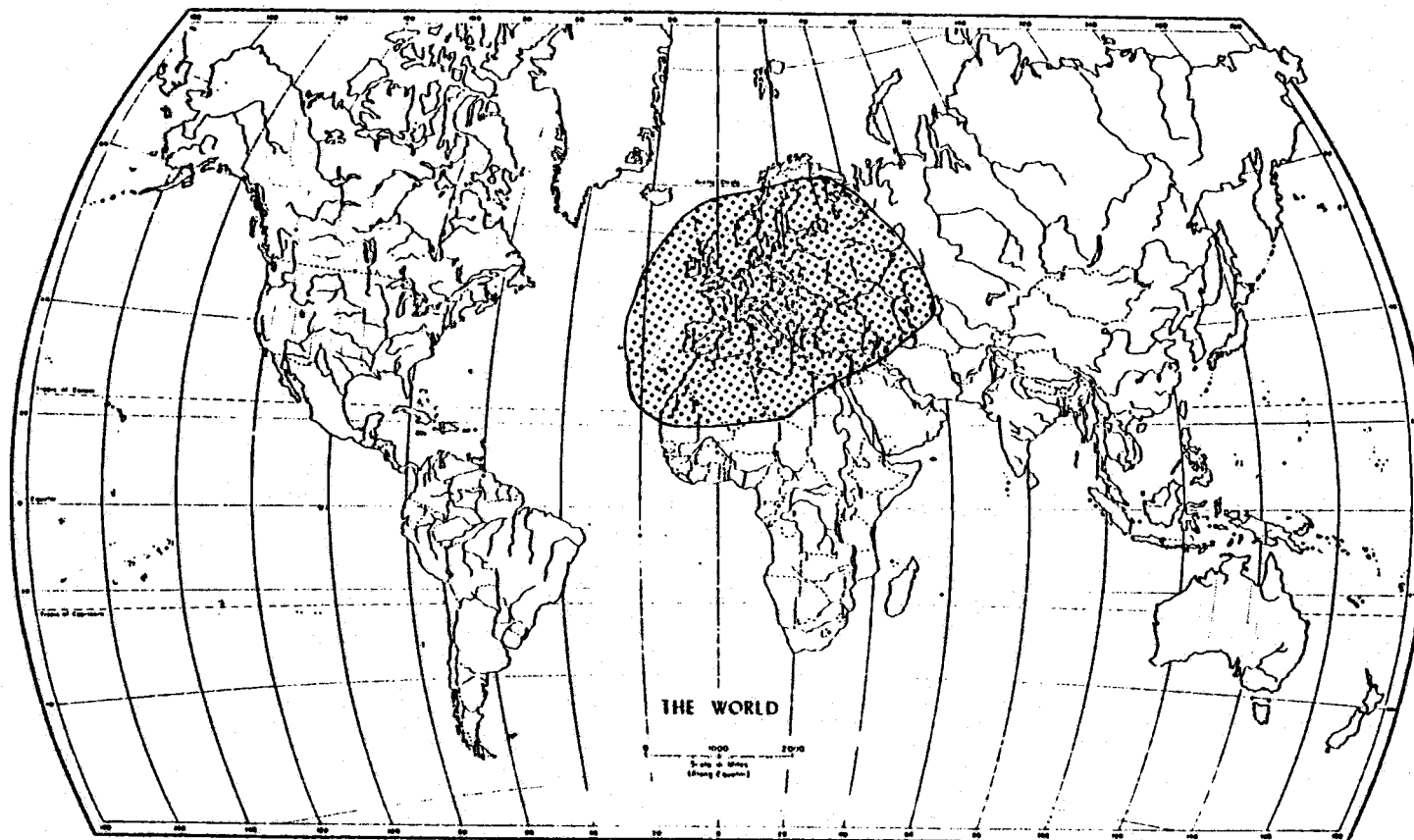


MAP II. 5.

MAP II. 6.

Dicyphus (Dicyphus).

6

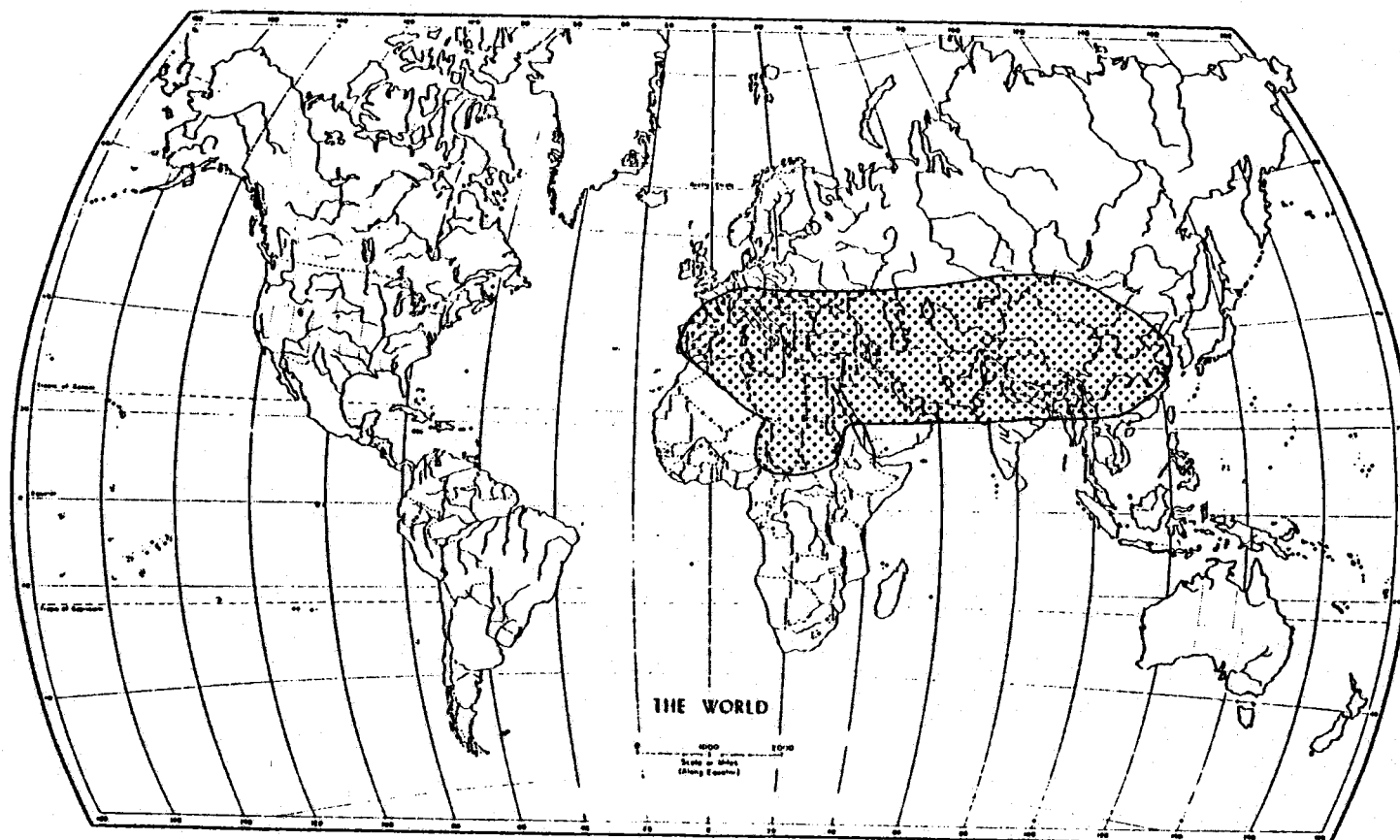


MAP II. 6.

MAP II. 7.

Dicyphus (Idolocoris).

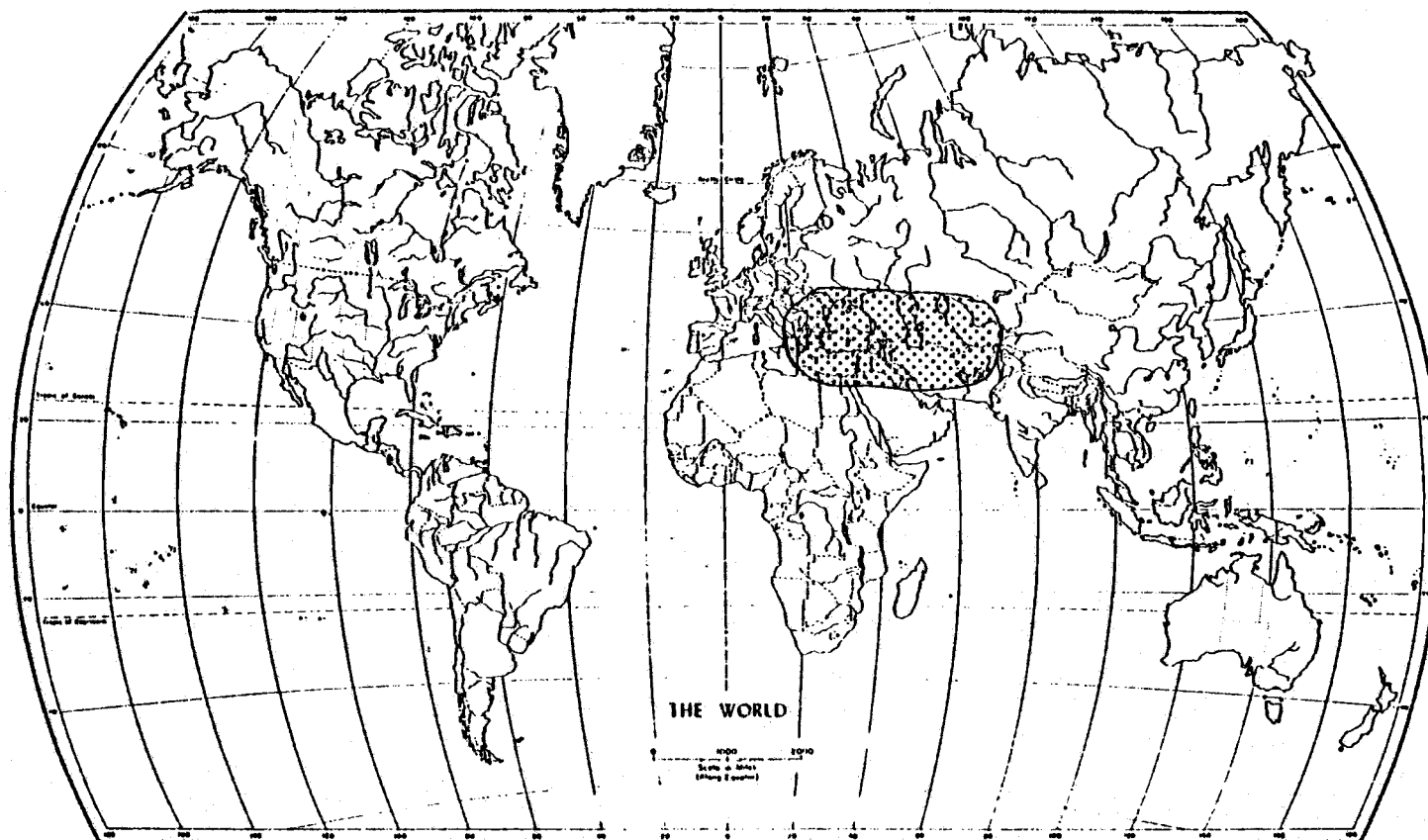
7



MAP II. 7.

MAP II. 8.

Dicyphus (Mesodicyphus).

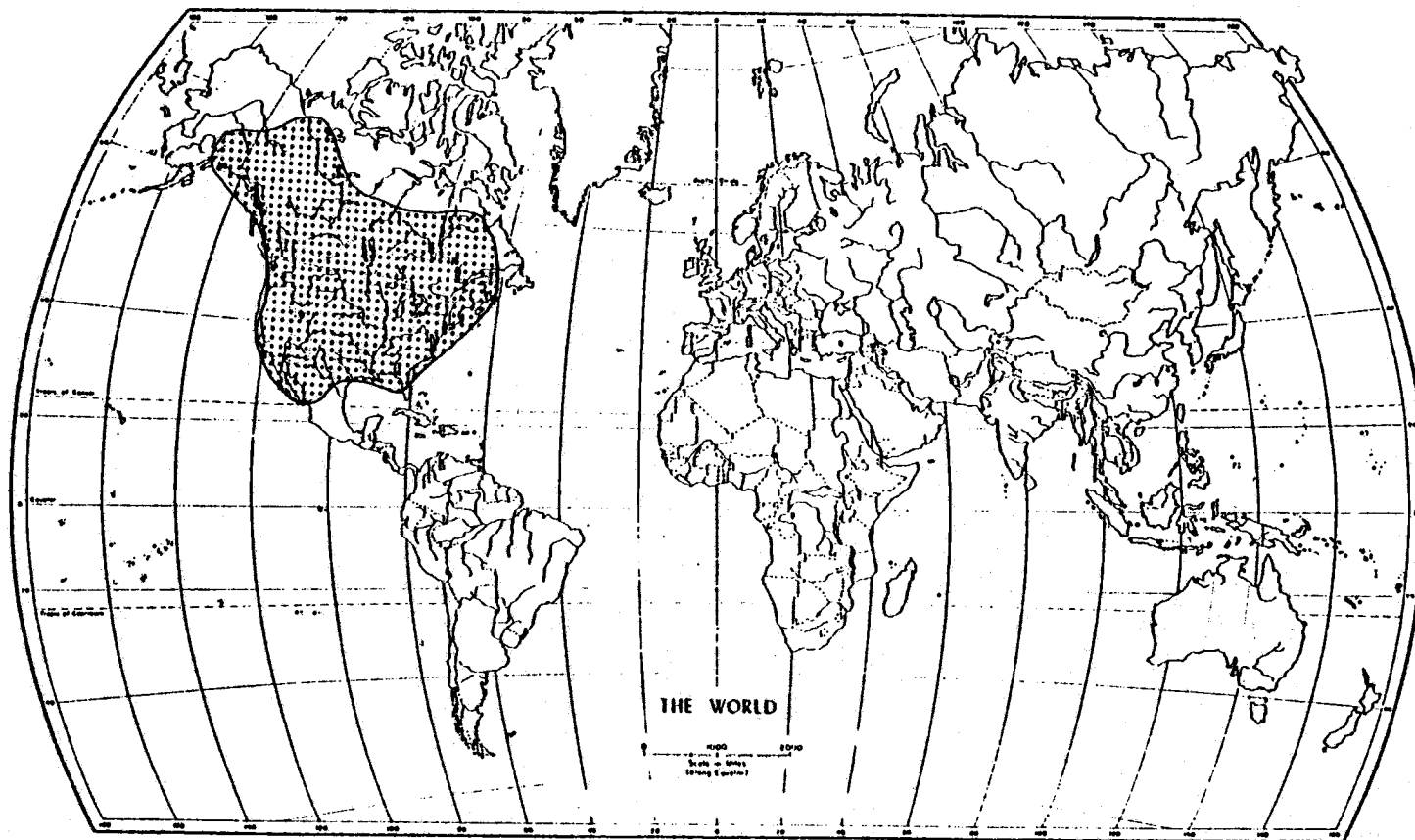


MAP II. 8.

MAP II. 9.

Dicyphus (Uhlerella).

9

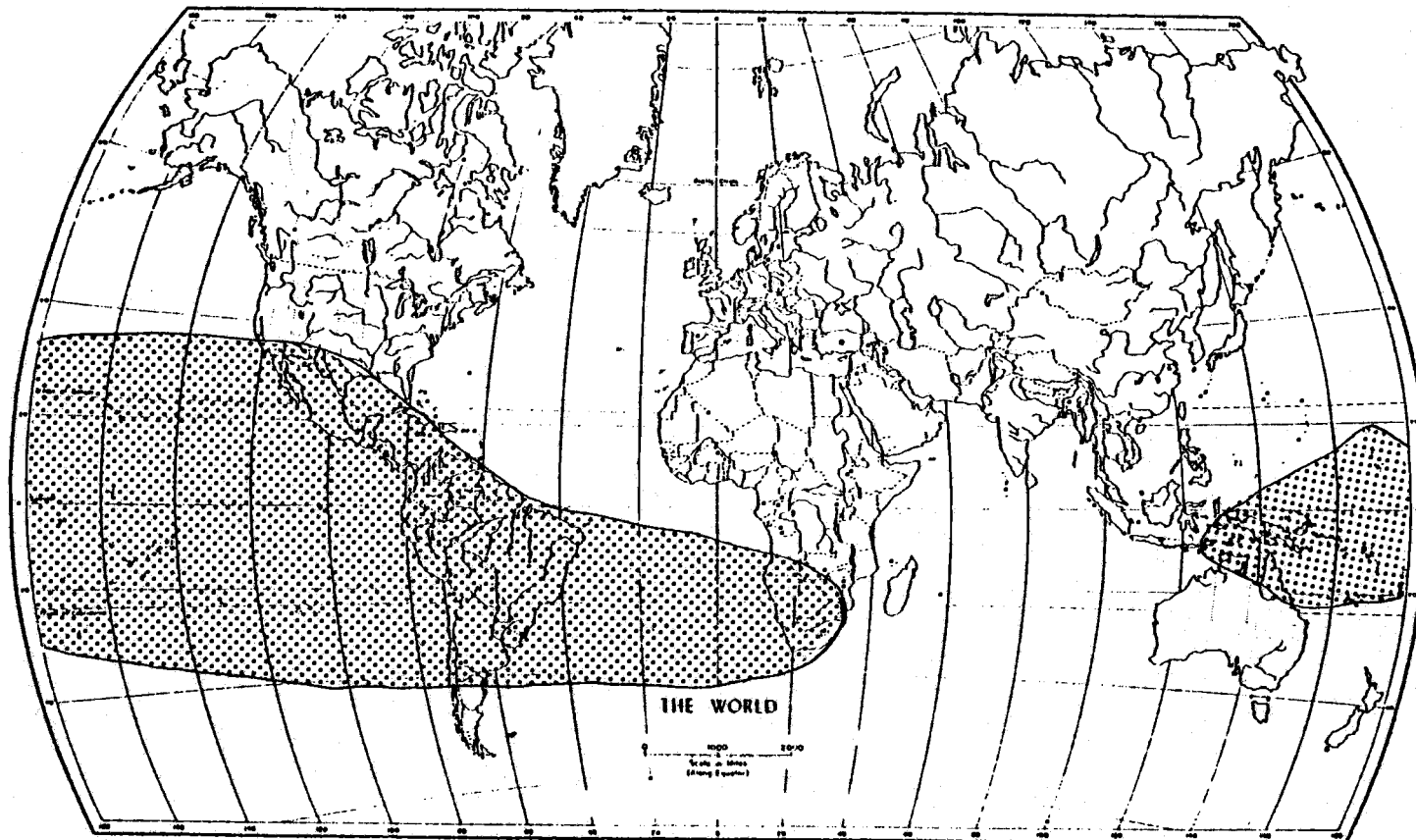


MAP II. 9.

MAP II. 10.

Engytatus.

10

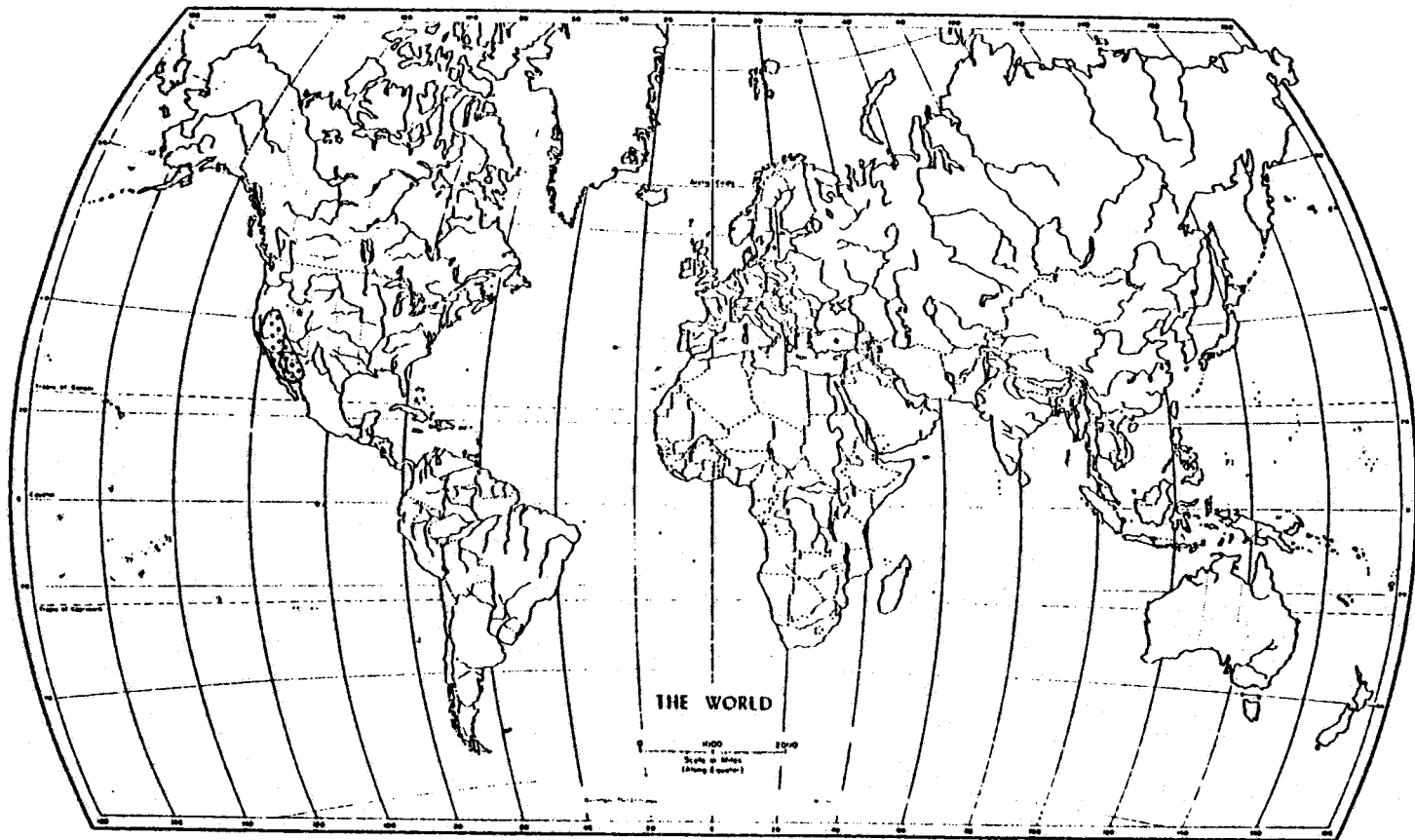


MAP II. 10.

MAP II. 11.

Glarisia.

11

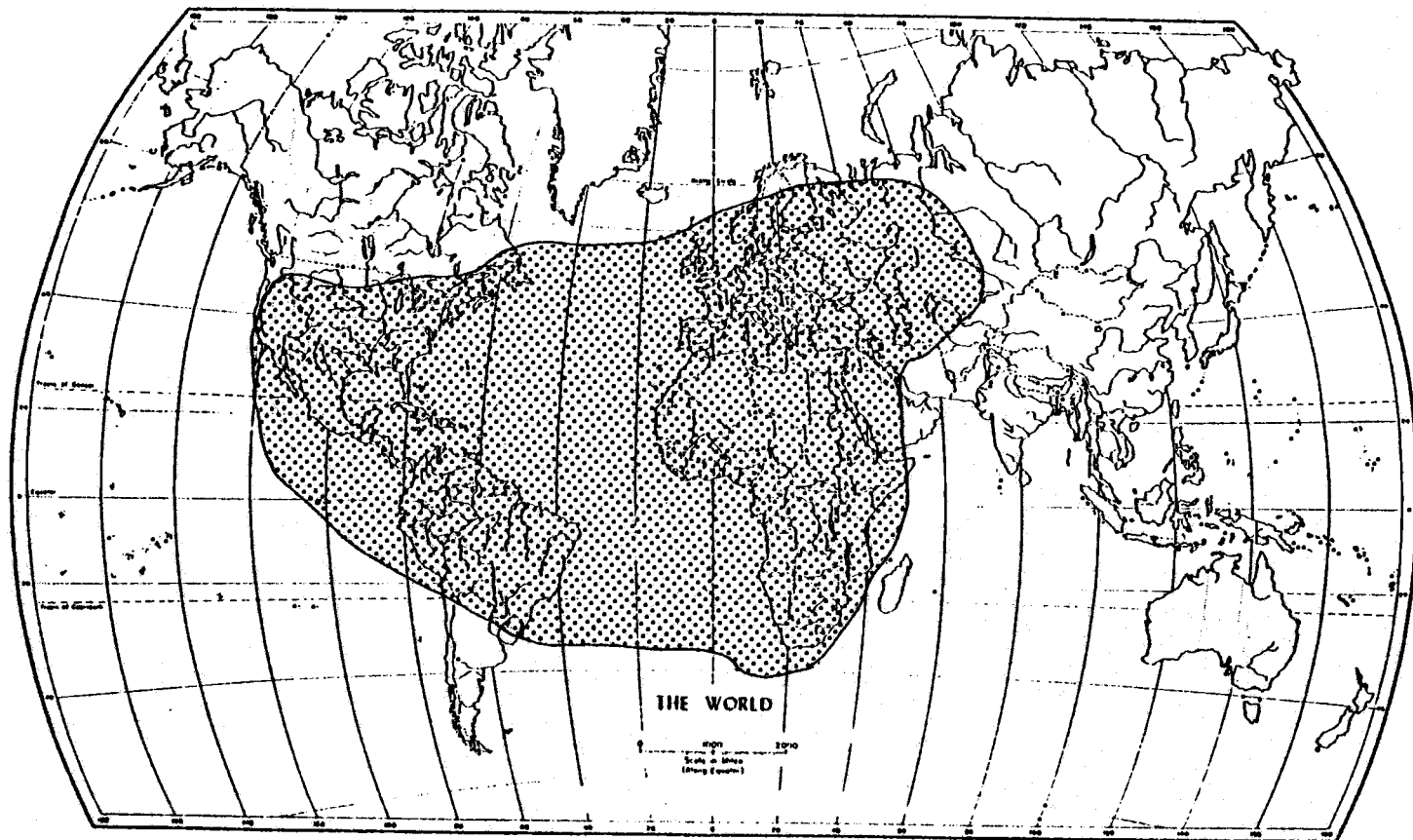


MAP II. 11.

MAP II. 12.

Macrolophus.

12

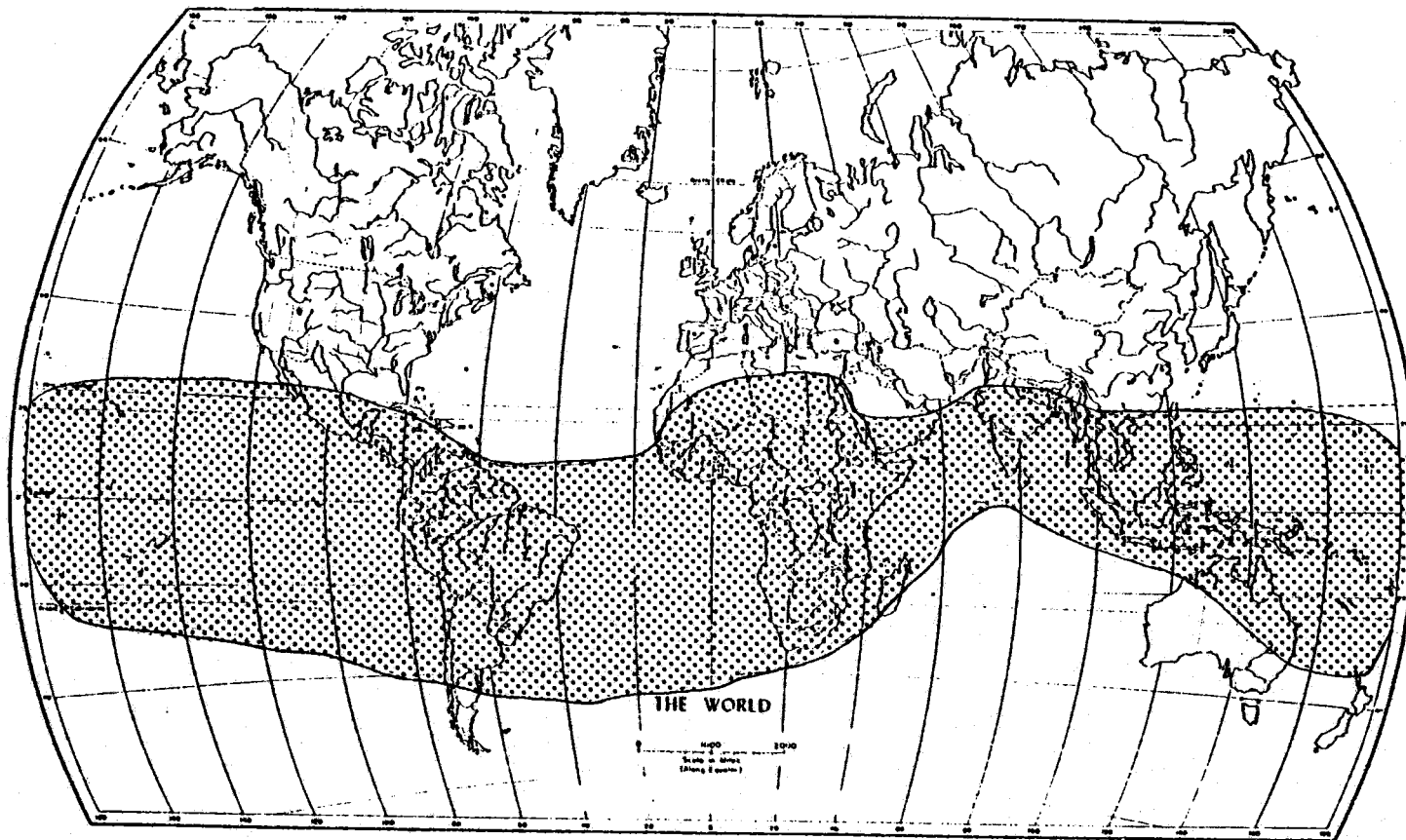


MAP II. 12.

MAP II. 13.

Nesidocoris.

13

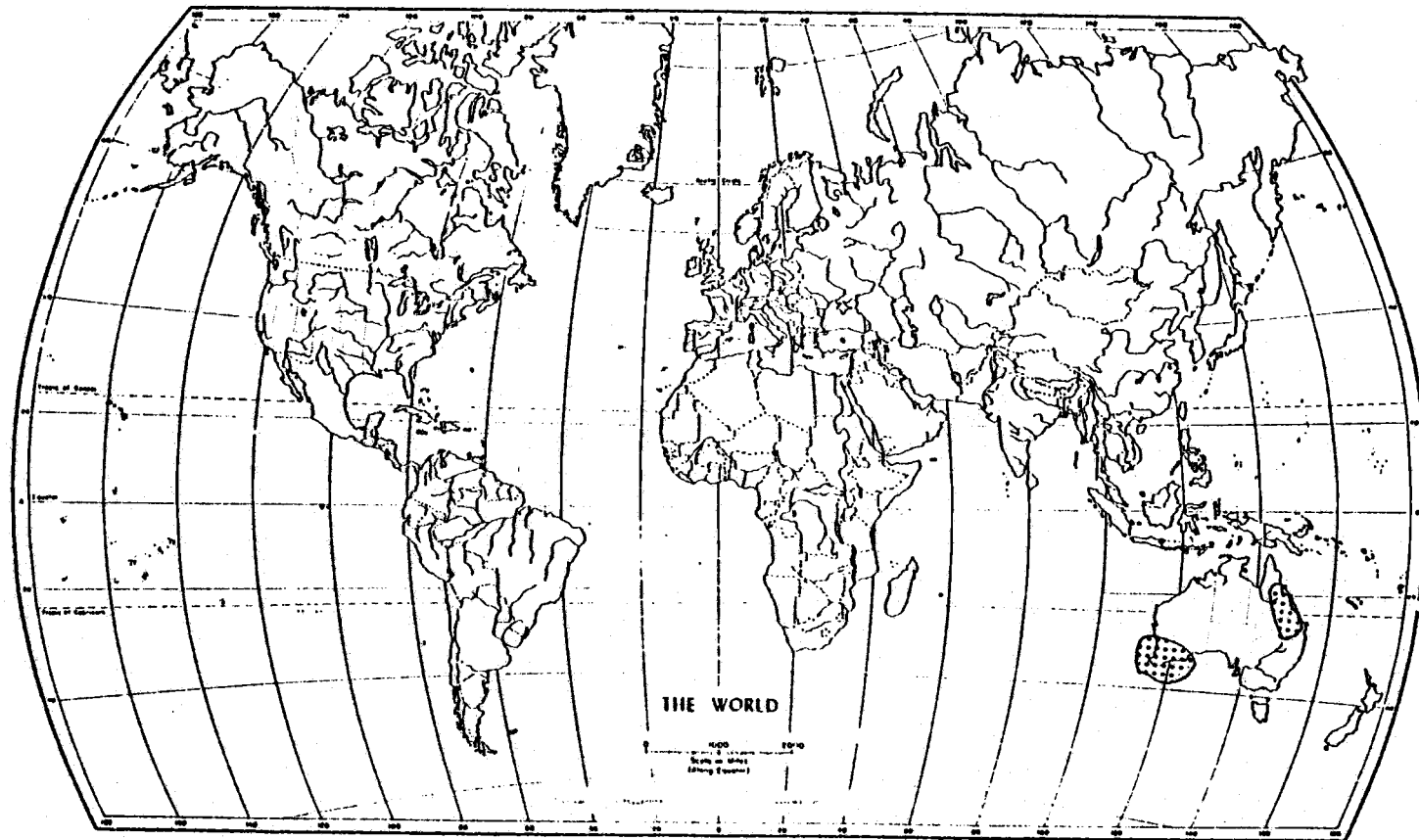


MAP II. 13.

MAP II. 14.

Setocoris.

14

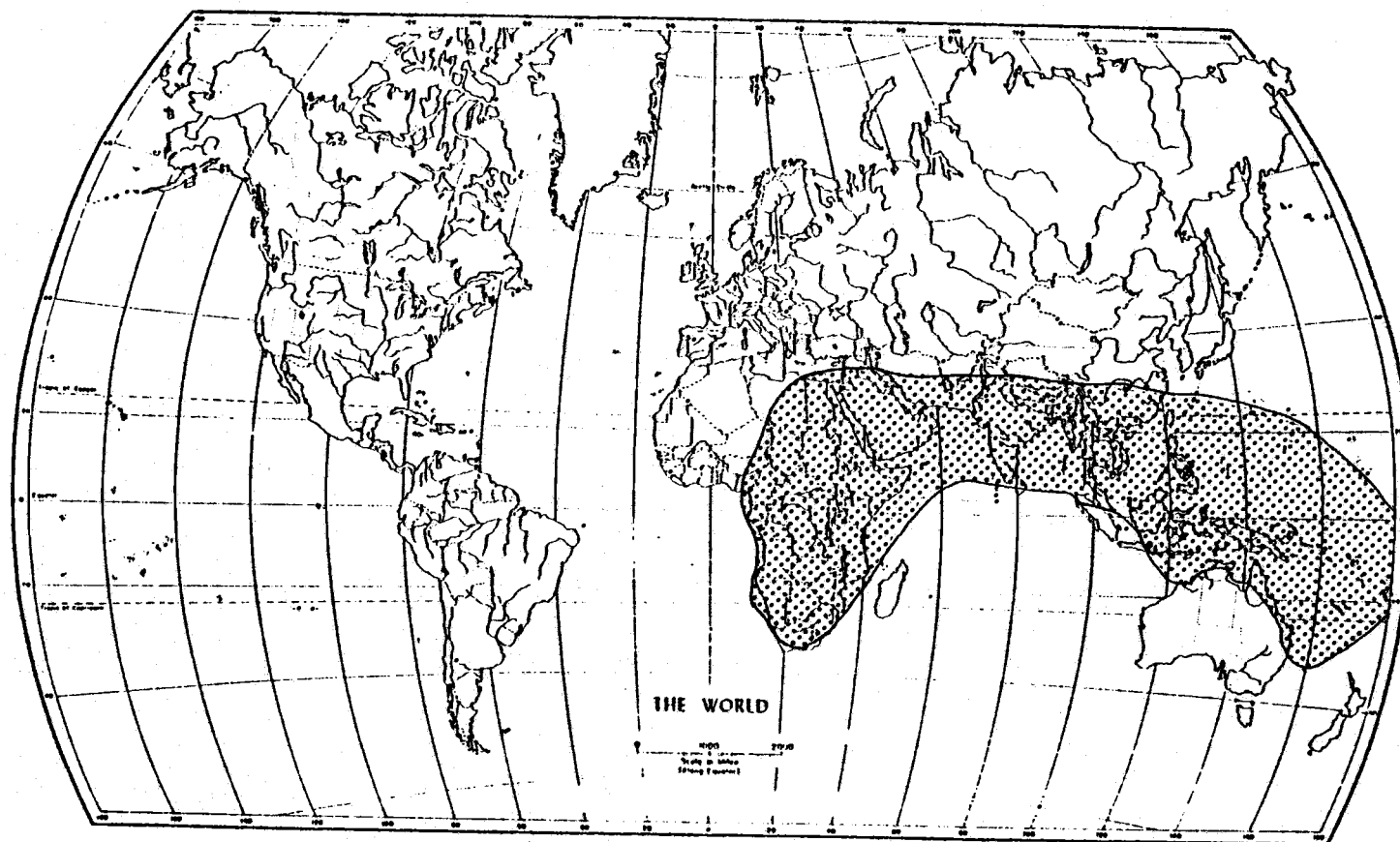


MAP II. 14.

MAP II. 15.

Singhalesia.

15

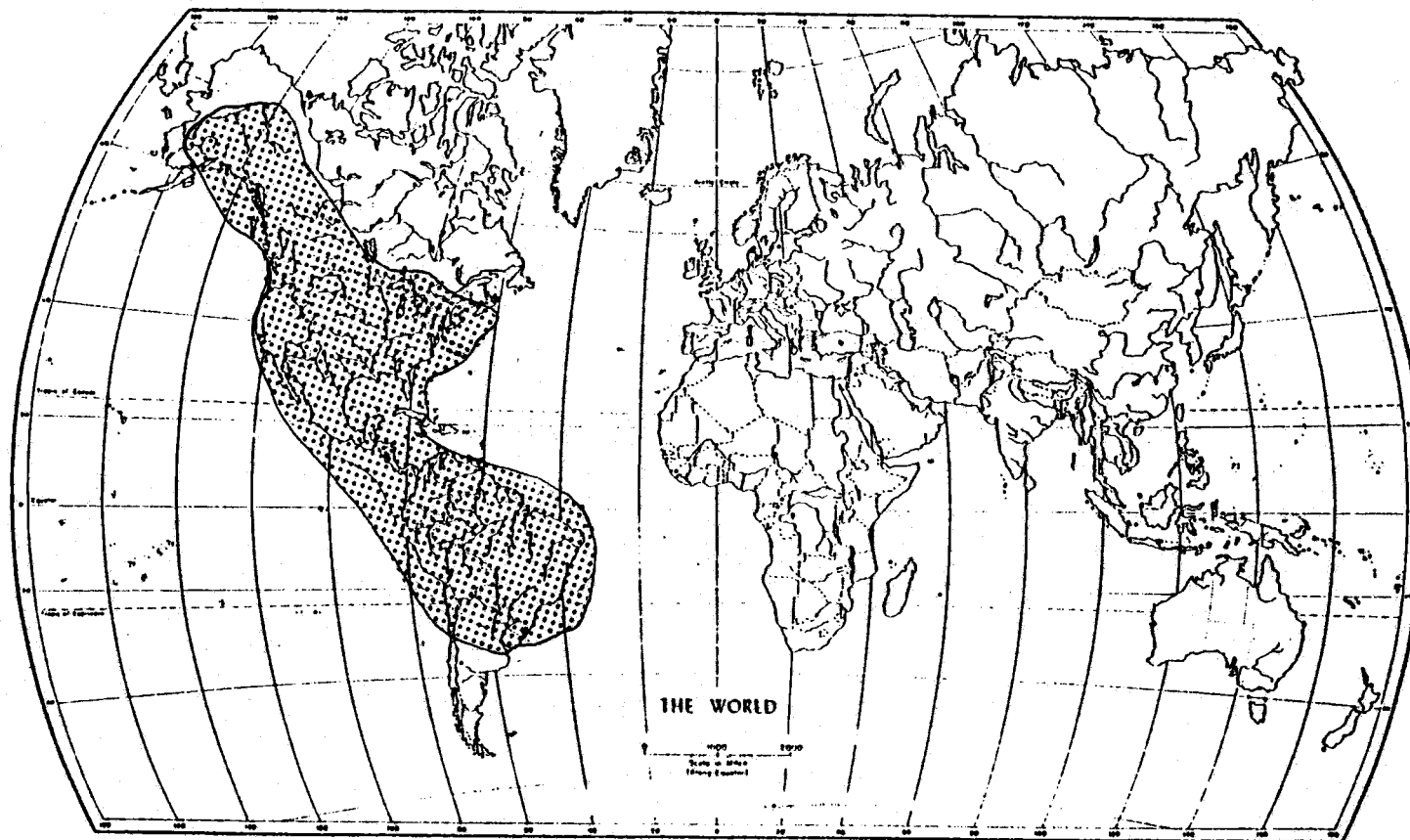


MAP II. 15.

MAP II. 16.

Tupiocoris.

16

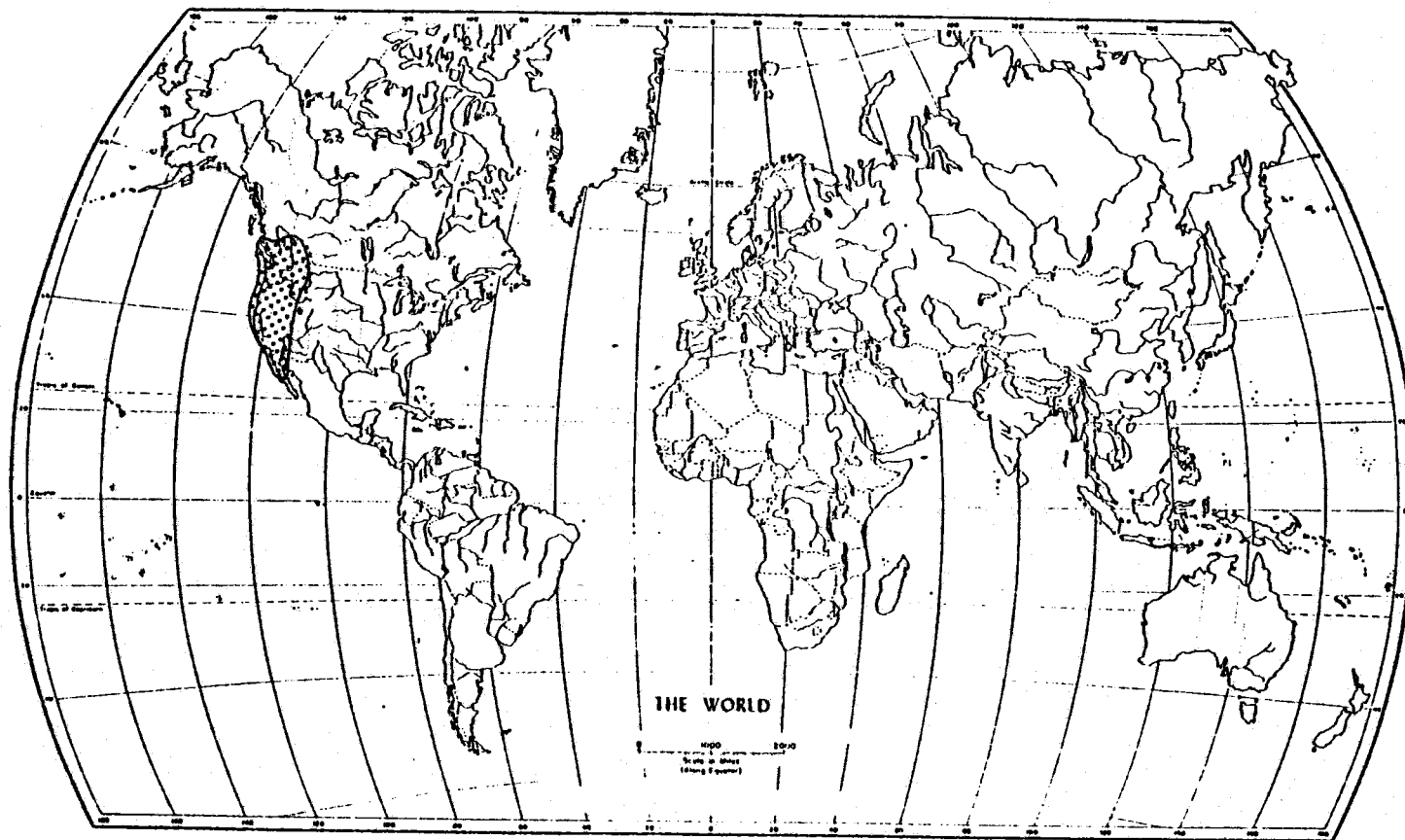


MAP II. 16.

MAP II. 17.

Usingerella.

17



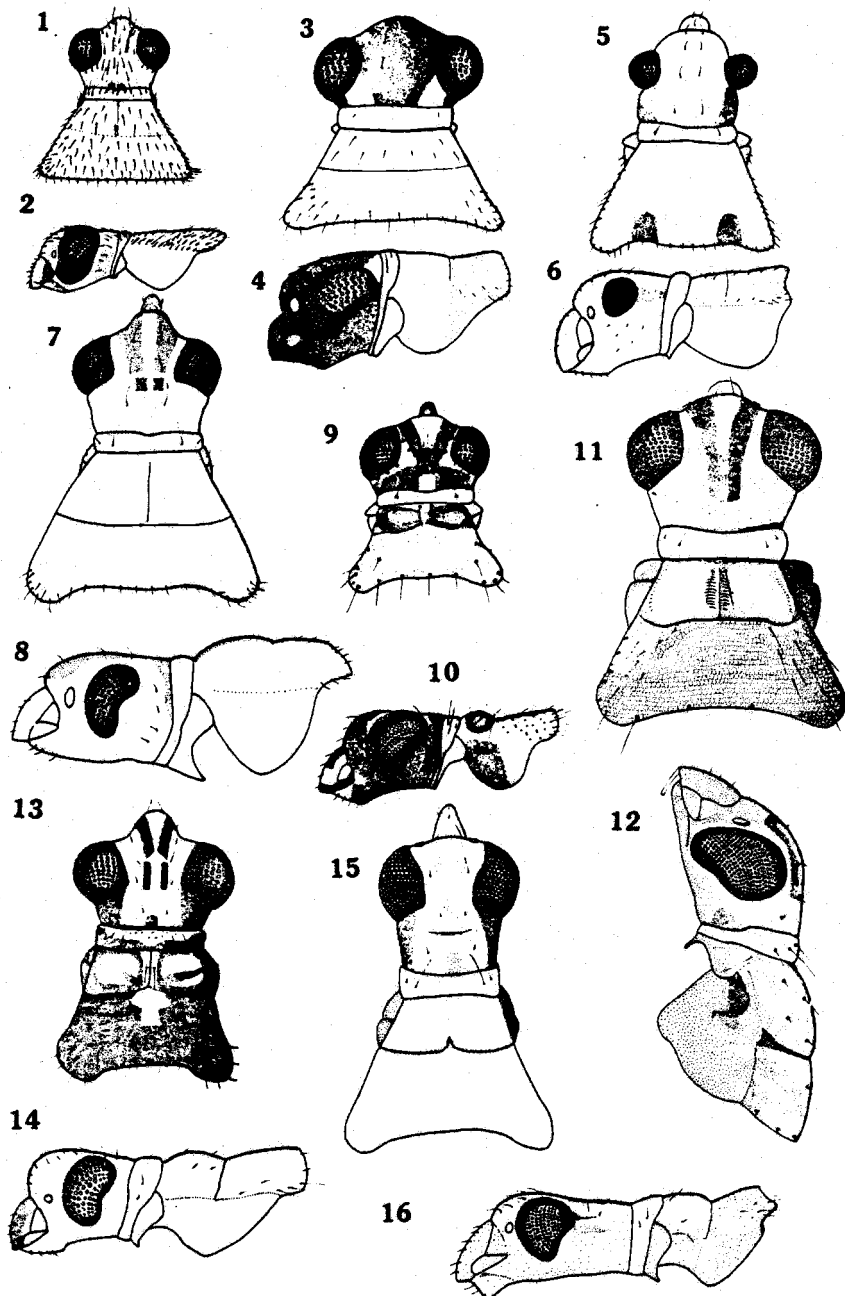
MAP II. 17.

FIGURES II. 1 - II. 16. Dorsal and lateral view of head
and pronotum.

Figures: 1, 3, 5, 7, 9, 11, 13, and 15, dorsal
view of head and pronotum, 16x.

Figures: 2, 4, 6, 8, 10, 12, 14, and 16, lateral
view of head, 16x.

- 1, 2. Campyloneuropsis annulata.
- 3, 4. Campyloneura virgula s. s.
- 5, 6. Chius maculatus.
- 7, 8. Cyrtopeltis geniculata.
- 9, 10. Dicyphus (Brachyceraea) globulifer.
- 11, 12. Dicyphus (Dicyphus) pallidus.
- 13, 14. Dicyphus (Idolocoris) pallicornis.
- 15, 16. Dicyphus (Uhlerella) famelicus.



FIGURES II. 1 - II. 16

FIGURES II. 17 - II. 32. Dorsal and lateral view of head
and pronotum.

Figures: 17, 19, 21, 23, 25, 27, 29, and 31,
dorsal view of head and pronotum, 16x.

Figures: 18, 20, 22, 24, 26, 28, 30, and 32,
lateral view of head and pronotum, 16x.

17, 18. Engytatus modestus.

19, 20. Glarisia melanocephala.

21, 22. Macrolophus nubilus s. s..

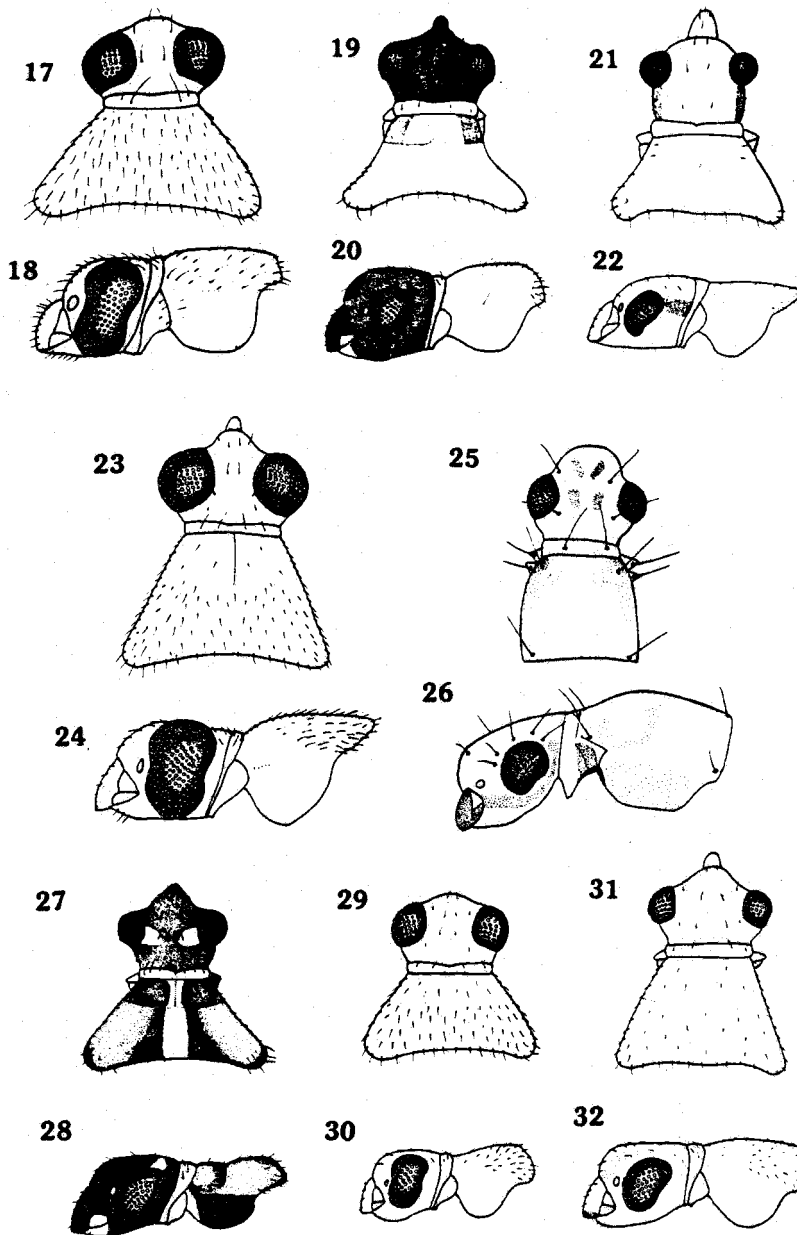
23, 24. Nesidocoris tenuis.

25, 26. Setocoris bybliphilus.

27, 28. Tupiocoris notata.

29, 30. Singhalesia indica.

31, 32. Usingerella simplex.



FIGURES II. 17 - II. 32

FIGURES II. 33 - II. 47. Thoracic structures.

Figures: 33 - 40: thoracic pleura, 40x.

B=basalare, ME=mesepimeron, MT=metaepisternum,

MTE=metaepimeron, O=osteole, P=postalare,

PD=peritremal disc, S=spiracle.

34. Chius maculatus.

35. Cyrtopeltis geniculata.

36. Dicyphus (Dicyphus) pallidus.

37. Engytatus modestus.

38. Engytatus rubescens.

39. Setocoris russelli.

40. Singhalesia indica.

41. Setocoris russelli, lateral view of
metafemur, 16x.

Figures: 42 - 47. Pretarsus.

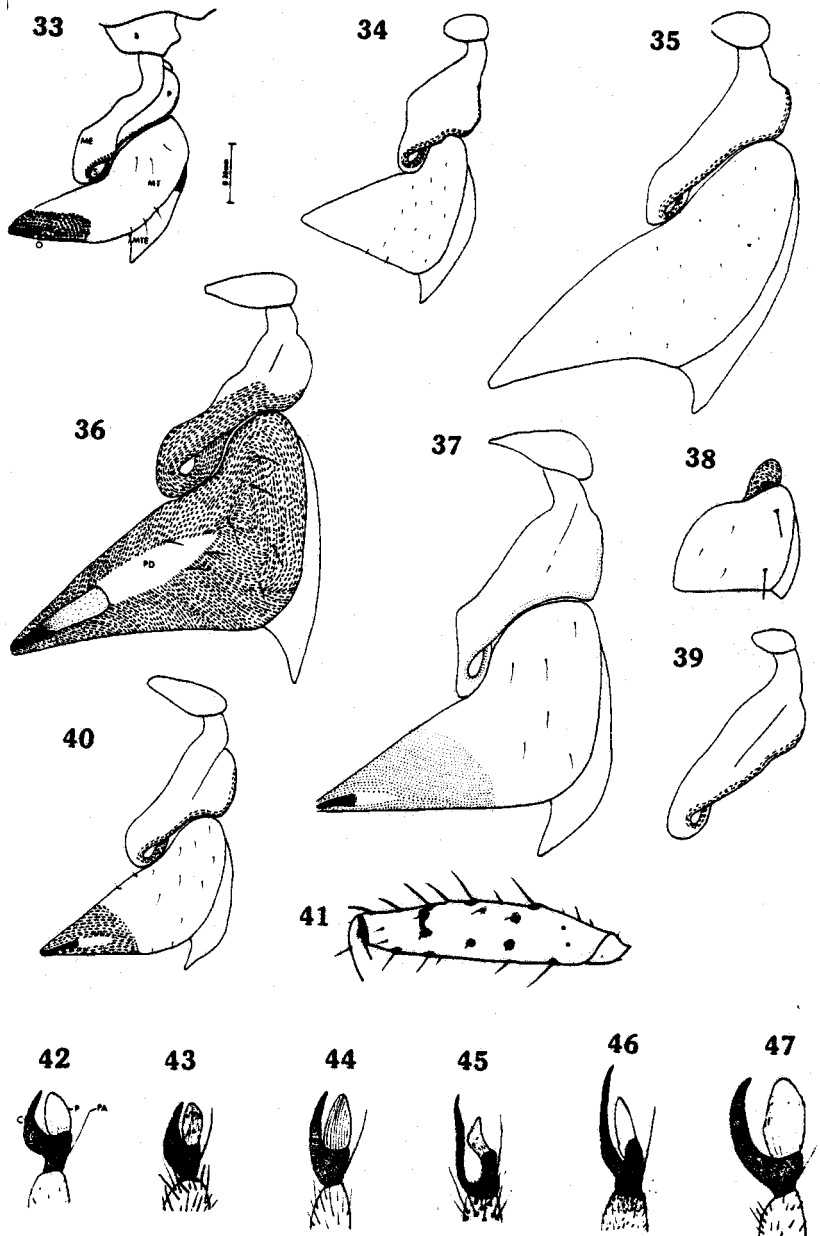
42. Campyloneuropsis annulata.

43. Cyrtopeltis geniculata.

44. Chius maculatus.

46. Dicyphus (Dicyphus) pallidus.

47. Setocoris bybliphilus.



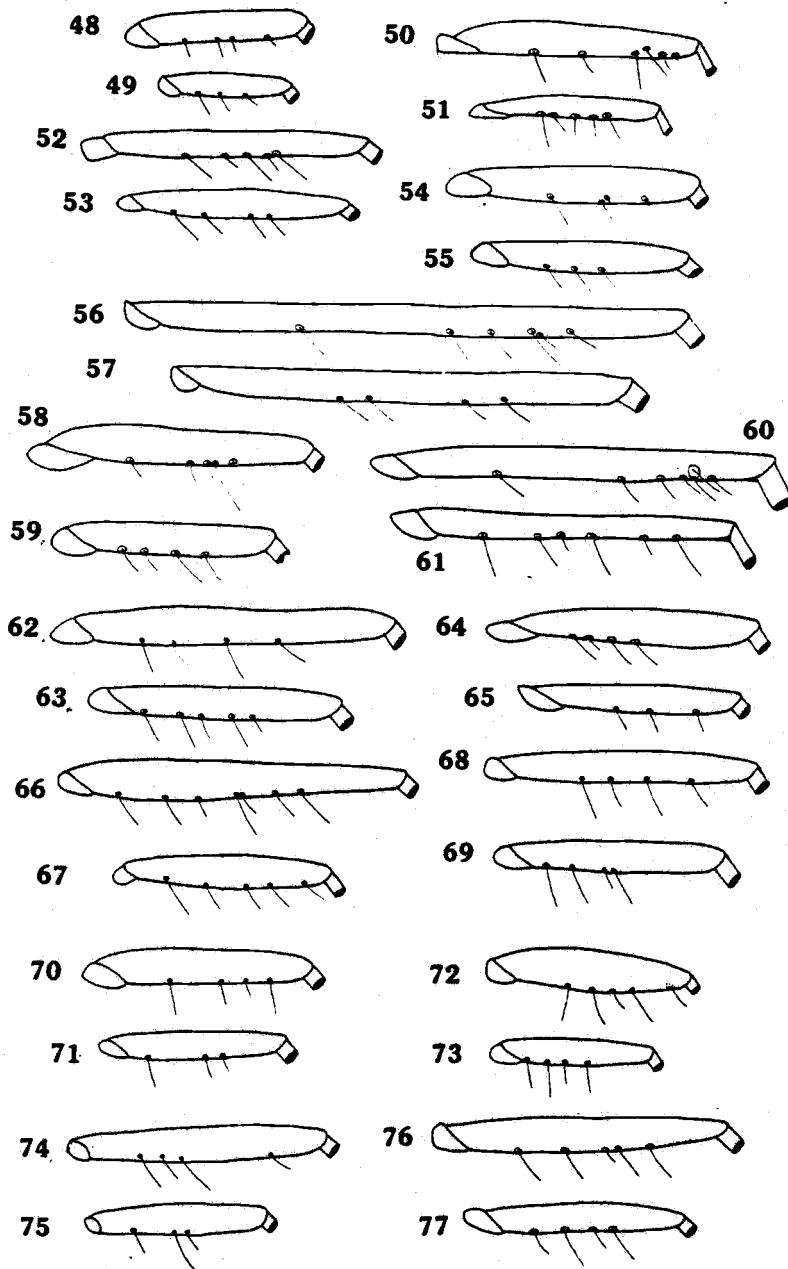
FIGURES II. 33 - II. 47

FIGURES II. 48 - II. 77. Femoral trichobothria.

Figures: 48, 50, 52, 54, 56, 58, 60, 62, 64, 66, 68, 70, 72, 74, and 76, metafemoral trichobothria, 16x.

Figures: 49, 51, 53, 55, 57, 59, 61, 63, 67, 69, 71, 73, 75, and 77, mesofemoral trichobothria, 16x.

- 48, 49. Campyloneuropsis annulata.
- 50, 51. Campyloneura virgula s. s..
- 52, 53. Chius maculatus.
- 54, 55. Dicyphus (Brachyceraea) globulifer.
- 56, 57. Dicyphus (Dicyphus) pallidus.
- 58, 59. Dicyphus (Idolocoris) pallicornis.
- 60, 61. Dicyphus (Uhlerella) famelicus.
- 62, 63. Engytatus modestus.
- 64, 65. Glarisia melanocephala.
- 66, 67. Macrolophus nubilus s. s..
- 68, 69. Nesidocoris tenuis.
- 70, 71. Setocoris bybliphilus.
- 72, 73. Singhalesia indica.
- 74, 75. Tupiocoris notata.
- 76, 77. Usingerella simplex.



FIGURES II. 48 - II. 77

FIGURES II. 78 - II. 92. Wings.

Figures: 78, 80, 81, 83, 85, 87, 89, 90, and 92,
hemelytron, 16x.

Figures: 79, 82, 84, 86, 88, and 91,
hindwing, 16x.

78, 79. Campyloneuropsis tacsia.

80. Campyloneuropsis hyalina.

81, 82. Campyloneura virgula s. s..

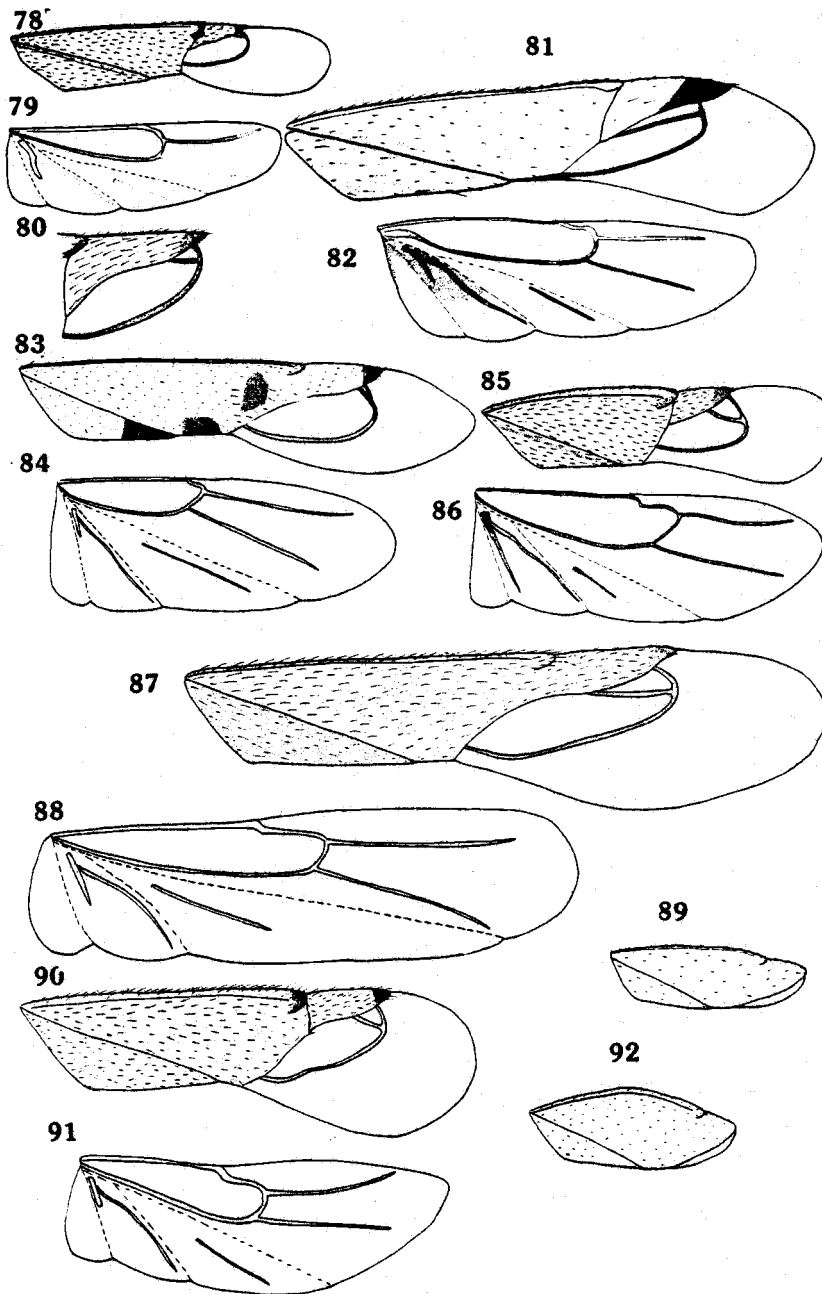
83, 84. Chius maculatus.

85, 86. Dicyphus (Dicyphus) globulifer.

87, 88. Dicyphus (Dicyphus) pallidus.

89. Dicyphus (Dicyphus) stachydis s. s..

90, 91, 92. Dicyphus (Idolocoris) pallicornis.



FIGURES II. 78 - II. 92

FIGURES II. 93 - II. 110. Wings.

Figures: 93, 95, 96, 98, 100, 102, 104, 105,
107, 109, hemelytron, 16x.

Figures: 94, 97, 99, 101, 103, 106, 108, and
110, hindwing, 16x.

93, 94, 95. Dicyphus (Uhlerella) famelicus.

96, 97. Engytatus modestus.

98, 99. Glarisia melanocephala.

100, 101. Nesidocoris tenuis.

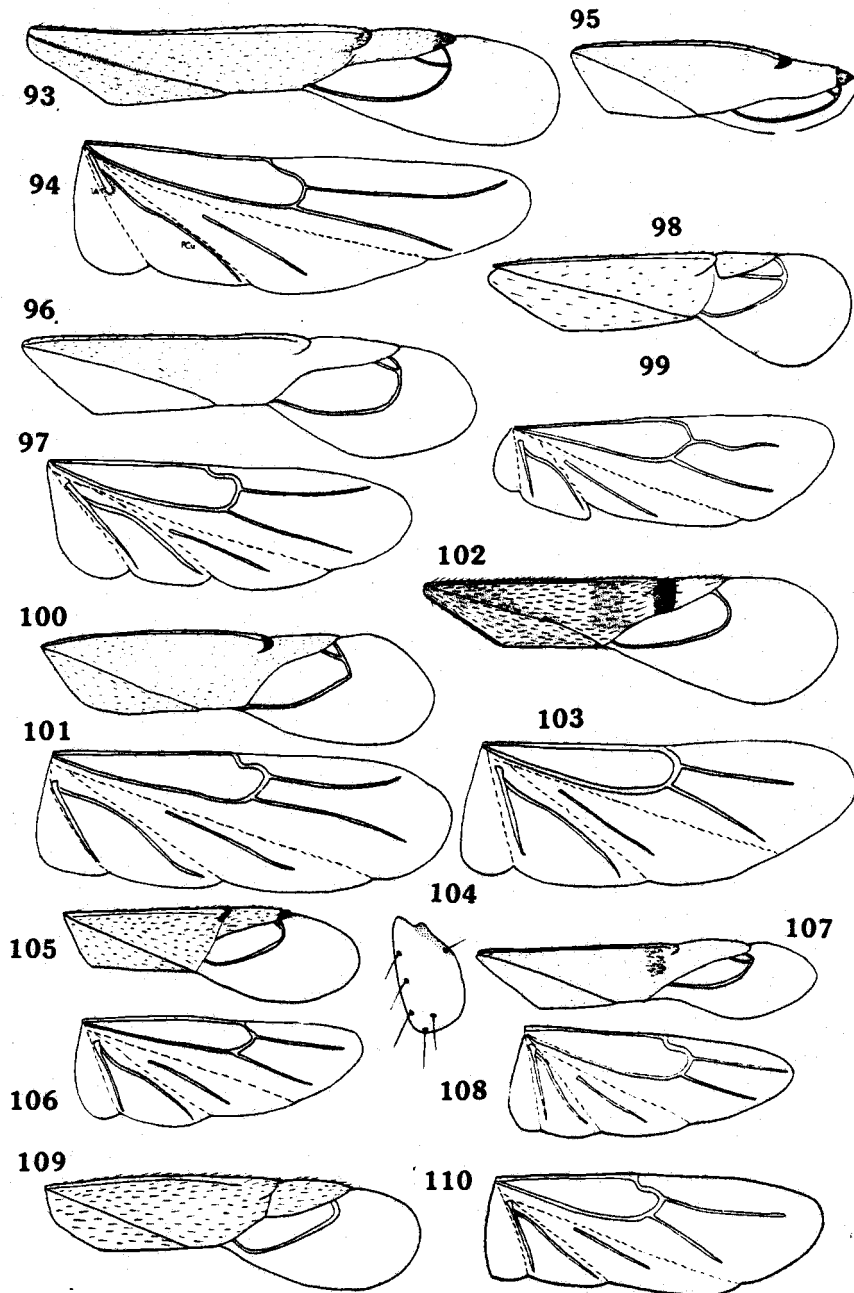
102, 103. Setocoris sp.

104. Setocoris bybliphilus.

105, 106. Singhalesia indica.

107, 108. Tupiocoris notata

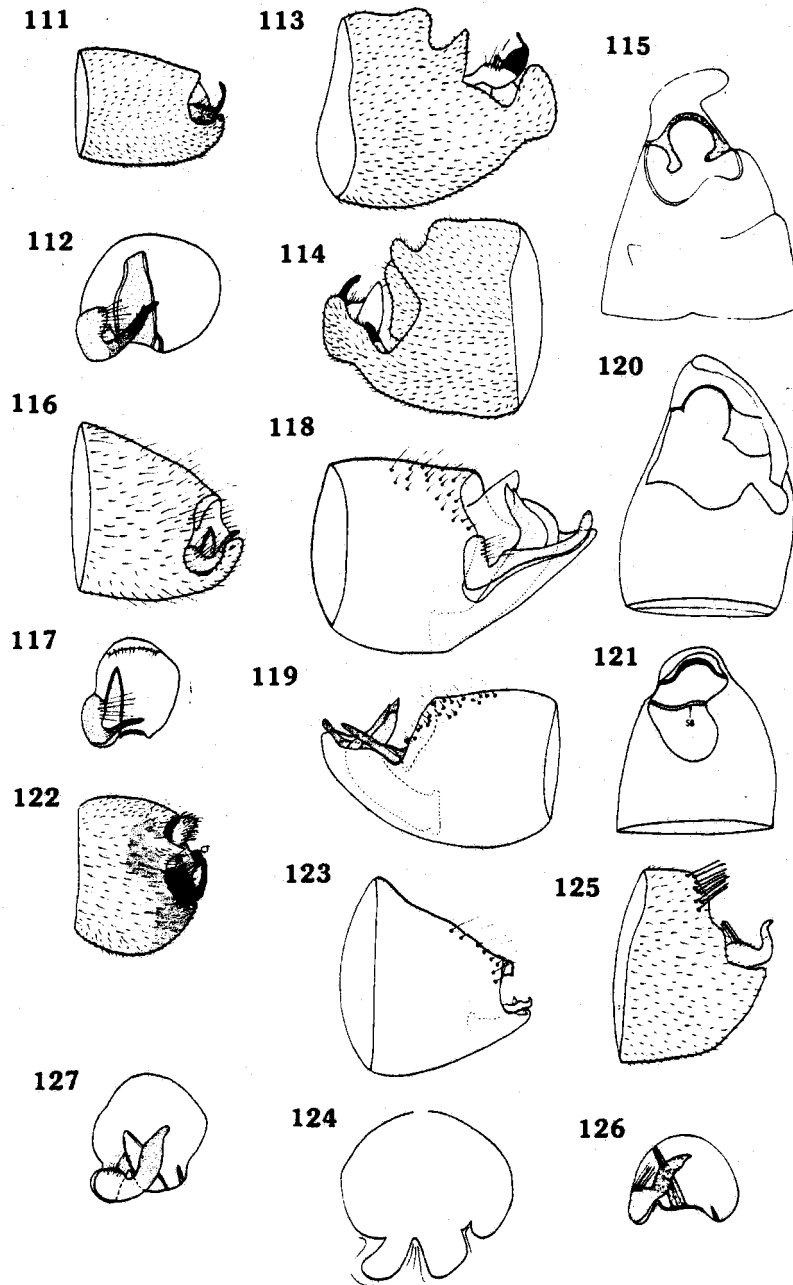
109, 110. Usingerella simplex.



FIGURES II. 93 - II. 110

FIGURES II. 111 - II. 127. Pygophore. 16x unless indicated otherwise.

111. Campyloneuropsis annulata,
sinistrolateral view
112. Ibid., terminal view, 40x.
113. Cyrtopeltis geniculata, sinistrolateral
view.
114. Ibid., dorsal view.
115. Ibid., dorsal view.
116. Chius maculatus, sinistrolateral view.
117. Ibid., terminal view.
118. Dicyphus (Dicyphus) pallidus, sinistro-
lateral view.
119. Ibid., dorsal view.
120. Ibid., dorsal view.
121. Dicyphus (Uhlerella) famelicus, dorsal
view
122. Glarisia melanocephala, sinistrolateral
view.
123. Setocoris bybliphilus, sinistrolateral
view, 40x.
124. Ibid., terminal view, 78x.
125. Singhalesia indica,
sinistrolateral view, 40x.
126. Ibid., terminal view, 40x.
127. Tupiocoris notata, 40x.



FIGURES II. 111 - II. 127

FIGURES II. 128 - II. 167. Left and right claspers.

Figures: 128, 131, 134, 137, 139, 140, 142, 144, 146, 149, 152, 155, 158, 161, 163, and 166, dorsal view of left clasper, 40x unless indicated otherwise.

Figures: 129, 132, 135, 147, 150, 153, 156, 159, and 164, lateral, internal view of left clasper, 78x.

Figures: 130, 133, 136, 138, 141, 143, 145, 148, 151, 154, 157, 160, 162, 165, and 167, dorsal view of left clasper, 78x unless indicated otherwise.

128, 129, 130. Campyloneruopsis annulata.

132, 132, 133. Cyrtopeltis geniculata.

134, 135, 136. Chius maculatus.

137, 138(40x). Dicyphus (Brachyceraea) globulifer.

139. Dicyphus (Brachyceraea) annulatus.

140(16x), 141(40x). Dicyphus (Dicyphus) pallidus.

142(16x), 143(40x). Dicyphus (Idolocoris)

pallicornis.

144(16x), 145(40x). Dicyphus (Uhlerella) famelicus.

146, 147, 148. Engytatus modestus.

149, 150, 151. Glarisia melanocephalus.

152, 153, 154. Macrolophus nubilis s. s..

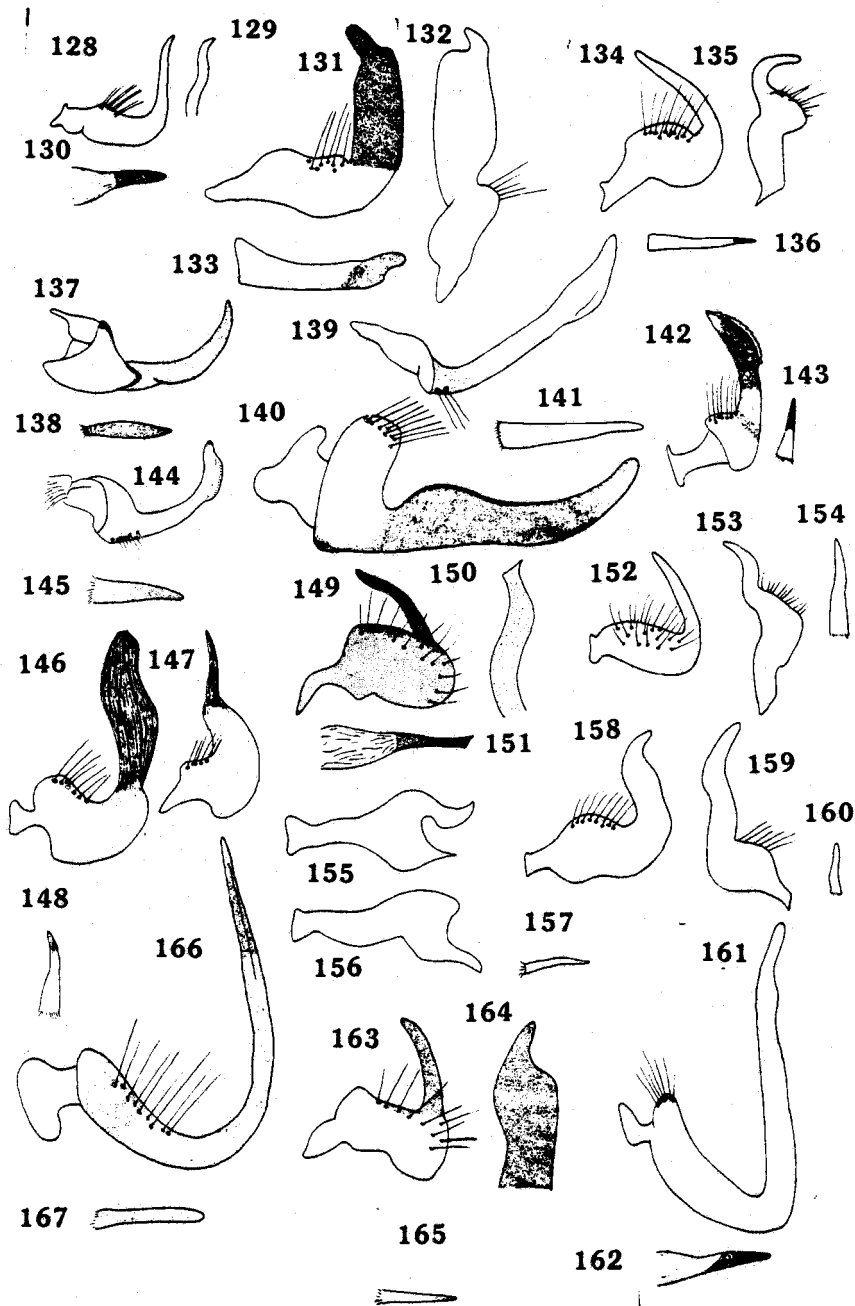
155, 156, 157. Setocoris bybliphilus.

158, 159, 160. Singhalesia indica.

161, 162. Nesidocoris tenuis.

163, 164, 164. Tupiocoris notata.

166, 167. Usingerella simplex.



FIGURES II. 128 - II. 167

FIGURES II. 168 - II. 186. Aedeagus.

Figures: 168, 170, 172, 174, 176, 177, 179, 181, 183, and 185, lateral view of vesica, 40x.

Figures: 169, 171, 173, 175, 178, 180, 182, 184, and 186, lateral view of phallosome unless indicated otherwise.

168, 169. Campyloneuropsis annulata,

figure 169 dorsal view.

170, 171. Cyrtopeltis geniculata.

172, 173. Chius maculatus.

174, 175. Dicyphus (Brachyceraea) globulifer.

176. Dicyphus (Brachyceraea) annulatus.

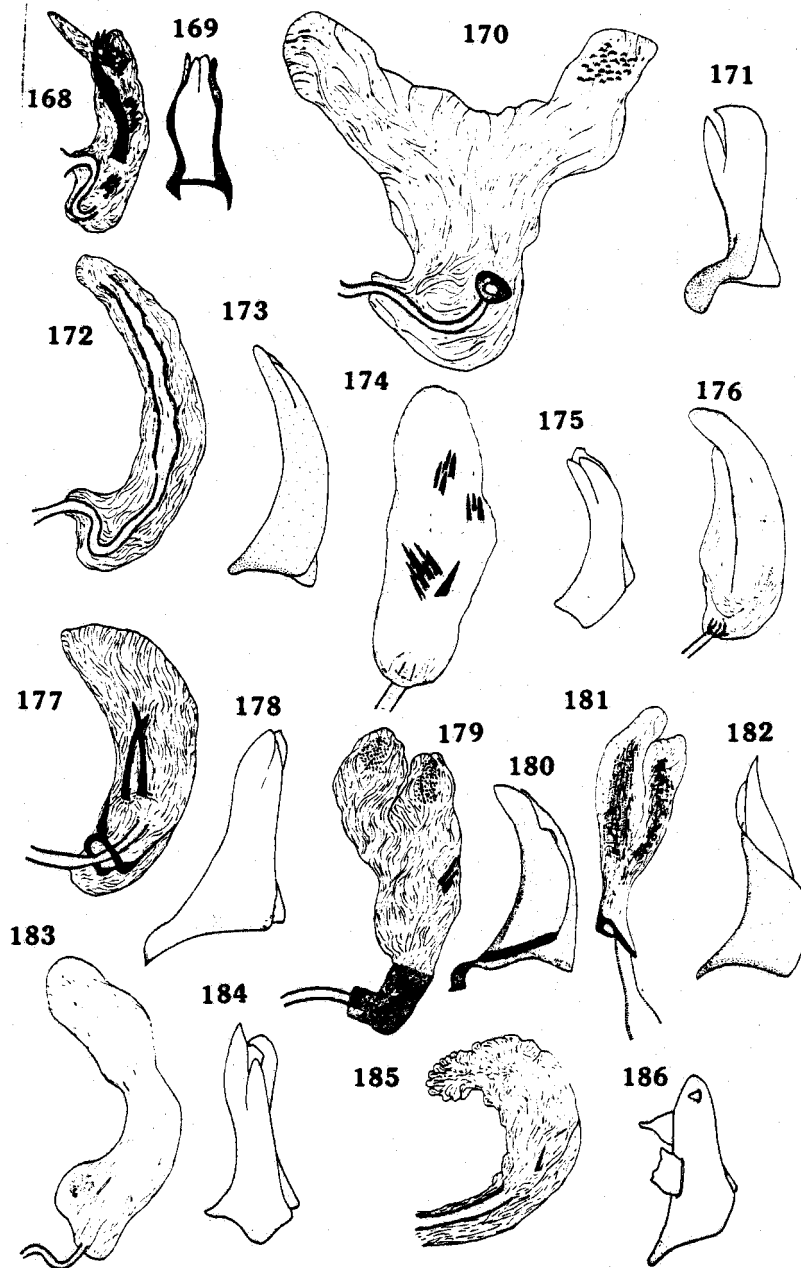
177, 178. Dicyphus (Dicyphus) pallidus.

179, 180. Dicyphus (Idolocoris) pallicornis.

181, 182. Dicyphus (Uhlerella) famelicus.

183, 184. Engytatus modestus.

185, 186. Glarisia melanocephala.



FIGURES II. 168 - II. 186

FIGURES II. 187 - II. 201. Aedeagus.

Figures: 187, 189, 190, 192, 193, 195, and 197,
lateral view of vesica, unless stated otherwise,
40x.

Figures: 188, 191, 194, 196, 198, and 201,
lateral view of phallosome unless indicated
otherwise, 40x.

187, 188. Macrolophus nubilus.

189. Macrolophus cuibanus.

190, 191. Nesidocoris tenuis.

192. Setocoris bybliphilus, lateral view
of aedeagus, 78x.

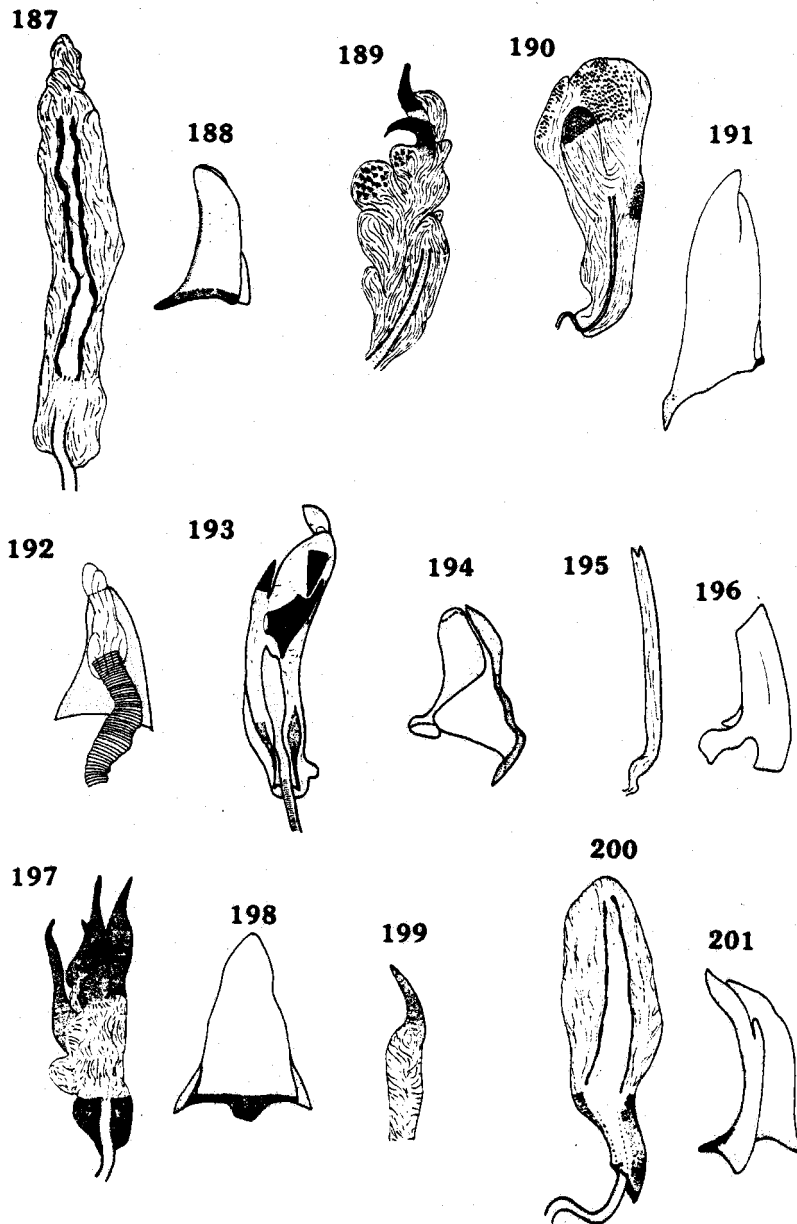
193, 194. Setocoris sp.

195, 196. Singhalesia indica, 78x.

197, 198. Tupiocoris notata.

199. Tupiocoris rubi.

200, 201. Usingerella simplex.

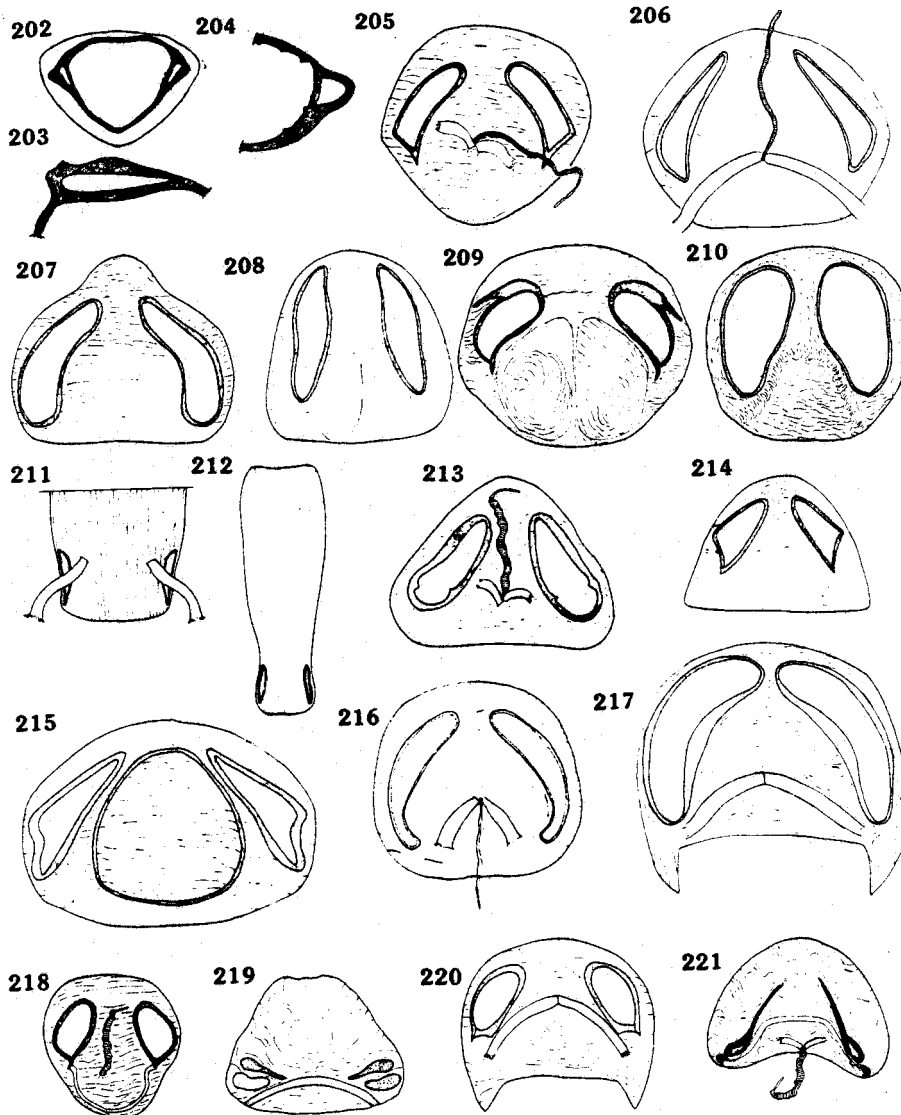


FIGURES II. 187 - II. 201

FIGURES II. 202 - II. 221. Female bursa copulatrix.

40x unless indicated otherwise.

- 202. Campyloneuropsis annulata, bursa
copulatrix.
- 203. Ibid., lateral view of sclerotized
ring, 78x.
- 204. Campyloneuropsis hyalina.
- 205. Campyloneura virgula.
- 206. Chius maculatus.
- 207. Dicyphus (Brachyceraea) globulifer.
- 208. Dicyphus (Dicyphus) constrictus.
- 209. Dicyphus (Idolocoris) pallicornis.
- 210. Dicyphus (Uhlerella) famelicus.
- 211. Engytatus modestus, only posterior
half of bursa copulatrix.
- 212. Engytatus rubescens.
- 213. Glarisia melanocephala.
- 214. Macrolophus costalis.
- 215. Macrolophus basicornis.
- 216. Nesidocoris tenuis.
- 217. Setocoris sp.
- 218. Singhalesia obscuricornis.
- 219. Tupiocoris notata.
- 220. Tupiocoris californica.
- 221. Usingerella simplex.



FIGURES II. 202 - II. 221

FIGURES II. 222 - II. 225. Thoracic pleura.

EA=evaporative areas, ME=mesepimeron,

MT=metaepisternum, O=osteole, P=peritremal disc,

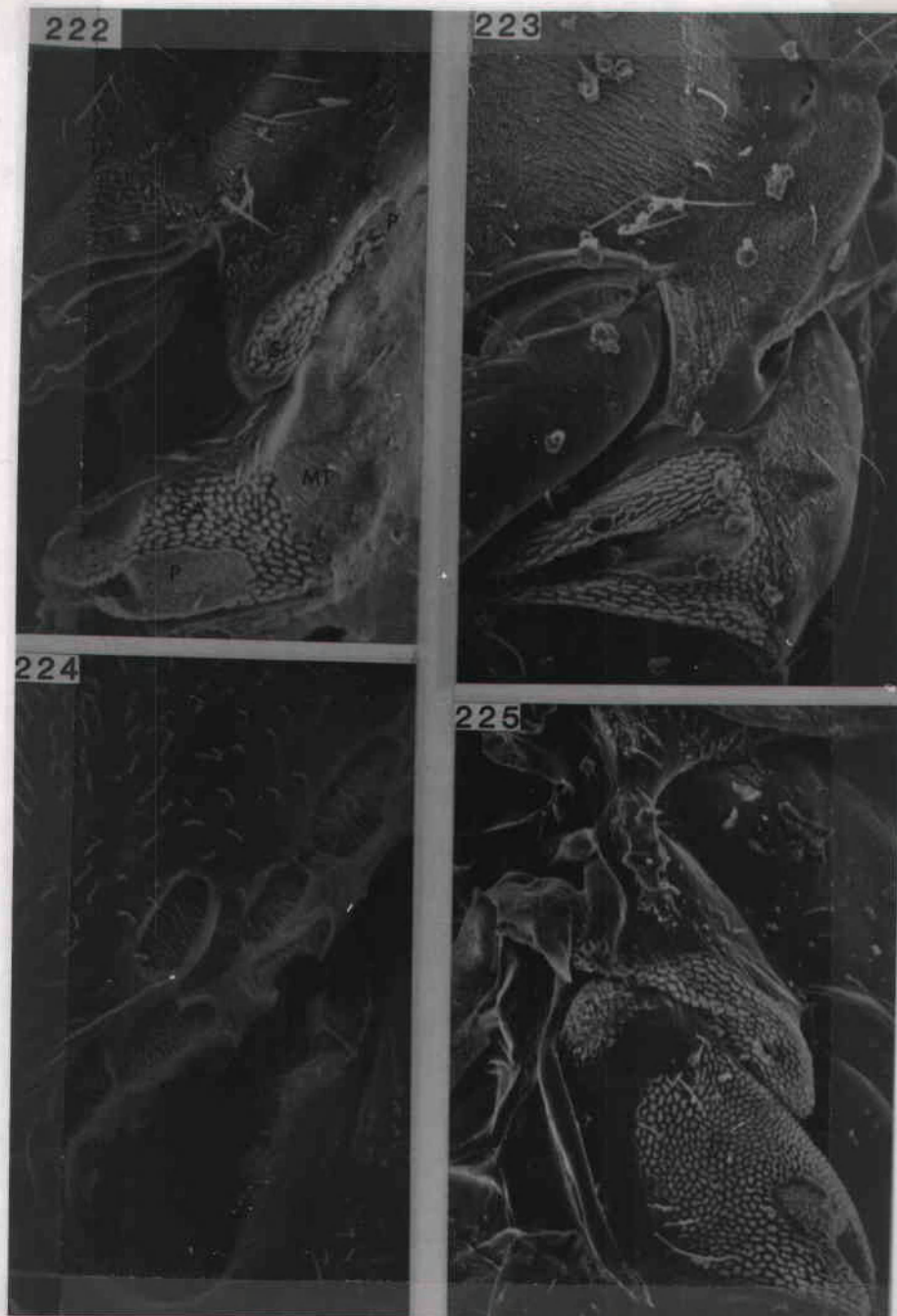
S=spiracle.

222. Campyloneuropsis hyalina, thoracic
pleura, 200x.

223. Campyloneura virgula, thoracic
pleura, 180x.

224. Ibid., mesepimeric spiracle, 1100x.

225. Dicyphus (Brachyceraea) globulifer,
thoracic pleura, 160x.

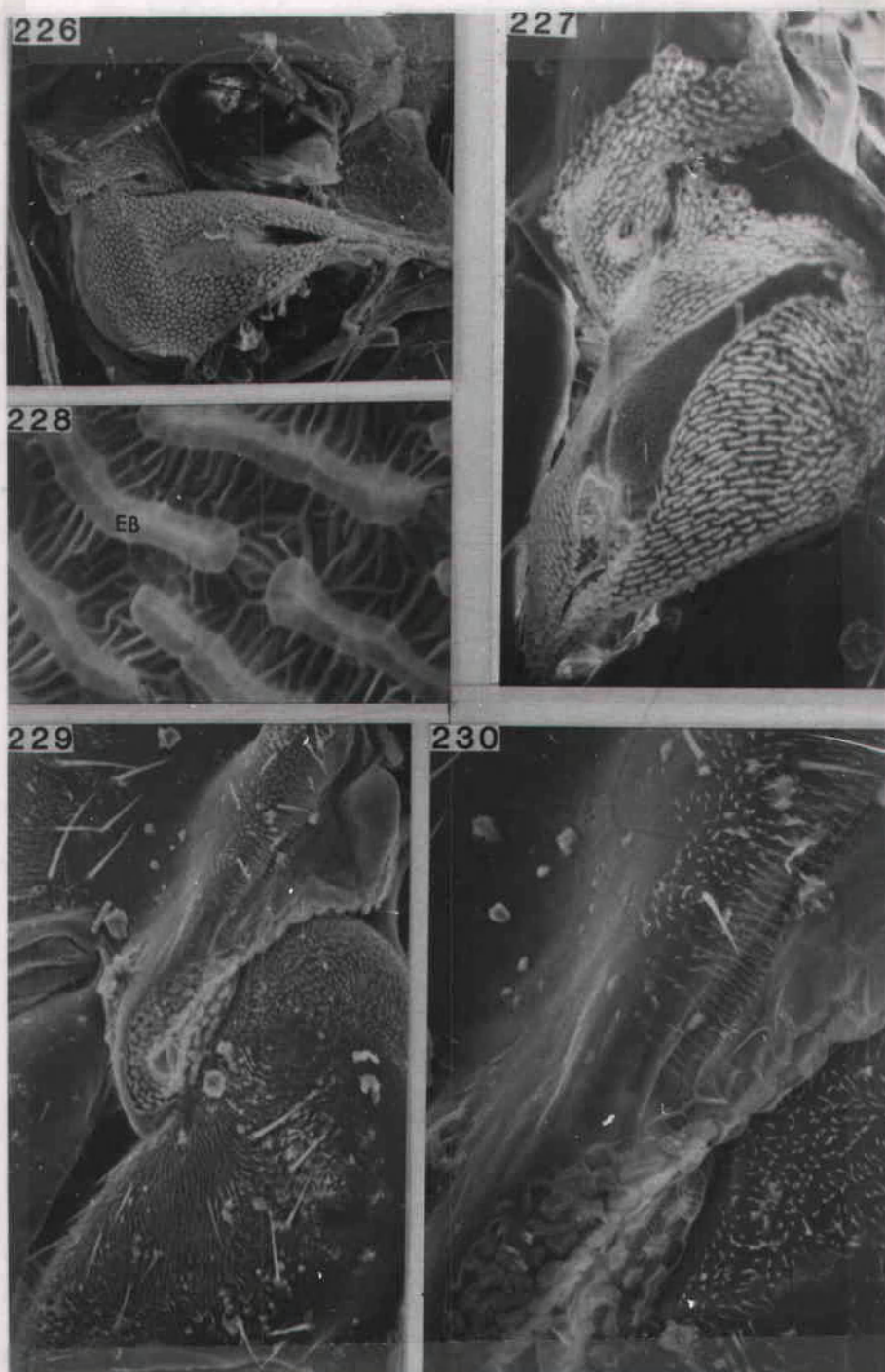


FIGURES II. 222 - II. 225

FIGURES II. 226 - II. 230. Thoracic pleura.

EB=evaporative areas.

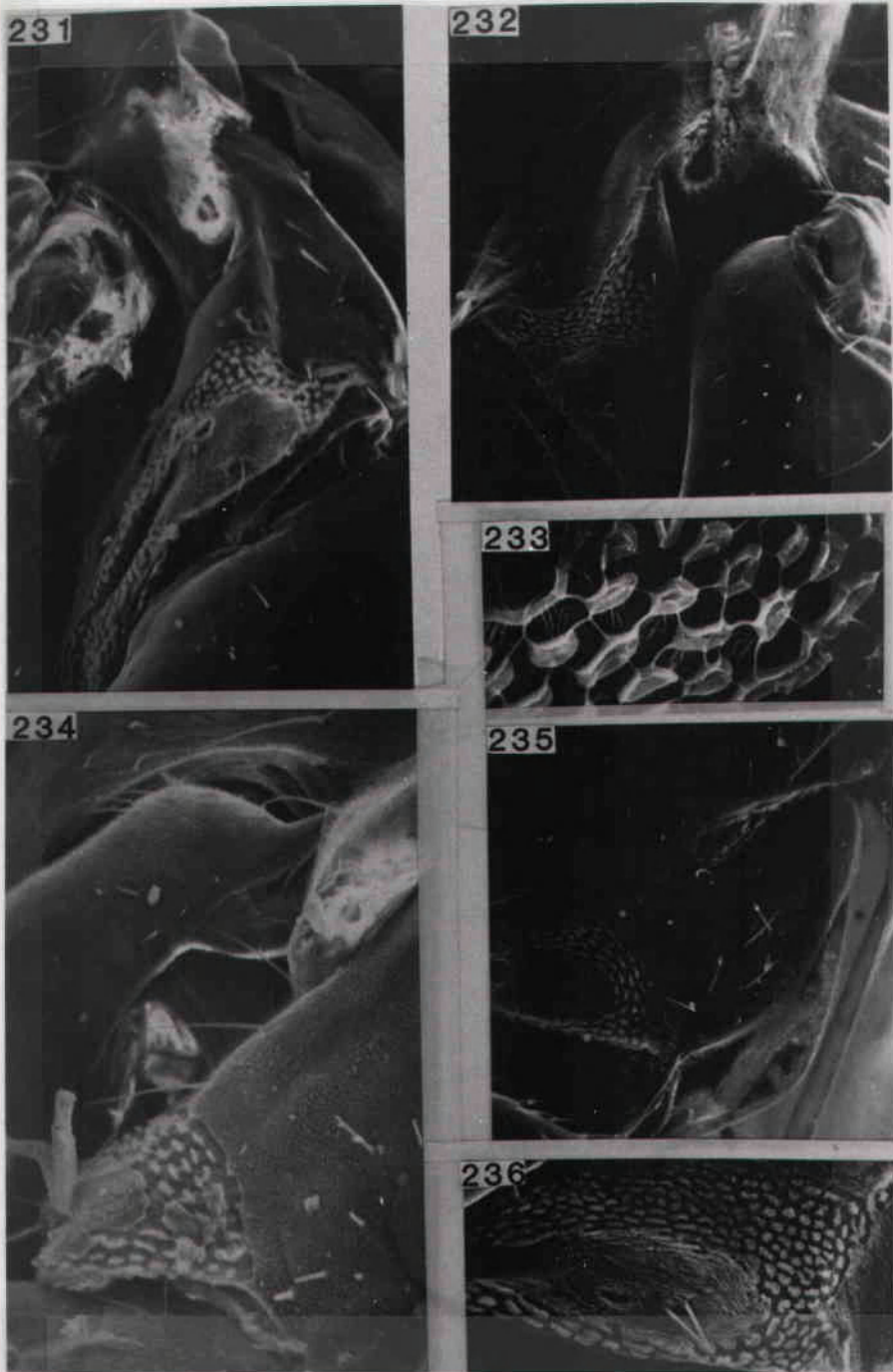
226. Dicyphus (Idolocoris) pallicornis,
thoracic pleura, 120x.
227. Dicyphus (Uhlerella) discrepans,
thoracic pleura, 200x.
228. Ibid., evaporative bodies on
metaepisternum, 2000x.
229. Engytatus modestus, thoracic pleura,
230x.
230. Ibid., mesepimeric spiracle and
evaporative bodies, 500x.



FIGURES II. 226 - II. 230

FIGURES II. 231 - II. 236. Thoracic pleura.

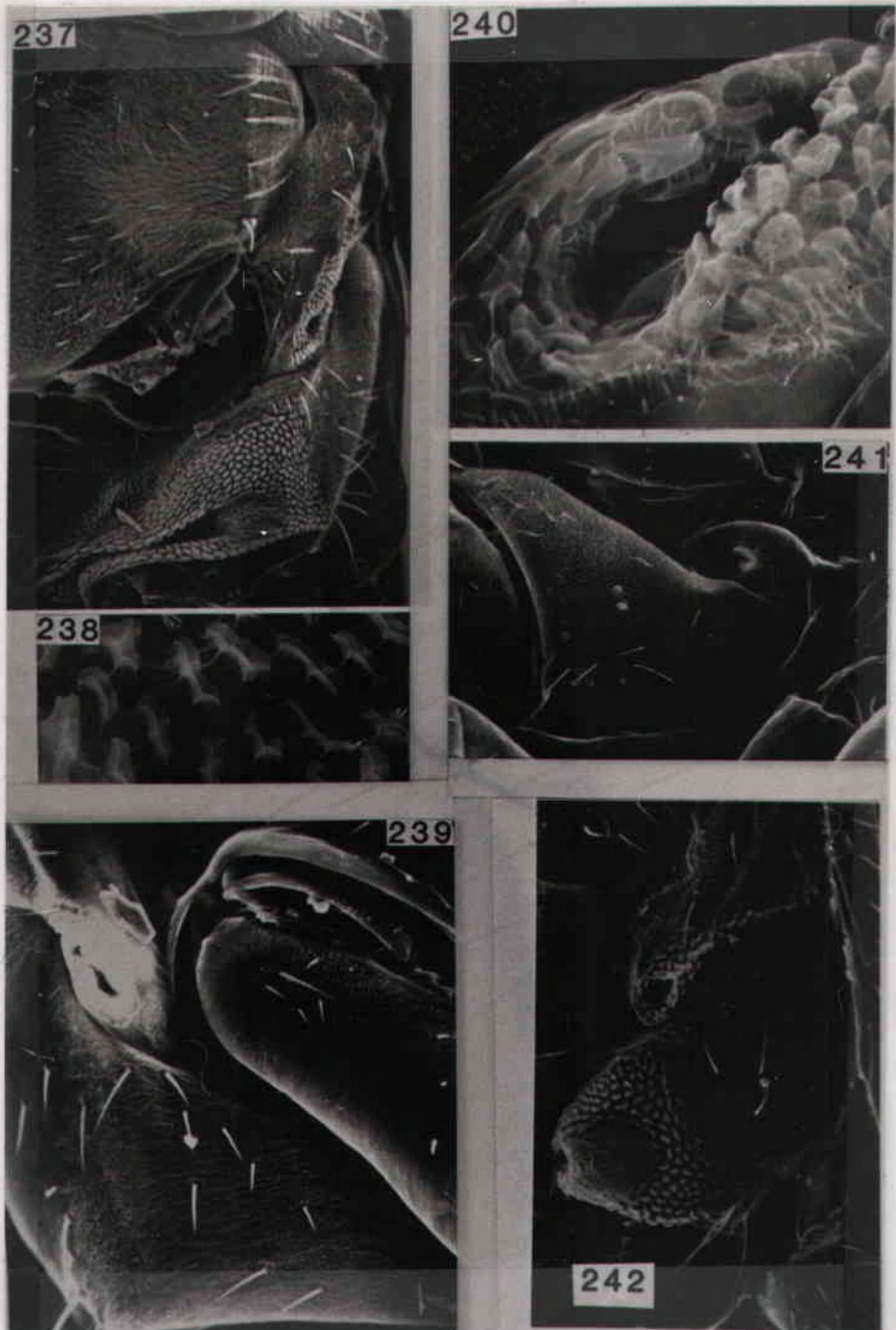
231. Glarisia melanocephala, thoracic pleura, 240x.
232. Glarisia sp., thoracic pleura, 200x.
233. Ibid., evaporative bodies on metaepisternum, 800x.
234. Macrolophus nubilus s. s., thoracic pleura, 330x.
235. Macrolophus sp. (from South Africa), pleura, 280x.
236. Macrolophus brevicornis, metaepisternum scent efferent system, 440x.



FIGURES II. 231 - II. 236

FIGURES II. 237 - II. 242. Thoracic pleura.

237. Nesidocoris tenuis, thoracic pleura,
170x.
238. Ibid., evaporative bodies on
metaepisternum, 1000x.
239. Tupiocoris confusa, thoracic pleura,
230x.
240. Ibid., mesepimeric spiracle, 1200x.
241. Ibid., fifth instar larva, thoracic
pleura, 170x.
242. Usingerella bakeri, thoracic pleura,
175x.



FIGURES II. 237 - II. 242

FIGURES II. 243 - II. 248. Pretarsus.

C=claw, CS=claw setae, P=pseudopulvilli,

PI=pulvilli, PA=parempodia.

243. Campyloneura virgula, s. s., lateral
view of pretarsus, 1100x.

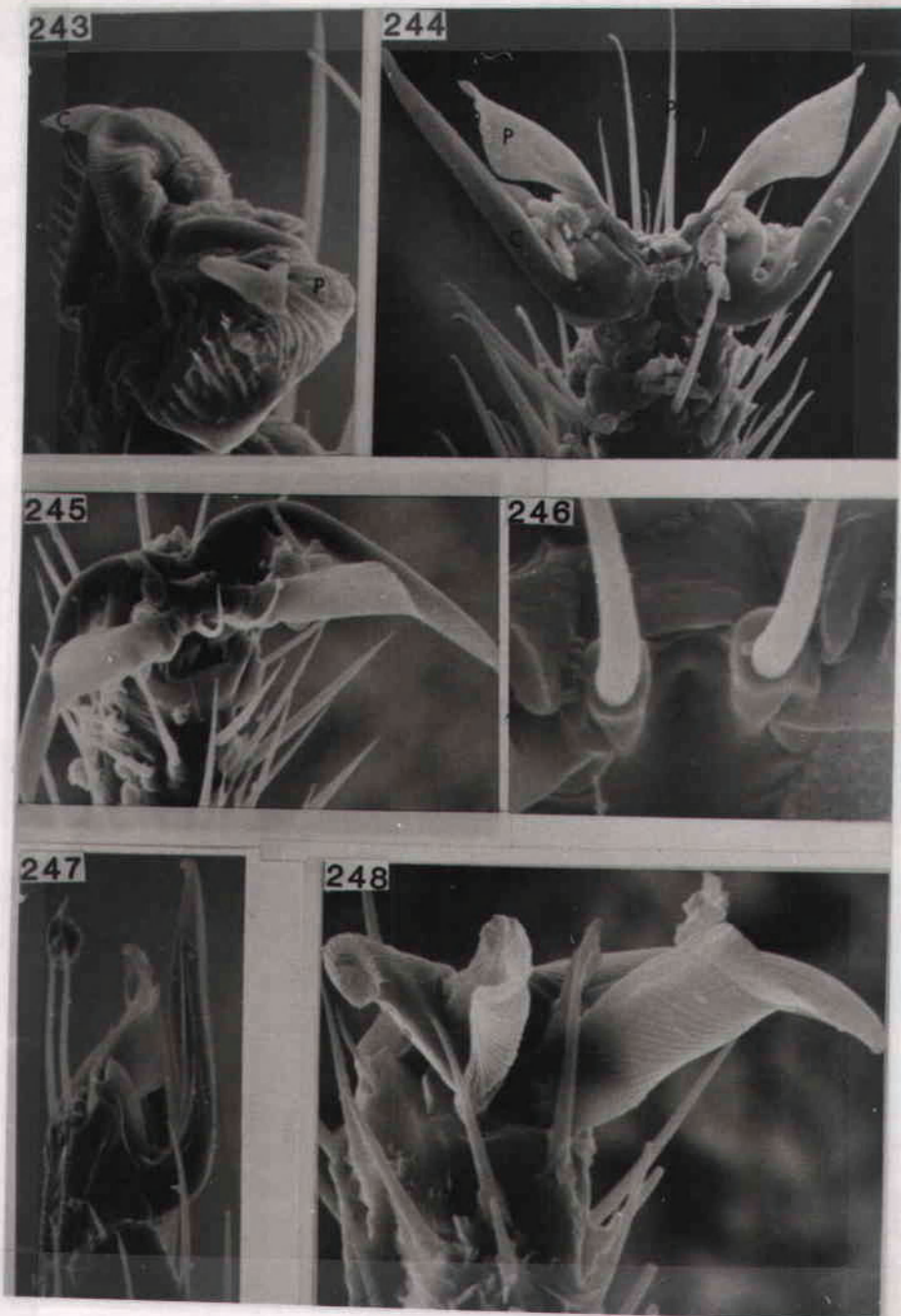
244. Dicyphus (Uhlerella) discrepans, dorsal
view of pretarsus, 700x.

245. Ibid., ventral view, 700x.

246. Ibid., unguitractor plate and
parempodia, 3800x.

247. Dicyphus (Idolocoris) pallicornis,
lateral view of pretarsus, 800x.

248. Engytatus modestus, ventral view of
pretarsus, 1600x.



FIGURES II. 243 - II. 248

FIGURES II. 249 - II. 256. Pretarsus.

p=pore.

- 249. Glarisia melanocephala, 1000x.
- 250. Macrolophus nubilus s. s., 1300x.
- 251. Macrolophus brevicornis, 1800x.
- 252. Nesidocoris tenuis, 1000x.
- 253. Tupiocoris notata, 1500x.
- 254. Tupiocoris confusa, 1500x.
- 255. Singhalesia obscuricornis, 1800x.
- 256. Usingerella bakeri, 1500x.

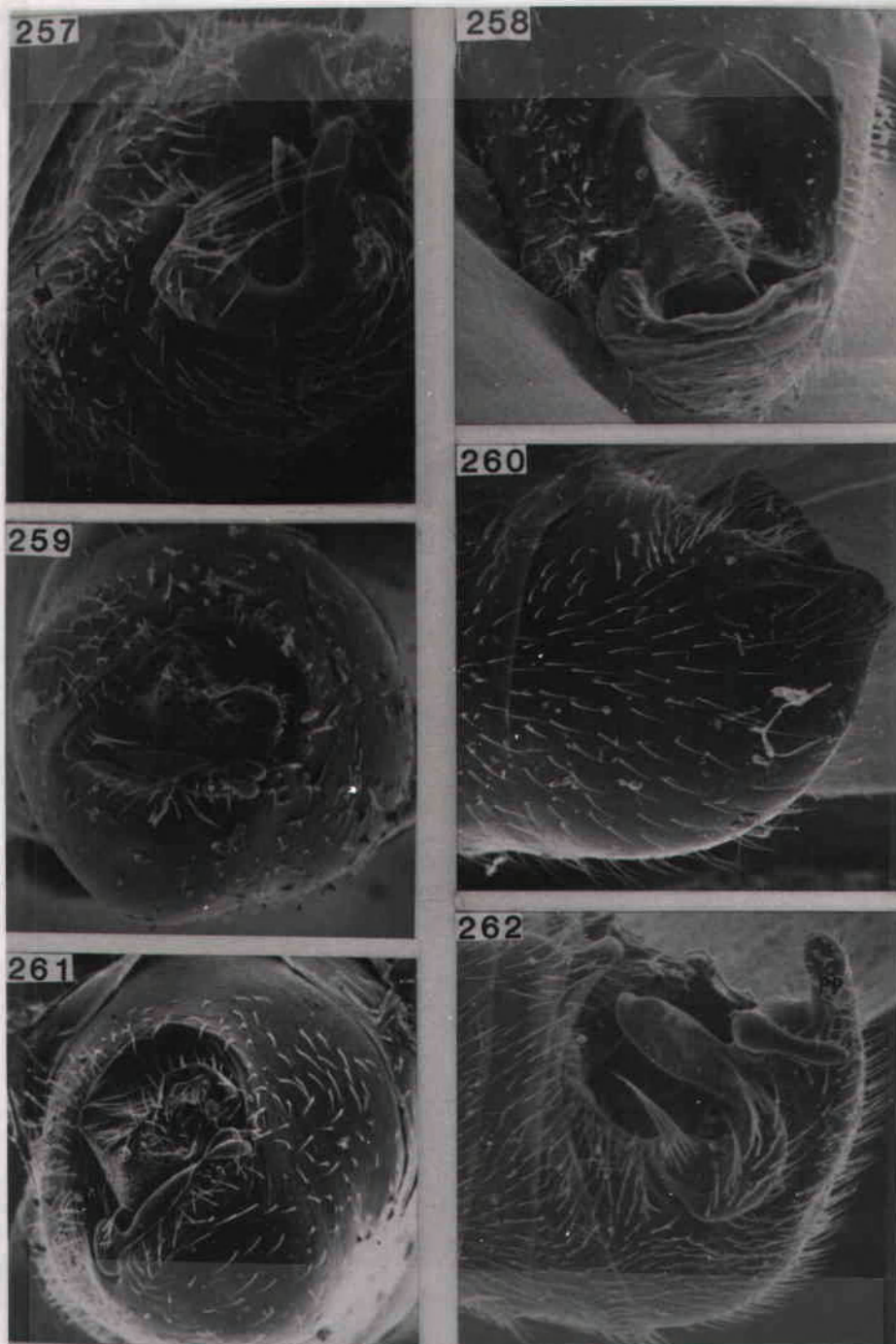


FIGURES II. 249 - II. 256

FIGURES II. 257 - II. 262. Pygophore.

T=tubercle.

257. Campyloneuropsis hyalina,
sinistrolateral view, 150x.
258. Dicyphus (Brachyceraea) globulifer,
dorsal view, 100x.
259. Dicyphus (Idolocoris) pallicornis,
terminal view, 100x.
260. Dicyphus (Uhlerella) discrepans,
sinistrolateral view, 150x.
261. Ibid., terminal view, 150x.
262. Engytatus modestus, sinistrolateral
view, 100x.



FIGURES II. 257 - II. 262

FIGURES II. 263 - II. 268. Pygophore.

T=tubercle, CT=chisel-like tubercle.

263. Glarisia melanocephala, sinistroterminal view, 130x.

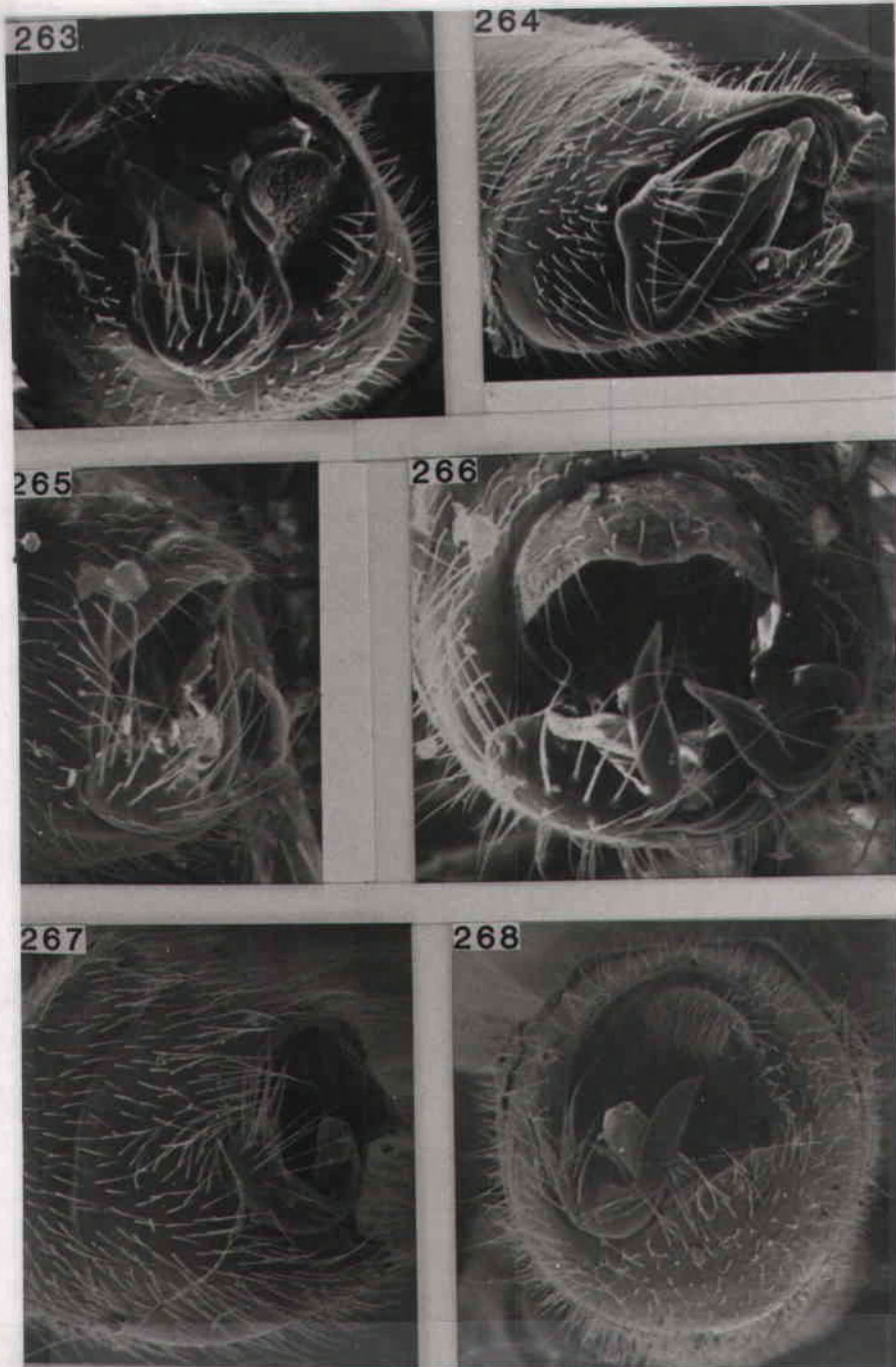
264. Nesidocoris tenuis, sinistrolateral view, 100x.

265. Macrolophus nubilus s. s., sinistrolateral view, 190x.

266. Ibid., terminal view, 240x.

267. Tupiocoris confusa, 110x.

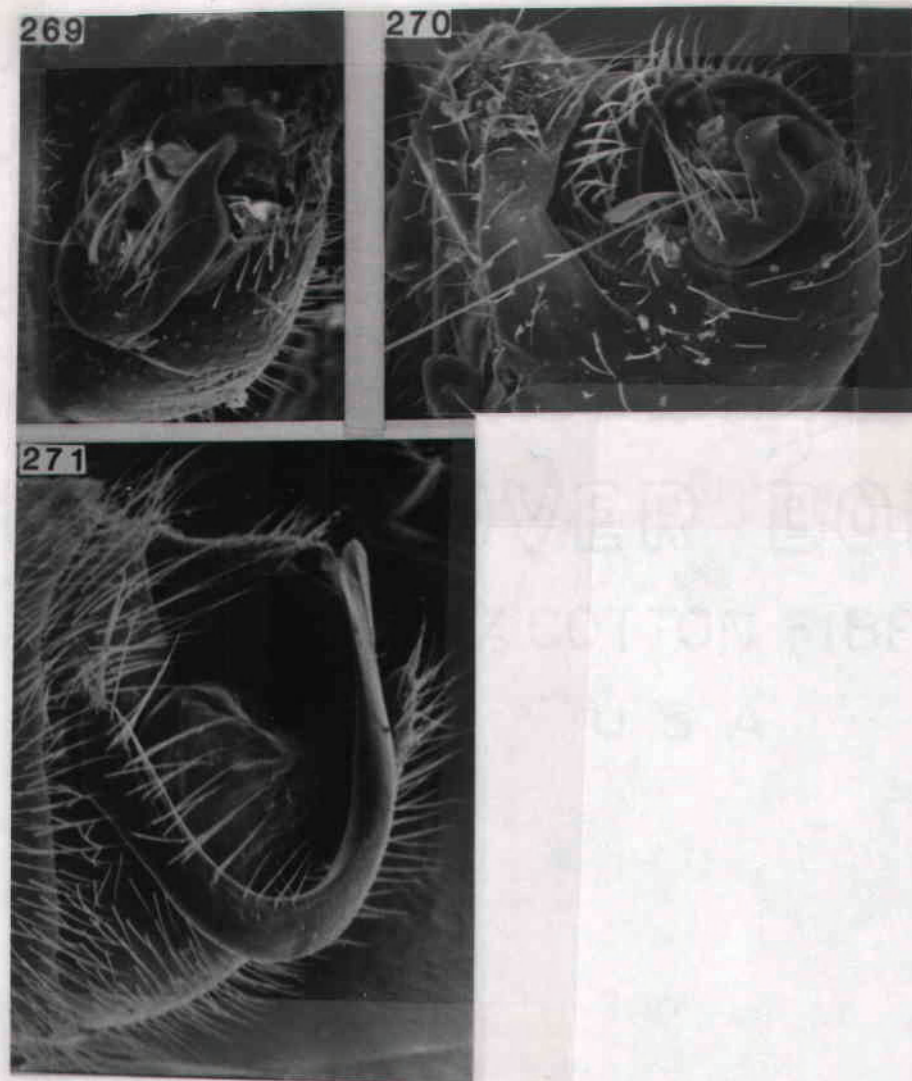
268. Ibid., terminal view, 100x.



FIGURES II. 263 - II. 268

FIGURES II. 269 - II. 271. Pygophore.

- 269. Tupiocoris notata, 200x.
- 270. Singhalesia indica, 250x.
- 271 Usingerella bakeri, 140x.



FIGURES II. 269 - II. 271

FIGURE II. 272.

Habitus of Dicyphus (Idolocoris) regulus, 10x.

272

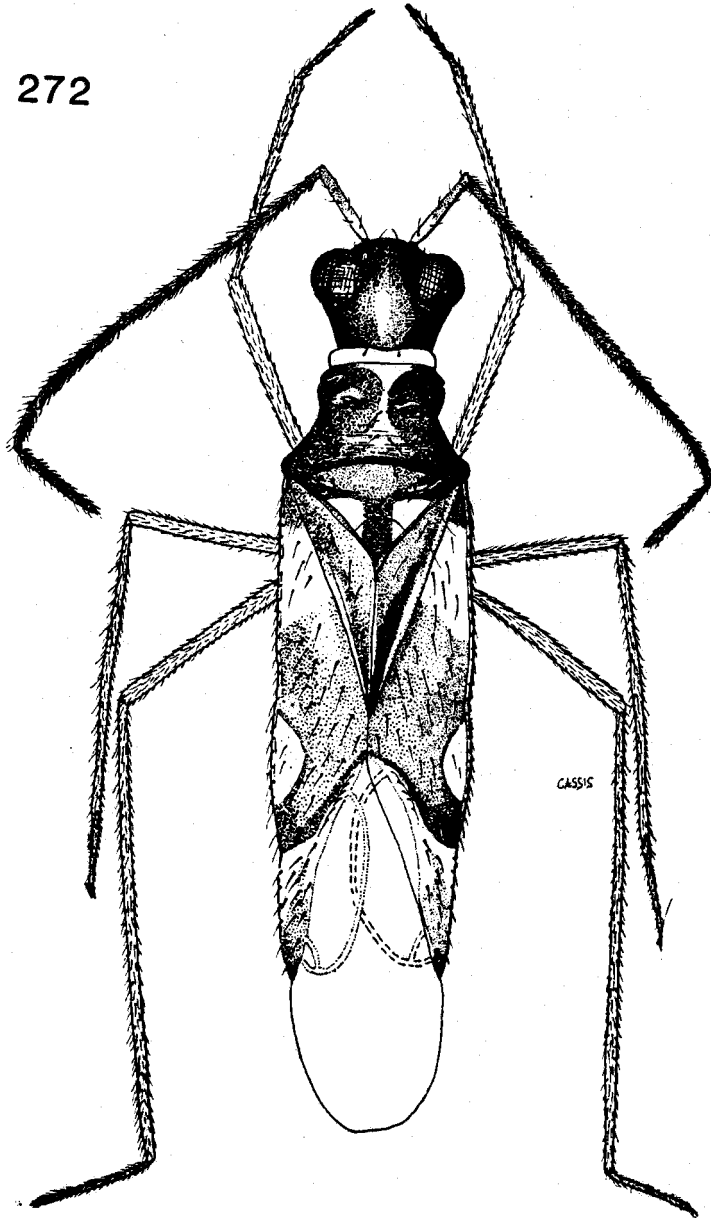


FIGURE II. 272

FIGURE II. 273.

Habitus of Dicyphus (Uhlerella) paddocki, 10x.

273

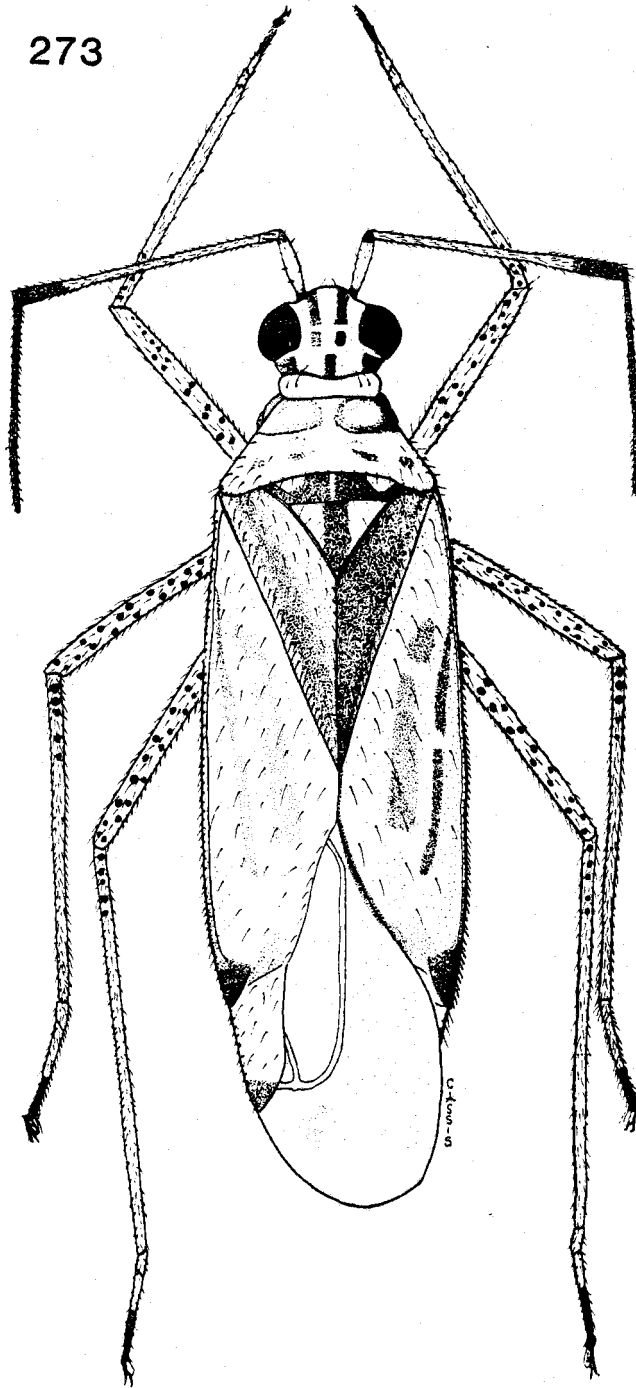


FIGURE II. 273

FIGURES II. 274.

Habitus of Tupiocoris californica, 10x.

274

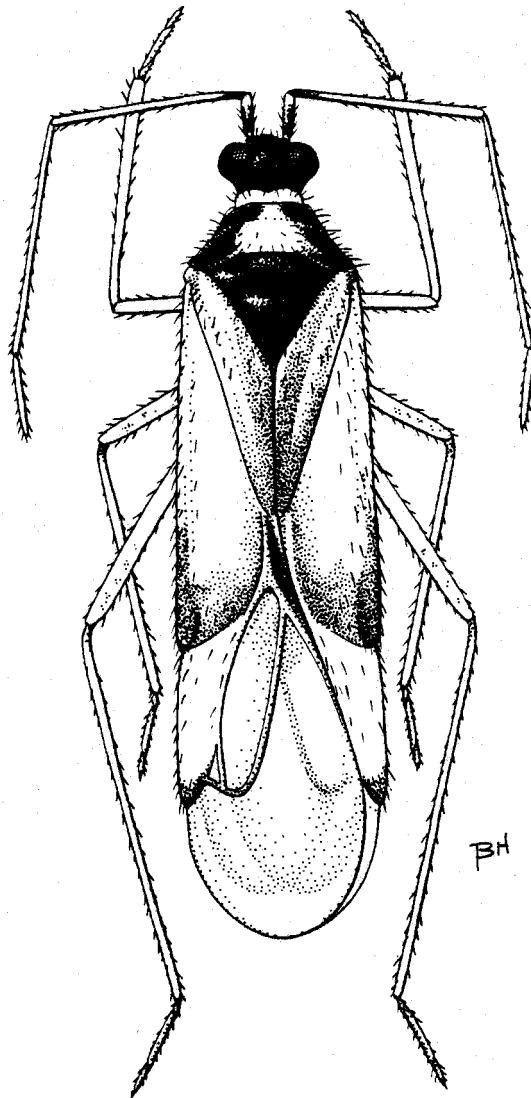


FIGURE II. 274

FIGURE 275. Cladogram showing the distribution of synapomorphies in Dicyphinae genera.

X = synapomorphy

X', X'' = synapomorphies of multistate characters

+X = parallelism

-X = reversal

Autapomorphies of terminal taxa are listed.

Characters are defined in Table 1.

275

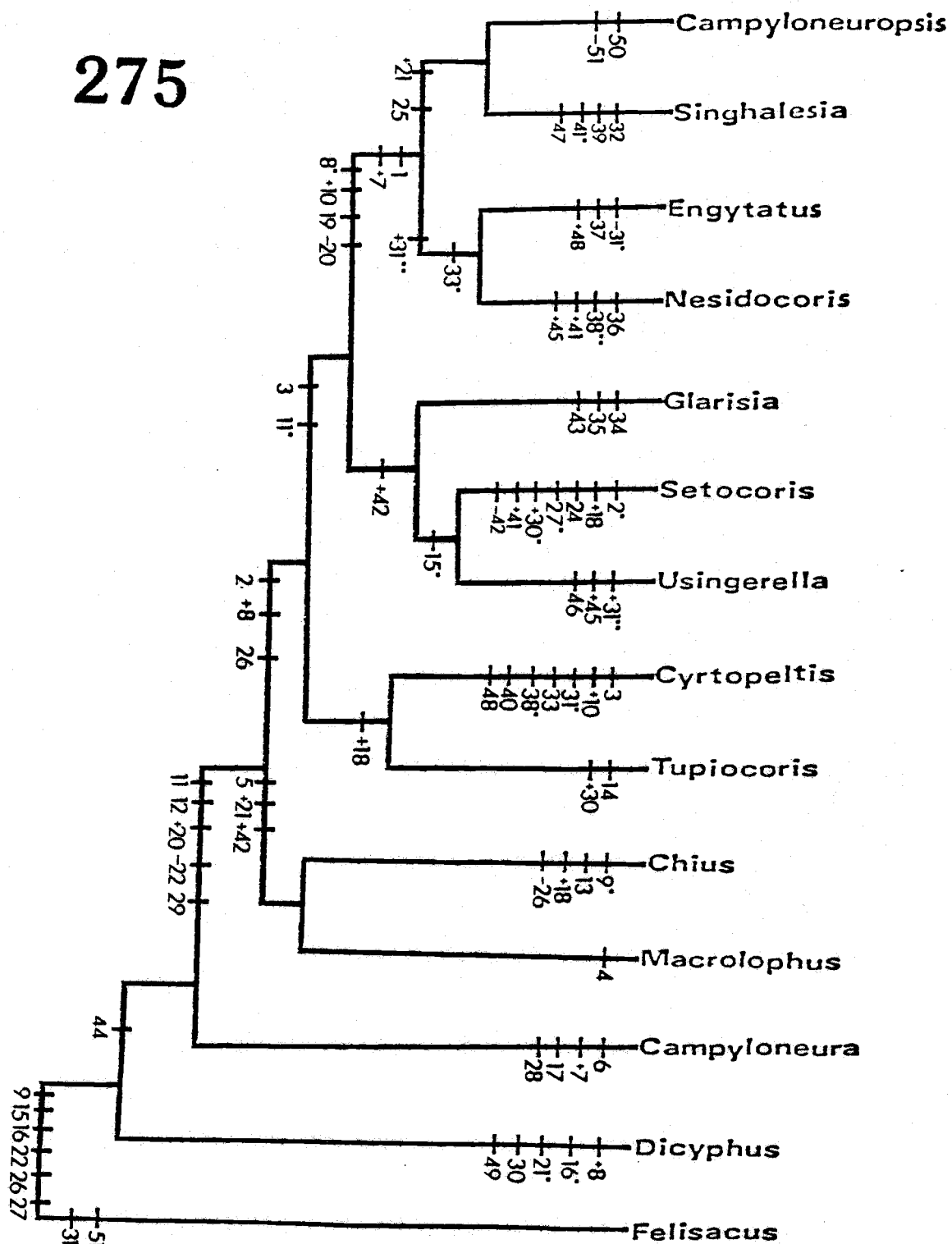


FIGURE 275

FIGURE 276. Cladogram showing the regional distribution of Dicyphinae genera.

The abbreviations in this figure are as follows:

P Palearctic

N Nearctic

E Ethiopian

NE Neotropical

O Oriental

A Australasian

OC Oceanic

276

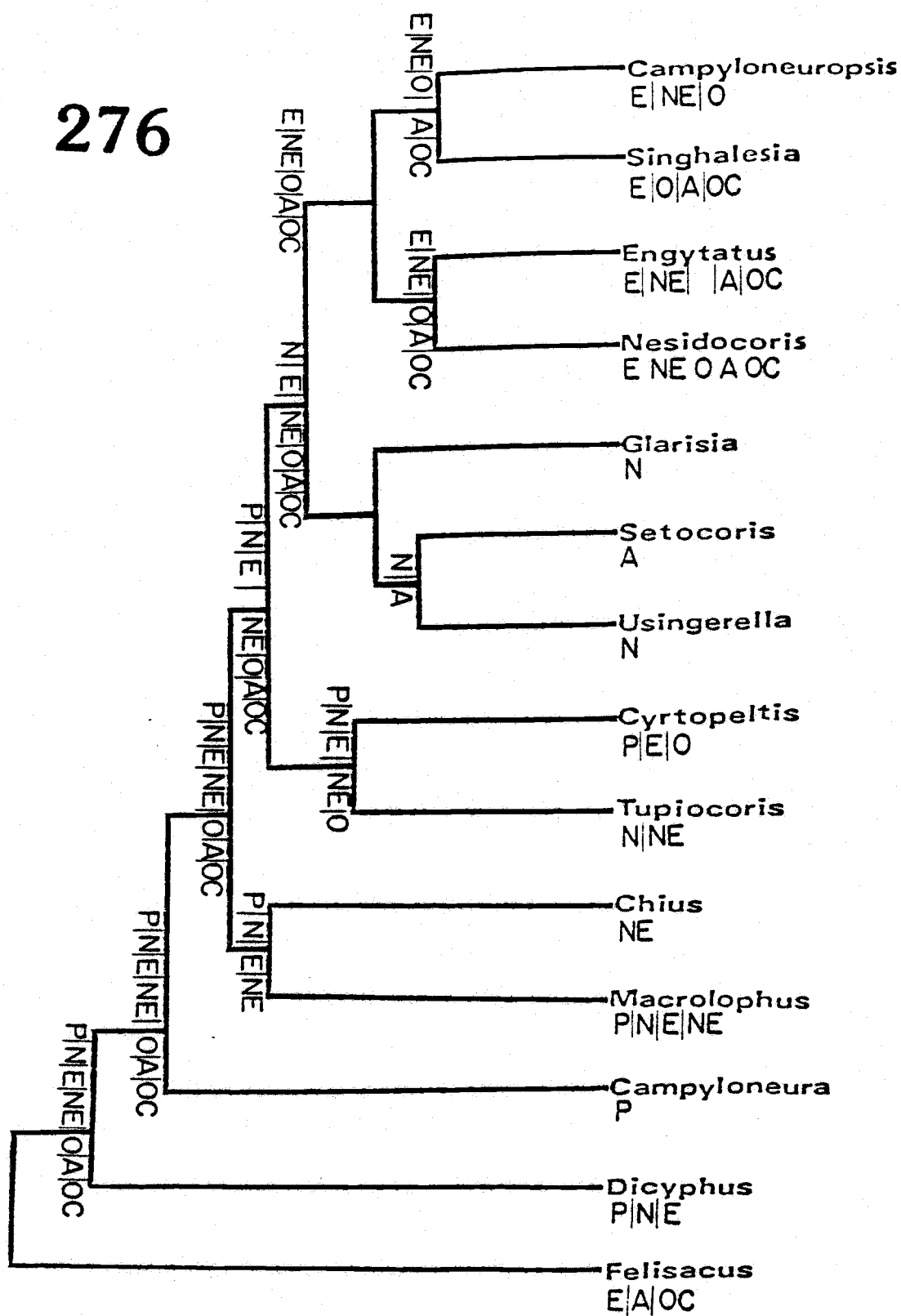


FIGURE 276

FIGURE 277. Cladogram showing the host plant family associations for Dicyphinae genera.

277

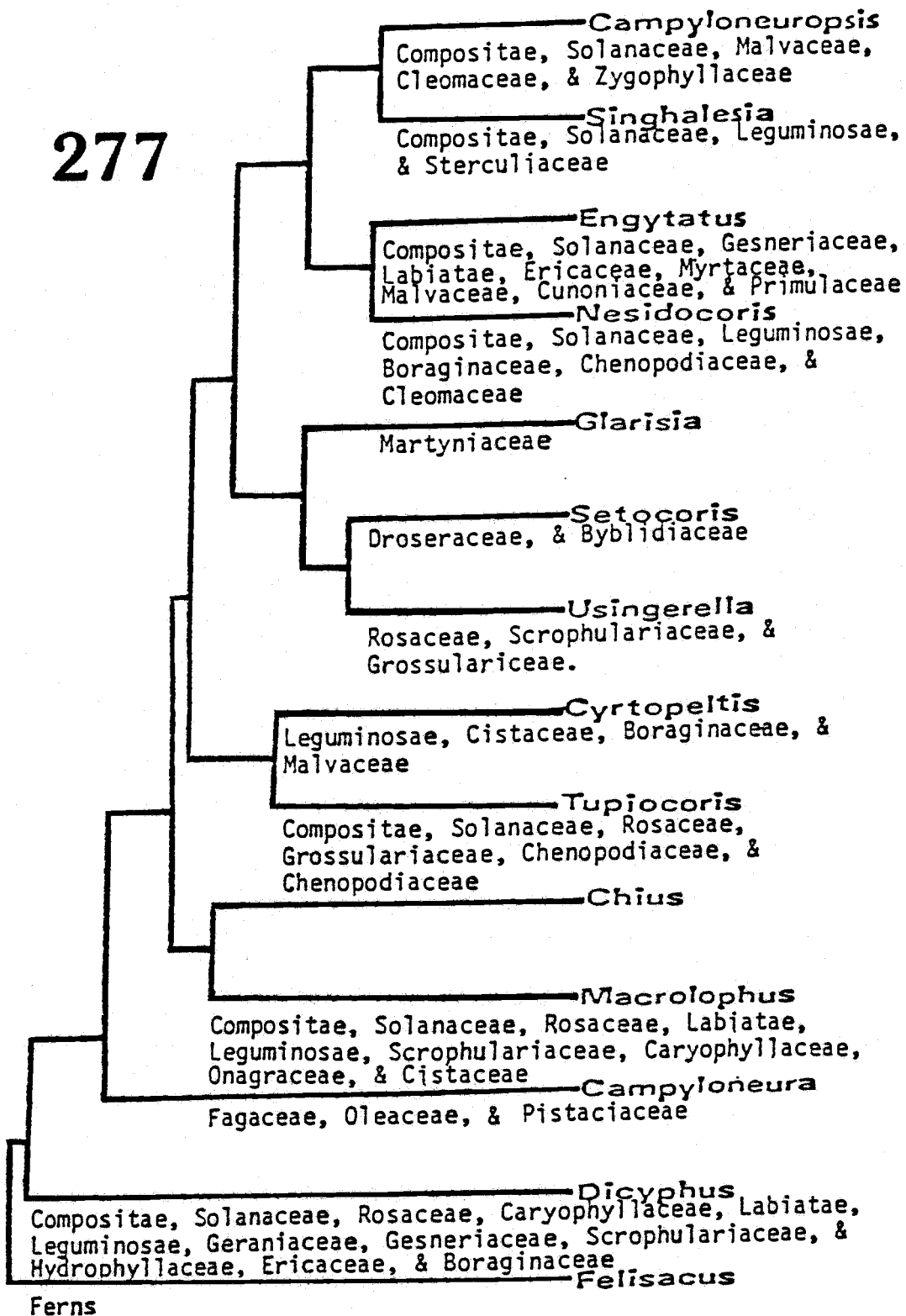


FIGURE 277

CHAPTER 3

A Systematic Study of the Genus Dicyphus Fieber
in the Western Hemisphere.

INTRODUCTION

This chapter contains the results of a systematic study of the genus Dicyphus Fieber in the Western Hemisphere. In a previous study, I proposed a new generic classification for the subfamily Dicyphinae (Cassis, Chapter 2), and considered this genus as a morphologically heterogeneous group. The species are usually pallid with fuscous, red or reddish-ochraceous markings, with a distinct tripartite pronotum (figs. 1, 2, 3), high femoral trichobothria number, fully developed metathoracic scent efferent system, presence of an osteolar peritremal disc, cleft claws, and small parempodia and pseudopulvilli. The genus has a Laurasian distribution with almost all the species confined to the Northern Hemisphere. Most of the species have some degree of host plant specificity, and the majority of the species are associated with plant genera in the families Labiatae, Rosaceae, Caryophyllaceae, Scrophulariaceae, and Compositae.

In a previous paper (Cassis, Chapter 2), I recognized five subgenera in Dicyphus, and described one new subgenus, Uhlerella, for the endemic Nearctic species of Dicyphus. This subgenus is defined morphologically by the presence of a long, narrow peritremal disc (figs. 1, 2), an internal sclerotized bar on the genital aperture of the male, and the tibiae are without spines.

The subgenus Uhlerella is broadly distributed in North America, and its southern limit of distribution is Baja California (Mexico). No species of this subgenus have been recognized in either Central or South America. There are no other North American species of Dicyphus that are considered to be endemic. Eight species belonging to Uhlerella are recognized. Two new species are described, occidentalis n. sp. and nigracorium n. sp. The former is restricted to coastal regions in California, and the latter is widely distributed in the western United States

One species, pallicornis (Meyer-Dur), belonging to the subgenus Idolocoris, is an introduction from Europe (Downes, 1957), and is widespread in coastal localities in British Columbia, Oregon and Washington (U. S. A.), on the introduced plant Digitalis purpurea L.

In this study, all the endemic species are redescribed, and a diagnosis is provided for pallicornis. A listing of host plant associations and distribution

(maps included) is given for each species. A key is provided to all the species, and it should be possible to identify all non-teneral specimens to species.

There was not enough morphological information to conduct a phylogenetic analysis. The group is characterized by considerable character reductions, even in characters that are of taxonomic significance in the genus Dicyphus in the Palearctic. Most of the species separations are based on subtle differences in the male genitalia.

MATERIALS

About 2,500 specimens were examined in this study. The following individuals and institutions loaned the specimens (acronyms in this listing are used in the text to indicate the housing of the type material):

American Museum of Natural History, New York, R. T. Schuh (AMNH); Arizona State University, Tempe, F. F. Hasbrouck; University of Arizona, Tucson, D. B. Thomas; Bernice P. Bishop Museum, Honolulu, Hawaii, W. C. Gagne; British Museum (Natural History), London, England, W. R. Dolling; University of British Columbia, Spencer Entomological Museum, Vancouver, Canada, S. G. Cannings and G. G. E. Scudder; California Academy of Science, San Francisco, P. H. Arnaud, Jr. (CAS); University of

California, Berkeley, J. A. Chemsak and J. B. Whitfield;
University of California, Davis, D. Ford; University
of California, Riverside, J. Pinto and S. I. Frommer
(UCR); University of Connecticut, Storrs, J. A. Slater
and J. E. O'Donnell; Canadian National Collection,
Ottawa, L. A. Kelton (CNC); Colorado State University,
Fort Collins, W. D. Fronk; Cornell University, Ithaca,
New York, L. L. Pechuman; Florida Department of
Agriculture and Consumer Services, Gainesville, F. W.
Mead; University of Georgia, Athens, C. L. Smith;
Harvard University, Museum of Comparative Zoology,
Cambridge, M. Hathaway (MCZ); University of Helsinki,
Zoological Museum, Finland, A. R. I. Jansson; Humboldt
State University, Arcata, California, R. L. Hurley;
University of Idaho, Moscow, W. F. Barr; Iowa State
University, Ames, R. E. Lewis (IWS); Kansas State
University, Manhattan, H. F. Blocker; University of
Kansas, Snow Entomological Museum, Lawrence, J. R.
Schrock and P. Ashlock (UK); R. Linnavouri private
collection, Somersoja, Finland; Los Angeles County
Museum of Natural History, California, C. L. Hogue;
Louisiana State University, Baton Rouge, J. B. Chapin;
University of Michigan, Ann Arbor, M. F. O'Brien;
University of Minnesota, St. Paul, P. E. Clausen (UMIN);
University of Missouri, Columbia, R. Blinn
and T. R. Yonke; Montana University, Bozeman, S. Rose;

Museu Nacional , Rio de Janerio, Brazil, J. C. M.
 Carvalho; Naturhistoriska Riksmuseet, Stockholm, Sweden,
 P. Lindskog; North Arizona University, Flagstaff, C. D.
 Johnson; North Dakota State University, Fargo, E. U.
 Balsbaugh, Jr.; Ohio State University, Columbus, C. A.
 Triplehorn; Oregon State University, Corvallis, J. D.
 Lattin, P. W. Oman, J. D. Oswald, and G. M. Stonedahl
 (OSU); J. T. Polhemus private collection, Engelwood,
 Colorado; University of Queensland, Brisbane, Australia,
 T. E. Woodward; San Diego Society of Natural History,
 California, D. K. Faulkner; Santa Barbara Museum of
 Natural History, California, S. E. Miller; Smithsonian
 Institution, National Museum of Natural History,
 Washington, D. C., W. Mathis and D. R. Smith, and T. J.
 Henry (USNM = main collection; USNM, HHK = H. H. Knight
 collection) ; Texas A. & M. University , College Station,
 J. C. Schaffner (TAM, JSC); United States Department of
 Agriculture, Beltsville, Maryland, T. J. Henry; Utah
 State University, Logan, M. Schwartz and W. J. Hanson
 (UTS); Washington State University, Pullman,
 R. S. Zack; University of Wisconsin, Madison, S. Krauth;
 Yale University, Peabody Museum of Natural History, New
 Haven, C. L. Remington and D. G. Fruth.

METHODS:

The taxonomic decisions in this study were based on comparative morphological studies of the left clasper and the pygophore of the male. Additionally, morphometric features were used as supportive evidence. All measurements in this study are maximum measurements, and are given in millimeters. Unless indicated otherwise, measurements refer to lengths. In some instances color characters were used as diagnostic features, however, its usage was limited to cases where the range of variation could be well documented.

Comparisons of distribution, host plant associations, and phenology were made for each species. The distribution of each species is described using the vegetational descriptors of Bailey (1978).

Dissecting methods and other general procedures are the same as presented in Cassis (Chapter 2).

SYNOPSIS OF THE GENUS DICYPHUS IN THE WESTERN HEMISPHERE:

Dicyphus (Uhlerella)

discrepans Knight

famelicus (Uhler)

gracilentus Parshley

hesperus Knight

nigracorium Cassis, new species

occidentalis Cassis, new species

paddocki Knight

vestitus Uhler

Dicyphus (Idolocoris)

pallicornis (Meyer-Dur)

KEY TO SPECIES OF DICYPHUS FOR WESTERN HEMISPHERE:

1. Ostiolar peritremal disc short; not extending
beyond lateral margin of mesepimeric spiracle
(fig. 3).....Dicyphus (Idolocoris)
pallicornis (Meyer-Dur), p. 338.
- Ostiolar peritremal disc long; extending almost
to metaepimeron (fig. 1,2).....2
2. Second antennal segment with annulations; mostly
testaceous or yellow, with fuscous, apical and/or
apical annulation(s).....3
- Second antennal segment concolorous; either
fuscous or fusco-red.....10
3. Head as long as wide when viewed from above.....
.....famelicus (Uhler)
p. 306.
Head always wider than long when viewed from
above.....4
4. Second antennal segment length smaller than the
posterior width of the pronotum;5

- Second antennal segment length equal to or greater than the posterior width of the pronotum.....
.....7
- 5. Body densely setate; femora with two rows of fuscous markings, sometimes tibiae with single row of fuscous spots on basal 1/5.....
.....paddocki Knight p. 329.
- Body not densely setate; femora sometimes with fuscous markings, but not developed into two rows; tibiae without dark markings.....
.....6
- 6. Hemelytra with black markings on endocorium and clavus; first antennal segment and frons pallid; rostrum extends to apices of mesocoxae; left clasper (figs. 16, 17, 18).....
.....nigracorium n. sp. p. 320.
- Hemelytra at most with light brown infusion; frons and first antennal segment mostly fuscous; rostrum extends to apices of mesocoxae; left clasper (figs. 13, 14, 15).....
.....hesperus Knight (both morphotypes)
p. 314.

7. Second antennal segment length, at least 1.6x in females, and 1.7x in males, greater than the width of the posterior margin of the pronotum....
occidentalis n. sp. p. 325.
- Second antennal segment length, either equal to or maximally 1.4x (both sexes) greater than the posterior width of the pronotum.....
8
8. Head when viewed from above black, with two yellow almost fused spots on postvertex; disc of pronotum black with yellow marking mesally; base of second antennal segment often with fuscous infusion.....
hesperus Knight (melanic morphotype) p. 314.
- Head when viewed from above with mesal red to fuscous markings.....9
9. Sensory lobe of left clasper entire (fig. 13); first antennal segment usually fusco-red to fuscous; macropterous females and males.....
hesperus Knight (pallid morphotype) p. 314.

- Sensory lobe of left clasper entire (fig. 7);
 first antennal segment mesally testaceous, with
 red apical and basal infusions, sometimes
 entirely red, except for endolateral
 margins.....discrepans Knight
 p. 299.

10. Second antennal segment longer than the posterior
 width of the pronotum; large species, males 4.
 25-4.75, females 4.15-4.60; genital aperture of
 males without tubercles.....
gracilentus (Parshley), p. 310.

- Second antennal segment smaller than the
 posterior width of the pronotum; moderately sized
 species, males 3.50-4.00, females 3.50-3.75;
 males with a small tubercle above the left
 clasper, on the genital aperture of males
 (fig. 5).....vestitus (Uhler),
 p. 334.

TAXONOMY

Dicyphus (Uhlerella) discrepans Knight

Figures: 1, 4, 7, and 8.

Dicyphus discrepans Knight 1923: 476 Kelton, 1980b: 373;
Kelton, 1982: 174.

DIAGNOSIS: This species is very similar to hesperus Knight, and can only be distinguished by characters of the male genitalia, antennae, and wing polymorphism. Both sexes can be macropterous, submacropterous, or brachypterous. The latter state is common in individuals from populations in the western United States. The length of the second antennal segment is 1.2x, or greater in males, and 1.1x, or greater in the females than the posterior width of the pronotum, whereas in hesperus specimens it is usually subequal to the basal width of the pronotum. Further, the first antennal segment in the former species is usually testaceous with the apex and base marked with red, however, in rare instances the entire segment can be red or fusco-red, which is the condition found in hesperus.

The two species are most definitely separated by differences in the sensory lobe of the left clasper (cf. figs. 7 and 13).

DESCRIPTION: Males. macropterous, length 3.75 (3.00-3.75), head-abdomen length 3.00 (2.60-3.00); or, brachypterous, length 2.15-3.00, head-abdomen length 1.95-2.75; testaceous with red and fuscous markings; sparsely covered with short, pale, adpressed setae.

Head: length 0.38 (0.33-0.45), width 0.53 (0.53-0.58), vertex width 0.20 (0.20-0.25); variable in color from pallid to fuscous; frons weakly produced in front of eyes, testaceous to entirely enbrowned; vertex testaceous, with red to fuscous band mesally, postocular margins red to fuscous; lateral and ventral surfaces of head brown, often with paler markings on clypeus, lorum and bucculae.

Eyes: large, protruding laterally, height 0.30 (0.28-0.33), width 0.25 (0.23-0.25); fuscous to red, latter condition more common in brachypterous morphotype.

Antennae: inserted at midheight of eyes. I, 0.33 (0.30-0.38), testaceous, with apical and basal red markings, sometimes with red markings along lateral margins, or rarely with entire segment red to fuscured. II, 0.95 (0.80-0.95), testaceous, with apical $1/3$ fuscous, tinged with red. III, 0.55-0.70, linear, basal $1/4$ testaceous, remainder fuscous, with erect setae as II, and apical $1/3$ with long, pale, adpressed setae. IV, 0.25-0.33, fuscous, vestiture as III.

Rostrum: length 1.56 (1.33-1.63), extending between apices of hind coxae and III antennal segment, testaceous, with apex of last segment fuscous.

Pronotum: macropterous, length 0.45 (0.35-0.45), anterior width 0.35 (0.33-0.45), posterior width 0.75 (0.60-0.80); brachypterous, length 0.30-0.38, anterior width 0.33-0.35, posterior width 0.60-0.65; collar large, anterior margin excavate, sometimes with longitudinal, mesal groove, pallid with basal and lateral margins often darker; calli quadrate, enlarged, confluent mesally, separated by fine groove, delimited posteriorly by deep depression, marked with red; disc coriaceous, pallid with posterior angles often fuscate; posterior margin deeply excavate; propleuron fuscate.

Scutellum: with mesal, fuscous band, lateral corners pallid.

Mesepimeron: enlarged, spiracle small, evaporative areas extensive, covering almost entire posterior region of segment and extending on posterior 1/2 and lateral margins of postalare; testaceous with fuscous and red markings (fig. 1).

Metaepisternum: osteole large, peritremal disc large, gradually recurved apically, often marked with red, but sometimes pallid, evaporative areas pallid to fuscous (fig. 1).

Legs: femora, 1.43 (1.30-1.56), yellow, uniformly covered with short, stout, dark setae, trichobothria, 5 meosfemoral and 6 metafemoral; tibiae, 1.95 (1.76-2.15), linear, sometimes brown spots at apex, uniformly covered with long, stout, erect, pale brown setae; tarsi, 0.63 (0.55-0.65), yellow, sometimes last segment infusate.

Hemelytron: length 2.75 (2.20-2.75); brachypterous, length 1.43-2.00; yellow to hyaline with fuscous to red markings on the clavus, claval suture; endocorium and apex of veins of membrane cells, corial fracture, and apex of cuneus marked with brown, sometimes infused with red.

Venter: brown to infusate laterally, sparsely covered with pale, suberect setae; pygophore usually lighter in color than remainder of abdomen.

Genitalia: pygophore (fig. 4), weakly dissected, genital aperture strongly dorsal in orientation, ventral lip with posterodextral orientation; left clasper (figs. 7, 8), sensory lobe strongly dissected on dorsodextral angle (fig. 7), shaft somewhat sinuate, apex not greatly expanded laterally; right clasper small, linear.

Females. brachypterous, rarely macropterous, similar to males in color, vestiture, and general morphology; length, macropterous 3.25-4.00, brachypterous 2.75-3.25; head-abdomen length, macropterous 2.75-3.50, brachypterous, 2.75-3.25. Head: length 0.38-0.50, width 0.53-0.60, vertex width 0.22-0.25. Eyes: height 0.30-0.35, width 0.23-0.28. Antennae: I, 0.30-0.38; II, 0.85-0.95. III, 0.55-0.68. IV, 0.25-0.35. Rostrum: 1.43-1.69. Pronotum: macropterous, length 0.35, anterior width 0.35-0.38, posterior width 0.60-0.65; brachypterous, length 0.45-0.50, anterior width 0.39-0.45, posterior width 0.68-0.90. Legs: femora 1.30-1.43; tibiae, 1.89-2.34; tarsi, 0.55-0.65. Hemelytra: macropterous, 2.50-3.00; brachypterous, 1.82-2.00.

TYPE DATA AND SPECIMENS EXAMINED: Holotype: Male, New York, Cranberry Lake, C. J. Drake (USNM, HHK). Allotype: female, same data as holotype. Paratypes: 2 topotypic (not seen); Minnesota, St Louis Co., Kawishiwi River (2 males, 6 females).

Knight (1923) reported 6 females and 2 males from the Minnesota locality, which, he designated as paratypes. I have seen 8 females with paratype labels with same data as paratypes (USNM, 4 females; CAS, 1 female; IWS, 1 female; UMIN, 2 females, 1 male). There are also

two female specimens from the same series (UMIN) that are not labelled as paratypes.

In addition to the type material, I have examined another 478 specimens from the following places in North America: U. S. A.: Alaska, Washington, Oregon, Idaho, Colorado, North Dakota, Minnesota, Michigan, Wisconsin, New York, Vermont, New Hampshire, and Maine; Canada: British Columbia, Yukon, and Quebec.

REMARKS: This species was described by Knight (1923) from a pair of specimens in copula. Because of the close similarity of hesperus Knight and discrepans Knight, I deemed it necessary to separate the types in copula to examine the left clasper of the male. This was achieved without any damage to either specimen, and the male was placed on a separate point, and on the same pin as the allotype female.

This species has a boreal distribution with a southern extension into the Rocky Mountains of Colorado, and is commonly found west of the Cascade Ranges in Oregon (see map 1). It is broadly sympatric with hesperus in the western United States, but it is apparently not found in California, nor does it extend into Utah and Arizona (as hesperus does).

The alary polymorphism in this species is intriguing. There is no apparent sexual pattern as Kelton (1980b) suggested. In the eastern and northern (Alaska only)

parts of its range, both sexes are always macropterous, whereas from Minnesota and westward both sexes are almost always brachypterous, although in some populations there are macropterous males and/or females. The diversity of wing conditions throughout this species range, and the non-sex polymorphism suggests that the condition is induced environmentally.

This species is most probably multivoltine in most parts of its range. In Oregon and in other temperate latitudes, adults are recorded from March to October. Knight (1927) suggested that this wide phenological range was indicative of overwintering adult behaviour, however, there is no biological reasoning to support this suggestion.

This species has a wide host plant range, like hesperus and has been collected from the following host plants: Horkelia sp., Aster sp. (Compositae), Scrophularia californica, Castilleja sp. (Scrophulariaceae), Rosa sp., Rubus sp., Ranunculus sp. (Rosaceae), and Stachys sp. (Labiatae).

Dicyphus (Uhlerella) famelicus (Uhler)

Figures: 9 and 10.

Idolocoris famelicus Uhler 1878: 413.

Dicyphus famelicus Atkinson 1890: 128; Carvalho 1958: 197; Kelton, 1982: 172.

DIAGNOSIS: This species is the largest of the North American species, and is easily distinguished from other species by the very elongate head, which is as long as wide, and the eyes are removed from the collar by the dorsal length of the eye.

DESCRIPTION: Males. macropterous; costal margins parallel, elongate, linear; length 4.50-4.80, head-abdomen length 3.00-3.50; testaceous with brown to red markings, sparsely covered with fine, long, pale setae.

Head: length 0.55-0.58, width 0.55-0.58, vertex width 0.20-0.23; elongate as long as wide; frons weakly produced in front of eyes; postocular margins of vertex linear, strongly convergent, red to brown; testaceous with meso-longitudinal red marking from midfrons to vertex, sometimes indistinct between eyes.

Eyes: height 0.33-0.35, width 0.25-0.30, large, strongly rounded, removed from collar by lateral width of eye; facets small; red.

Antennae: inserted at midheight of eyes. I, 0.45-0.55, with subapical and subbasal red markings, remainder

testaceous, with simple, adpressed setae. II, 1.37-1.43, apical 1/3 dark brown to fuscous with reddish tinge, evenly covered with erect, brown setae, apical 1/3 with small, pale adpressed setae. III, 0.91-0.98, thinner than II, basal 1/4 testaceous, remainder fuscous with reddish tinge, vestiture as apex of II. IV, 0.42-0.48, fuscous, vestiture as III.

Rostrum: length 1.82-1.95, extending to apices of metacoxae, testaceous, darker toward apex of last segment.

Pronotum: length 0.53-0.58, anterior width 0.35-0.40, posterior width 0.85-0.96; calli strongly rounded, confluent mesally, separated by fine, linear groove; posterior margin deeply excavate; posterior angles fuscous, remainder testaceous.

Scutellum: mesally ochraceous to reddish, outer anterior angles testaceous to yellow.

Thoracic pleura: same as discrepans.

Legs: femora, length 1.76-1.98, testaceous, sometimes with brown markings, or with subapex enbrowned, simple, stout, dark setae; trichobothria, 6 mesofemoral and 7 femoral; tibiae, length 2.47-2.80, testaceous, with small, stout setae, and rows of spinelets, but devoid of large spines; tarsi, length 0.60-0.72, testaceous, last segment fuscous.

Hemelytra: length 3.20-3.50, macropterous, rarely submacropterous; yellow to whitish with red markings on clavus, endocorium, corial fracture, and apex of cuneus, sometimes variable, or ochraceous or dark brown.

Genitalia: pygophore, genital aperture dorsal; left clasper (figs. 9, 10), sensory lobe small, setae restricted to ventral margin, shaft small, tip of shaft strongly expanded laterally; right clasper small, linear.

Females. similar to males in shape, color, and vestiture; length 4.50-5.00, head-abdomen length 3.50-4.00. Head: length 0.50-0.63, width 0.55-0.58, vertex width 0.20-0.23. Eyes: height 0.33-0.35, width 0.25-0.27. Antennae: I, 0.45-0.50; II, 1.30-1.37; III, 0.88-1.04; IV, 0.39-0.42. Rostrum: length 1.75-1.95, extending to apices of metacoxae. Pronotum: length 0.55-0.65, anterior width 0.38-0.43, posterior width 0.85-0.98. Legs: femora, length 1.69-1.82; tibiae, length 2.41-2.80; tarsi, length 0.55-0.72.

TYPE DATA AND SPECIMENS EXAMINED:

"Type" male: New Hampshire, Mr. Leonard, No. 101, Harris Collection; "Capsus famelicus Say", manuscript name (not seen, see Remarks section).

I have examined 254 specimens from the following places in North America: U. S. A.: Maine, New Hampshire, Vermont, Massachusetts, Connecticut, New York, New Jersey, West Virginia, North Carolina, Pennsylvania, Ohio, Michigan, Wisconsin, Minnesota, and Iowa; Canada: Quebec and Ontario.

REMARKS: Uhler (1878) designated a type specimen, however, I have not as yet located it. It is most probably in the Harris collection at MCZ. Despite the absence of the type, there is no doubt as to the identity of this species, based on the original description, and identified material (by H. H. Knight).

This is the most distinctive Nearctic species of the genus Dicyphus (Uhlerella), having an elongate head which is somewhat similar to that found in Macrolophus Fieber species. Caution is advised with the use of this character, as it is variable within this species, and depends to a great degree on the "telescoping" of the head.

This species is distributed in eastern North America (see map 2), and is restricted to the Laurentian Mixed Forest, and Eastern Deciduous Forest Provinces. Collection dates range from April 18 to November 9. The only recorded host plant is Rubus odoratus (Rosaceae), and this species is apparently host specific.

Dicyphus (Uhlerella) gracilentus Parshley

Figures: 11 and 12.

Dicyphus gracilentus Parshley 1923: 21.

DIAGNOSIS: This species is clearly distinguished from other eastern North American species of Dicyphus by the predominately black to fuscous head and scutellum, and the concolorous first and second antennal segments. It is superficially similar to famelicus, but is generally darker in color, smaller in size, and the head is never as long as wide. It can be confused with vestitus on the basis of color, however, the latter species is generally broader and has a small tubercle above the left clasper on the genital aperture, which is absent in gracilentus.

DESCRIPTION: Males. macropteorus; costal margins almost parallel, elongate; length 4.25-4.75, head-abdomen length 3.00-3.25, base color yellow with fuscous, fuscured and orange markings; almost devoid of setae. dorsum sparsely clothed with pale, fine, adpressed setae.

Head: length 0.45-0.50, width 0.60-0.65, vertex width, 0.23-0.26, highly polished, shiny, mostly fuscous, posterior margin of vertex with yellow to ochraceous markings; dorsum sometimes subdivided by fine, brown, longitudinal line; laterally fuscous, gula yellow, sometimes bucculae marked with yellow.

Eyes: large, strongly protruding, height 0.38-0.40, width 0.30-0.32; dull red.

Antennae: inserted below midheight of eyes. I, 0.40-0.45, red, sometimes with yellow markings on mesolateral areas, with stout, dark, adpressed setae; II. 1.17-1.37, fuscous to fusco-red, uniformly covered with pale brown setae; III, 0.91-0.98, fuscous, vestiture as II. IV, 0.38-0.45, fuscous.

Rostrum: 1.76-1.95, reaching between apices of metacoxae and third abdominal segment, yellow, fuscous at apex.

Pronotum: subtriangular, length 0.55-0.60, anterior width 0.38-0.40, posterior width 0.88-0.98; collar large, yellow, mesally constricted; calli large, subquadrate, yellow, shiny, confluent mesally; disc concolorous with calli, posthumeral angles sometimes enbrowned, posterior margin deeply excavate, coriaceous; propleuron fuscous, shiny.

Scutellum: brown to fuscous, with anterolaterad angles yellow.

Thoracic pleura: same as for discrepans.

Legs: femora, 1.69-1.82, linear, yellow, sometimes with row of brown spots on apical half, uniformly covered with stout, brown, suberect setae; tibiae, 2.60-2.93, linear, yellow, uniformly covered with pale brown, erect

setae; tarsi, 0.60-0.78, last segment fuscous, remainder yellow.

Hemelytra: length 3.25-3.65, hyaline with endocorium and clavus enbrowned, tip of cuneus and corial fracture with fuscous spots, membrane with coriaceous texture.

Venter: concolorously yellow, except for fuscous spot on ventral aspect of pygophore, sparsely covered with fine, suberect setae.

Genitalia: pygophore strongly dorsal in orientation, ventral margin of genital aperture produced into a dextral oriented lip; left clasper (figs. 11, 12) simple, sensory lobe entire, apex of shaft expanded laterally.

Females. macropterous, similar to males in color, shape, and general morphology; length 4.00-4.50; head-abdomen length 3.00-3.25. Head: length 0.40-0.45, width 0.60-0.65, vertex width 0.23-0.25. Eyes: height 0.33-0.35, width 0.25-0.30. Antennae: I, 0.40-0.45; II, 1.00-1.15; III, 0.90-0.95; IV, 0.38-0.48. Rostrum: length 1.69-1.89. Pronotum: length 0.50-0.55, anterior width 0.38-0.43, posterior width 0.85-0.90. Legs: femora 1.56-1.69; tibiae 2.21-2.47; tarsi 0.65-0.72. Hemelytra: length 3.00-3.25.

TYPE DATA AND SPECIMENS EXAMINED: Holotype male:

Illinois, Champaign Co., Urbana, July 14, 1922, P. A.

Glick (CAS, type # 9348, male; type seen). Allotype:, same data as holotype (CAS, female; type seen).

Paratypes: same data as holotypes. Parshley (1923)

reported numerous male and female paratypes, of which I have examined six males (USNM, 3; UMIN, 1; CAS, 1; IWS, 1), and five females (USNM, 4; UMIN, 1). There are also 3 males (USNM, HHK, 2; CAS, 1), and eight females (USNM, HHK, 5; CAS, 3) which have the same data as the holotype, but have no paratype labels. I have designated these as paratypes because Parshley (1923) did not indicate the designated number of paratypes. Parshley (1923) also recognized paratypes with the same locality data, but with the collection dates: July 8, 1887 (C. A. Hart collector), July 2, 1921, and September 26, 1921 (A. O. Weese collector). I have observed one badly damaged specimen without head or abdomen, and one female with the July 2 date (USNM). Also, there are an additional eight males and six females with this data which have no paratype labels. One female with the September date (UMICH) has also been examined. All the above specimens, I have designated as paratypes. Two additional male specimens with the collection dates, September 18, 1921 and August 8, 1922, have paratype labels (CAS), however, Parshley (1923) did not refer to these specimens.

An additional 102 specimens have been examined from the following U. S. A. states: Indiana, Michigan, Wisconsin, and Illinois. Knight (1943) reports that this species is also known from Ohio, however, I have not seen specimens of this species from this state.

REMARKS: This species has a restricted distribution in the eastern United States (see map 3), and is found in the Eastern Deciduous Forest province, and the Oak-Hickory Bluestem Parkland Section of the Prairie Parkland Province. Collection dates range from April 28 to October 13. It is apparently restricted to one host plant, Polymnia canadensis (Compositae), and Knight (1941) reports that it inhabits, deep, shady woods.

Dicyphus (Uhlerella) hesperus Knight

Figures: 13, 14, and 15.

Dicyphus hesperus Knight 1943: 56; Carvalho 1958: 197; Knight 1968: 73; Kelton 1980b: 374; Kelton 1982: 176.

DIAGNOSIS: This species shows extreme variation in color, size, and is consequently difficult to separate from both, discrepans Knight and nigracorum, n. sp..

It differs from the latter two by the fuscous, fusco-red or red first antennal segment, but in some instances it may be pallid mesally which will cause misidentification if this character is used exclusively. The lateral expansion of the left shaft clasper (fig. 15) of the male

is the most distinguishing feature. The second antennal segment is variable in length relative to the posterior width of the pronotum, but is most often subequal to it. There are two color morphs in this species: a melanic and a pallid form. The former is readily recognized by the almost entirely blackened head and pronotum, and is restricted geographically to Idaho, Utah and California. The pallid form is ubiquitous and where it is sympatric with discrepans, the left clasper character should be examined in combination, with the ratio of the second antennal segment to the posterior width of the pronotum for a proper identification. This species does not have the color pattern of nigracorium.

DESCRIPTION-PALLID MORPHOTYPE: Males. length 3.50 (3.25-4.00), head-abdomen length 2.40 (2.25-2.80), macropterous, very rarely brachypterous, abdomen terminates at corial fracture; testaceous with fuscous to black, and red markings on dorsum, sparsely covered with pale to brown, erect, long setae.

Head: length 0.35 (0.33-0.40), width 0.55 (0.50-0.60), vertex width 0.22 (0.20-0.23), pentagonal; frons moderately produced in front of eyes, black to fuscous, sometimes light brown, often produced into two longitudinal, posteriorly converging bands, separated mesally, and areas adjacent to eyes by yellow to

testaceous markings; vertex pallid, with meso-longitudinal red to light brown marking, postocular margins linear, convergent, fuscous to black, rarely red.

Eyes: large, height 0.33 (0.30-0.35), width 0.25 (0.23-0.25); red to fusco-red.

Antennae: inserted at midheight of eyes. I, 0.25 (0.25-0.33), fuscous, fusco-red or red, rarely pallid mesally; II, 0.85 (0.75-1.05), with apical 1/4 to 1/3 fuscured, remainder testaceous; III, 0.55 (0.45-0.60), with apical 1/5 testaceous, remainder red to brown; IV, 0.25 (0.25-0.30), fuscured to brown.

Rostrum: length 1.37 (1.37-1.56), extending between apices of metacoxae and third abdominal segment; testaceous with tip of last segment, and sometimes basal 1/2 of first segment embrowned to fuscous.

Prontoum: length 0.35 (0.35-0.45), anterior width 0.33 (0.33-0.40), posterior width 0.78 (0.70-1.00); collar large, anterior margin weakly excavate, testaceous, lateral margins marked with black; calli small, mesal confluence often obscure, widened anteriorly, posterior margin weakly sinuate, pale brown to testaceous, with mesal separation often yellow; disc pale brown to testaceous, sometimes marked with fuscous, but never entirely, pallid mesally, longitudinal band; posterior margin excavate; propleuron entirely black.

Thoracic pleura: structurally identical to discrepans; mesepimeron, evaporative areas yellow to whitish, often with reddish infusion; metaepisternum, evaporative areas testaceous to brown, osteolar peritremal disc reddish, rarely yellow.

Legs: femora, length 1.37 (1.34-1.56), linear, yellow, sometimes marked with brown spots, uniformly covered with pale to dark, stout setae; trichobthria, 5 mesofemoral, 6 metafemoral; tibiae, 1.82 (1.76-2.08), yellow, covered with stout, suberect setae; tarsi, 0.55 (0.55-0.63), testaceous, last segment fuscous.

Hemelytra: length 2.75 (2.60-3.25), but mostly testaceous with light brown markings on corium, regions posterad to clavus often fuscous; corial fracture and apex of cuneus marked with red.

Venter: pale to brown, if brown then pygophore with testaceous markings.

Genitalia: pygophore not deeply dissected, genital apterure dorsal; left clasper (figs. 13, 14, 15), dorsal margins of sensory lobe entire, sometimes weakly truncate at junction of shaft, shaft recurved, linear, apex greatly expanded laterally, arising as a ridge off the shaft.

Females. similar to males in shape, color, vestiture, and general morphology; macropterous; length 3.25-4.00, head-abdomen length 2.50-2.95; hemelytra terminates at apex of cuneus. Head: length 0.35-0.43, width 0.55-0.60, vertex width 0.22-0.24. Eyes: height 0.30-0.35, width 0.23-0.28. Antennae: I, 0.25-0.30; II, 0.83-0.90; III, 0.53-0.60; IV, 0.25-0.30. Rostrum: length 1.44-1.56. Pronotum: length 0.35-0.40, anterior width 0.35-0.40, posterior width 0.80-1.00. Legs: femora 1.30-1.43; tibiae 1.82-1.95; tarsi 0.50-0.55. Hemelytra: length 2.50-3.00.

COLOR DESCRIPTION-MELANIC MORPHOTYPE: mostly black, sometimes fuscous, with yellow to testaceous markings. Head black with two yellow markings on vertex. Eyes fusco-red to fuscous. Rostrum testaceous with apical half of first segment and apex of last segment fuscous. Antennae, coloration similar to pallid morphotype, except II is often embrowned on basal 1/3. Pronotum, collar testaceous; calli fuscous to brown, separated by wide testaceous marking mesally; disc black to fuscous mesally, separated by mesal, yellow band. Thoracic pleura black to fuscous, osteolar peritremal disc dark, sometimes red. Hemelytra similar to pallid form, except corial fracture marked with brown. Venter black to fuscous, sometimes pygophore with pallid markings.

TYPE DATA AND SPECIMENS EXAMINED:

Holotype: Male, Idaho, Moscow, T. A. Brindley, April 19, 1933 (USNM, HHK). Allotype: female, same data as holotype (USNM, HHK). Paratypes: 2 males and 2 females, same data as holotype (USNM, HHK); same locality and collector, male and female, April 4, 1933 (USNM, HHK); same locality and collector as holotype, one female, May 7, 1936 (USNM, HHK); same locality and collector, female, October 28, 1938. Knight (1943) lists another 91 paratypes (which I have not seen), from Idaho, Montana, North Dakota, Washington, Oregon, Utah, Colorado, and California.

I have examined an additional 721 specimens from the following states in North America, U. S. A.: Montana, Idaho, Utah, Arizona, Washington, Oregon, and California; Canada: British Columbia; Mexico: Baja California.

REMARKS: This species is broadly distributed in western North America. From the specimens examined the eastern limit is Montana (Bear Paw Mountain), the southern limit is Mexico (Baja California, Cedros I.), and the northern limit is Canada (British Columbia, Fort St. John, map 4). This species is not apparently restricted to vegetational provinces, and is recognized from 15 different provinces. Knight (1968) also records this species from Colorado and Wyoming, and Kelton (1980b) reports it as far east as western Manitoba (Canada).

There is no altitudinal zonation recognized for hesperus as it is found in coastal, desert, and montane situations (maximum altitude 6500 feet).

Furthermore, the collection data of specimens examined indicates that this taxon is probably multivoltine. For example, it is recorded from Oregon from late February to November.

The ubiquity of this taxon is partly explained by the wide host plant range. It is associated with the following plants: Verbascum thapsus (Scrophulariaceae), Rubus strigosus (Rosaceae), Stachys rigida, S. albens (Labiatae), Arctostaphylos sp. (Ericaceae), Phacelia distans (Hydrophyllaceae), Ribes sp. (Grossulariaceae), and tomato (Solanaceae).

The two color morphotypes are not considered separate species, as there are no structural differences between them, nor are there any distributional disjunctions. The melanic morphotype is most commonly found in California, Idaho and Colorado, between April and September, whereas the pallid form is most common in the northern sections of its range, from southern Oregon north, and is commonly found between March and November.

Dicyphus (Uhlerella) nigracorium Cassis. New species.

Figures: 16, 17, and 18.

DIAGNOSIS: This taxon is very similar to hesperus,

however, it is generally much broader and larger, and has a distinctive coloration pattern. The second antennal segment is always smaller than the posterior width of the pronotum. In specimens of hesperus where the latter character state is present, then the frons and vertex are fuscous to fusco-red, whereas in this species the frons is always pallid. Furthermore, in nigracorium the apex of the left clasper is not greatly expanded laterally (cf. figs. 15, 18).

DESCRIPTION: Males. macropterous, hemelytra terminating at corial fracture; length 4.00 (3.75-4.25), head-abdomen length 3.00 (3.00-3.25); testaceous with fuscous to black markings, sometimes with reddish infusions; setation regular, pale, erect.

Head: length 0.38 (0.38-0.48), width 0.60 (0.60-0.63), vertex width 0.25 (0.25-0.28); broad, mostly testaceous, often with mesal, red longitudinal marking on dorsum, sometimes frons with indistinct, pale brown infusion; postocular margins of vertex black to fuscous; clypeus testaceous dorsally, remainder of lateral aspect of head fuscous to black.

Eyes: protrudent; height 0.30 (0.30-0.35), width 0.23 (0.23-0.26); fusco-red.

Antennae: inserted below midheight of eyes; I, 0.35 (0.35-0.38), mostly testaceous, with subbasal fusco-red ring, sometimes apex with light red infusion; II, 0.90 (0.85-0.90), testaceous, with apical 1/4 fusco-red; III, 0.55 (0.55-0.65), basal 1/4 testaceous, remainder brown to fuscous; IV, 0.30 (0.30-0.35), brown to fuscous.

Rostrum: length 1.37 (1.33-1.43), yellow to testaceous, sometimes base of first segment embrowned, apex of last segment fuscous.

Prontoum: trapezoidal, length 0.50 (0.45-0.53), anterior width 0.45 (0.43-0.45), posterior width 0.93 (0.93-0.98); collar weakly constricted mesally; calli subquadrate, mesal separation obscure, posterior sulcus indistinct mesally, with red infusion mesally, remainder testaceous; disc coriaceous, testaceous, often posterior angles fuscous; posterior margin deeply excavate; propleuron fuscous.

Mesonotum: black with lateral angles yellow.

Scutellum: with broad, mesal, black marking, anterolaterad angles yellow.

Thoracic pleura: basalare anteriorly red, remainder black; mesepimeron, evaporative areas whitish; metaepisternum, evaporative areas black to fuscous, osteolar peritremal disc red.

Legs: femora, 1.37 (1.37-1.56), testaceous to yellow, sometimes with one row of brown spots, variable in position, often with subapical enbrowment; trichobothria, 6 mesofemoral, 6 metafemoral; tibiae, 1.95 (1.95-2.08), testaceous to yellow; tarsi, 0.55 (0.55-0.65), small, last segment fuscous, remainder testaceous with first segment with brown infusion.

Hemelytra: length 3.00 (3.00-3.25), mostly testaceous to whitish, color pattern distinctive; corial fracture and corium with black to fuscous markings; clavus black mesally, apex fusco-red.

Venter: fuscous to black, pygophore with testaceous markings.

Genitalia: similar to hesperus, except apex of left clasper is not greatly expanded (fig. 18).

Females. macropterous; similar to males in color, shape, setation, and general morphology; length 3.75-4.50, head-abdomen length 3.00-3.75. Head: length 0.40-0.45, width 0.60-0.65, vertex width 0.25-0.30. Eyes: height 0.30-0.33, width 0.22-0.25. Rostrum: length 1.30-1.43. Pronotum: length 0.50-0.55, anterior width 0.40-0.45, posterior width 0.93-1.10. Legs: femora, 1.33-1.56; tibiae, 1.95-2.34; tarsi, 0.55-0.65. Hemelytra: length 3.00-3.40.

TYPE DATA: Holotype male: New Mexico, Otero Co., 4 miles E. Cloudcroft, June 22, 1979, Delorne, McHugh Carrola, Friedlander, and J. C. Schaffner collectors (TAM, JSC). Paratypes: same data as holotype, 1 male and 4 females (TAM, JSC); Colorado, Adams Co., Denver, N. Banks collection, 1 female (AMNH); Idaho, Franklin Co., Thomas Springs, June 28, 1974, Knowlton, Hanson, 1 male (UTS); same county as latter, Cub River Canyon, Preston Campground, June 24, 1976, Knowlton, Cazier, 1 female (UTS); Utah, Utah Co., Provo, Environs, May 27, 1957, G. L. Wielsen, 1 male (UTS); same locality and collector as latter, May 8, 1954, 1 female (UTS); Weber Co., Ogden Canyon, Snow Basin, Maple Forest Camp, June 24, 1962, C. W. O'Brien, 1 female (UCR); Box Elder Co., Welsville, C. L. Allen, May 19, 1948 (UTS). California, Modoc Co., Modoc Lava Caves, June 23, 1946, J. C. Schuh, ex. Scrophularia sp., 1 male, 5 females (OSU); Los Angeles Co., Sawtelle, March 17, 1930, C. H. Hicks, J. C. Lutz collection, 7 males, 2 females (USNM); New Mexico, Mountainhair, April, 1925, J. C. Lutz, 1 female (USNM); Arizonia, Santa Cruz Co., Santa Rita Mountains, Trail from Madera Canyon to Aqua Caliente Saddle, August 26, 1980. J. Pinto, 2 females (UCR); Pima Co., Santa Catalina Mountains, Mt. Lemmon, July 27, 1917, H. H. Knight, 1 female (USNM< HHK).

This species is described from 40 specimens. Three specimens from Colorado have no locality or date information (OSU, accession #'s 566, 2463, and 2465) and are therefore not included as type material.

REMARKS: This taxon has a puzzling distribution pattern (see map 5) being confined to montane regions in California, Idaho, Colorado, Arizona, and New Mexico. One series of specimens is recorded from low elevations in California (Los Angeles Co., Sawtelle), however, there is no doubt to its conspecificity with the other specimens examined. This suggests that this species may be more widely distributed, but is poorly sampled.

The only recorded host plant for this species is Scrophularia sp. (Scrophulariaceae), and collection dates range from March 17 to August 26.

Dicyphus (Uhlerella) occidentalis Cassis. New species.

Figures: 19 and 20.

DIAGNOSIS: This species is described from ten specimens from four coastal localities in California, and is readily distinguished by the enlarged clypeus, jugum, and the narrow, anteriorly produced lorum. Furthermore, the appendages are very long; the first antennal segment is almost as long as the width of the head across the eyes, the second antennal segment is at least 1.7x in males,

and 1.6x in females, greater than the posterior width of the pronotum, and the hind femora are almost as long as the body. The pygophore in the males is greatly expanded dorsoventrally and the left clasper is enlarged (figs. 19, 20), although of a similar type to that found in discrepans. Both sexes are known only from brachypterous individuals.

DESCRIPTION: Males. brachypterous, hemelytra terminating just beyond tip of abdomen; testaceous with extensive fuscous markings, and with red to reddish or ochraceous markings on dorsum; length 3.10 (3.00-.3.25); sparsely covered with pale, suberect setae.

Head: length 0.40 (0.40-0.45), width 0.60 (0.58-0.63), vertex width 0.30 (0.28-0.30); frons evenly rounded in front of eyes, with longitudinal, fuscous to red markings; vertex red mesally, remainder testaceous, postoccular margins fuscous to red; clypeus strongly protruding, testaceous dorsally, sometimes fuscous ventrally; jugum enlarged, triangular; lorum produced anteriorly, fuscous.

Eyes: height 0.33, width 0.23-0.25, produced weakly.

Antennae: very long, subequal to body length; inserted below midheight of eyes; I, 0.55 (0.55-0.58), long, 0.92x or greater than the width of head across eyes, yellow mesally, with basal and apical, fuscous

markings; II, 1.43 (1.30-1.48), at least 1.7x width of posterior margin of pronotum, testaceous, with apical, red to fuscured band, sometimes with mesal, red infusion; III, 0.78 (0.78-0.83), fuscous, with small, basal, yellow band; IV, 0.39 (0.35-0.39), fuscous.

Rostrum: length 1.82 (1.82-1.95), extending to fourth abdominal segment; testaceous, fuscous at tip.

Pronotum: length 0.45 (0.45-0.50), anterior width 0.43 (0.40-0.43), posterior width 0.75 (0.73-0.78); collar enlarged, constricted mesally, testaceous with mesal, red infusion, fuscous laterally; calli enlarged, raised, longer than disc, quadrate, confluent mesally, testaceous mesally to entirely brown; disc small, dark brown to fuscous, always testaceous mesally, posterior margin almost linear; propleuron fuscous.

Scutellum: brown, lateral angles testaceous.

Thoracic pleura: identical to discrepans, peritremal disc red.

Legs: very long; femora, 2.02 (1.95-2.08), linear, testaceous, with subapical brown band, uniformly covered with pale brown suberect setae; trichobothria, 5 mesofemoral, 5 metafemoral; tibiae, 3.00 (2.73-3.06), testaceous; tarsi, 0.78 (0.73-0.78), last segment fuscous.

Hemelytra: length 2.25-2.35; clavus coriaceous, reddish-brown mesally, extremities yellow; corial

fracture and apex of cuneus brown.

Venter: testaceous mesally, fuscous laterally.

Genitalia pygophore with dorsal and ventral, fuscous markings; ventral margin of genital aperture strongly projecting dextrally; left clasper (figs. 19, 20), lobe small, weakly dissected at junction with shaft, shaft long with a long ridge, outer margin not greatly expanded (fig. 20).

Females. similar to males in color, shape, setation, and general morphology; length 3.00-3.20; head-abdomen length 3.00-3.20; brachypterous. Head: length 0.40-0.45, width 0.58-0.63, vertex width 0.23-0.25. Eyes: height 0.28-0.30, width 0.20-0.23. Antennae: I, 0.45; II, 1.17-1.20; III and IV missing on all female specimens. Rostrum: length 1.82-1.89. Pronotum: length 0.40-0.43, anterior width 0.40-0.43, posterior width 0.65-0.70. Legs: femora, 1.69-1.82; tibiae, 2.47-2.60; tarsi, 0.75-0.78. Hemelytra: length 2.08-2.15.

TYPE DATA: Holotype male: California, San Mateo Co., Crystal Lakes, April 25, 1916, E. P. Van Duzee, 1 male (CAS). Paratypes: same county as latter, April 25, 1917, 300-1200 feet, W. M. Giffard, 2 males (CAS); Monterey Co., Monterey, July 22, 1935, R. H. Beamer, 5 females (KU); Humboldt Co., Falk, B. P. Bliven, August 9, 1959, BBP 579, 1 male (CAS, BBP); Marin Co., November 8,

1953, V. Roth, 1 male (CAS).

REMARKS: This species is distributed in coastal California between Humboldt Co. and Monterey Co. (see map 7). The female specimens of this species are only recorded from the latter locality, and their association with the males from the more northern areas is adjudged from structural similarities, particularly the long appendages.

This taxon is apparently restricted to the Redwood Forest Section of the Pacific Forest Province, and the Monterey locality most likely represents the southern limit of its range. The collection dates for occidentalis range from July 17 to November 8. There is no recorded host plant for this species.

Dicyphus (Uhlerella) paddocki Knight

Figures: 2, 21, and 22.

Dicyphus paddocki Knight 1968: 73.

DIAGNOSIS: This species is readily distinguished from other Californian species of Dicyphus (Uhlerella) by its elongate-ovoid shape, and broadness of the head across the eyes. The second antennal segment is always shorter than the posterior width of the the pronotum, in both sexes. Further, the head has a distinctive coloration pattern and the entire body, particularly the venter,

is covered with fine, long, erect to suberect setae. The left clasper is similar to discrepans (figs. 21, 22), and is distinct from the left clasper of, hesperus, which is not dissected at the junction between the lobe and the shaft.

DESCRIPTION: Males. macropterous, costal margins weakly convex, hemelytra terminates at corial fracture; length 3.75-4.00, head-abdomen length 2.60-2.75; pallid with brown markings; uniformly covered with pale to dark, long, erect setae.

Head: length 0.33-0.43, width 0.60-0.63, vertex width 0.23-0.25; frons broadly rounded anteriorly, with two converging black to fuscous markings, yellow mesally; vertex yellow with two brown spots mesally, base and postocular margins marked with brown; ventral aspect of clypeus, jugum, lorum brown; gula and buccula yellow to light brown.

Eyes: height 0.33-0.35, width 0.23-0.25; brownish-red.

Antennae: inserted at midheight of eyes, antennal insertions raised; I, 0.35-0.38, yellow, with a basal, brown to brown-red band, and apical, red band; II, 0.95, weakly expanded distally, apical $1/4$ - $1/3$ brown, remainder yellow to testaceous, sometimes with subbasal enbrowment.

Rostrum: length 1.43, reaching apex of metacoxae, apex of last segment fuscous.

Pronotum: length 0.45-0.50, anterior width 0.40-0.43, posterior width 1.00-.105; subquadrate, lateral margins strongly divergent; collar strongly constricted mesally, whitish to yellow; calli subdivided mesally, brown, yellow mesally; disc brown, posterior angles often fuscate, posterior margin weakly excavate; propleuron concolorous with calli, never fuscous.

Scutellum: coriaceous, brown mesally, lateral angles yellow.

Thoracic pleura: similar to discrepans structurally, evaporative areas on both mesepimeron and metaepisternum yellow; osteolar peritremal disc testaceous.

Legs: coxae, base fuscous, remainder yellow; femora, 1.50-1.56, somewhat fusiform, yellow, with two rows of brown spots; trichobothria, 6 mesofemoral, 7 metafemoral; tibiae, 2.08-2.28, apical 1/5 with diffuse, brown spots, basally infused with brown, remainder testaceous; tarsi, 0.55-0.65.

Hemelytra: length 2.95-3.20, hyaline, infused with brown on endocorium, clavus, corial fracture, and apex of cuneus; minor cell large.

Genitalia: pygophore more dissected than discrepans; left clasper (figs. 21, 22) large, lobe large, dorsal surface dissected, apex of shaft skewed and moderately

expanded laterally.

Females. similar to males in color, shape, vestiture, and general morphology; macropterous, abdomen terminates at apex of cuneus; length 4.10 (3.70-4.10), head-abdomen length 3.25 (2.85-3.25). Head: length 0.38 (0.38-0.42), width 0.63-0.65, vertex width 0.25. Eyes: height 0.33 (0.33-0.38), width 0.25 (0.23-0.25). Antennae: I, 0.33 (0.33-0.38); II, 0.90 (0.83-0.90); III, 0.60 (0.48-0.60); IV, 0.25. Rostrum: length 1.56 (1.50-1.56). Pronotum: length 0.48 (0.45-0.50), anterior width 0.43 (0.40-0.45), posterior width 0.95 (0.95-1.00). Legs: femora, 1.43-1.48; tibiae, 2.02-2.08; tarsi, 0.55-0.65. Hemelytra: length 3.20 (2.85-3.20).

TYPE DATA AND SPECIMENS EXAMINED: Female holotype: California, San Diego Co., El Modeno, E. L. Paddock, August 16, 1935 (USNM, type seen). Allotype: California, San Diego Co., False Bay, C. L. Hubbs, June 11 1918, collected on sand spit, 1 male (USNM, not seen).

An additional 15 specimens were examined from the following counties in California: San Diego Co., Los Angeles Co., Riverside Co., Monterey Co., Contra Costa Co., and Ventura Co..

REMARKS: Knight (1968) described this species from two specimens from San Diego Co. and Orange Co.. It is here redescribed with reference to the type material and additional material. This taxon is distributed from Contra Costa Co. (Clayton) to San Diego Co. (see map 6), and is chiefly found in the Californian Chaparral Province. There is no apparent altitudinal zonation, as it is known from coastal localities to montane regions (Ventura Co., Mt. Pinos, 8000 feet).

The only recorded host plant is Solanum sp. (Solanaceae), and collection dates range from March 26 to August 16. From the label data both sexes are recorded as being collected at light.

Knight (1968) suggested that this species was allied to Dicyphus (Idolocoris) pallicornis Meyer-Dur, however there is no doubt that this species has the following synapomorphies with other Dicyphus (Uhlerella) species: peritremal disc elongate, narrow, apically recurved, hind tibiae without spines, and vesica of males without spiculi or tuberculations.

Dicyphus (Uhlerella) vestitus Uhler

Figures: 23 and 24.

Dicyphus vestitus Uhler 1895: 46; Carvalho 1958: 200.

DIAGNOSIS: This species is most closely allied to gracilentus, but is smaller in size, and more ovoid in shape. It can be further distinguished from the latter by the following combination of characters: second antennal segment shorter than the posterior width of the pronotum; collar, calli, and hemelytra with red to reddish-ochraceous infusion; genital aperture of male with a small, linear tubercle above the left clasper (fig. 5).

DESCRIPTION: Males. macropterous, elongate-ovoid; length 2.60-3.00, base color fuscous, with testaceous, brown, and red to reddish-ochraceous markings; sparsely clothed with long, pale, suberect setae.

Head: length 0.35-0.40, width 0.52-0.58, vertex width 0.23-0.25; highly polished, fuscous, with two yellow markings on the postvertex that may be fused mesally; frons evenly rounded in front of eyes.

Eyes: moderately large, height 0.30-0.33, width 0.23-0.25; red.

Antennae: inserted below midheight of eyes; I, 0.30-0.33, testaceous with basal red infusion, and apical enbrowment; II, 0.70-0.80, expanded weakly toward apex, fuscous to fusco-red, concolorous to segments III and

IV; III, 0.55-0.65; IV, 0.28-0.30.

Rostrum: length 1.43-1.50; extending between middle and apices of metacoxae; testaceous, apical 1/2 of last segment fuscous.

Pronotum: length 0.45-.50, anterior width 0.35-0.38, posterior width 0.78-0.88; subquadrate; collar yellow anteriorly, posteriorly with reddish infusion; calli subquadrate, confluent mesally, posterior margin indistinct mesally, fuscous laterally, testaceous mesally with reddish infusion; disc fuscous, testaceous mesally, posterior margin emarginate deeply; propleuron fuscous to black.

Scutellum: fuscous to black, lateral angles testaceous.

Thoracic pleura: fuscous; peritremal disc ochraceous to reddish.

Legs: femora, 1.12-1.30, sometimes with brown markings; trichobothria, 5 mesofemoral, 5 metafemoral; tibiae, 1.69-1.95; tarsi, 0.59-0.65, last segment fuscous.

Hemelytra: length 2.60-3.00, pale to testaceous, sometimes exocorium hyaline, reddish markings on endocorium, clavus, and veins of membrane cells; often with brown markings mesad to corial fracture and midlength region of corium adjacent to clavus; corial fracture and apex of cuneus reddish to brown.

Venter: strongly tapered towards apex; testaceous to fuscous, if fuscous then pygophore testaceous ventrally; sparsely covered with pale, suberect setae.

Genitalia: pygophore (fig. 5) small, strongly tapered, strongly dissected, linear tubercle present on genital aperture above the left clasper, ventral margin of genital aperture strongly produced dorsally; left clasper (figs. 23, 24), lobe narrow, broadly connected to shaft, tapered toward apex, tip weakly recurved.

Females. similar to males in color, shape, setation, and general morphology; macropterous; length 3.45-3.75, head-abdomen length 2.70-3.25. Head: length 0.38-0.45, width 0.53-0.58, vertex width 0.23-0.26. Eyes: height 0.30-0.35, width 0.23-0.25. Antennae: I, 0.30-0.33; II, 0.65-0.80; III, 0.50-0.60; Iv, 0.25-0.33. Rostrum: length 1.43-1.50. Pronotum: length 0.42-0.50, anterior width 0.35-0.40, posterior width 0.80-0.93. Legs: femora 1.24-1.36; tibiae, 1.69-.82; tarsi, 0.60-0.65. Hemelytra: length 2.75-3.00.

SPECIMENS EXAMINED: There is no designated type specimen for this species, and I have deferred the designation of a lectotype, because of the uncertainty of the original material (see Remarks section). I have examined 91 specimens belonging to this species from the following

states: Colorado, North Dakota, South Dakota, Kansas, and Iowa.

REMARKS: Uhler (1895) described this species from one male and one female, from Colorado (Fort Collins, and Montrose). As there was no type designation, I obtained all the available Uhler material (mostly USNM). The locality and date information from the original description is as follows: "Fort Collins, May 20th to June 4th (Baker and Gillette)", and "Montrose, June 24th (Gillette)". To date I have not been able to locate specimens with this information, and there remains some doubt as to the identity of this species. However, from the original description, and the junior synonym, notatus Parshley, and specimens from COSU and USNM collections, it is most likely that the above description, and the specimens examined represent Uhler's vestitus.

This species is known from the mid-western States (Map 7), and there is no recorded host plant for this species.

Dicyphus (Idolocoris) pallicornis (Meyer-Dur)

Figures: 3, 6, and 25.

Capsus pallicornis (Meyer-Dur) 1843: 110.

DIAGNOSIS: This species is easily separated from the D.

(Uhlerella) species, by the following differences:

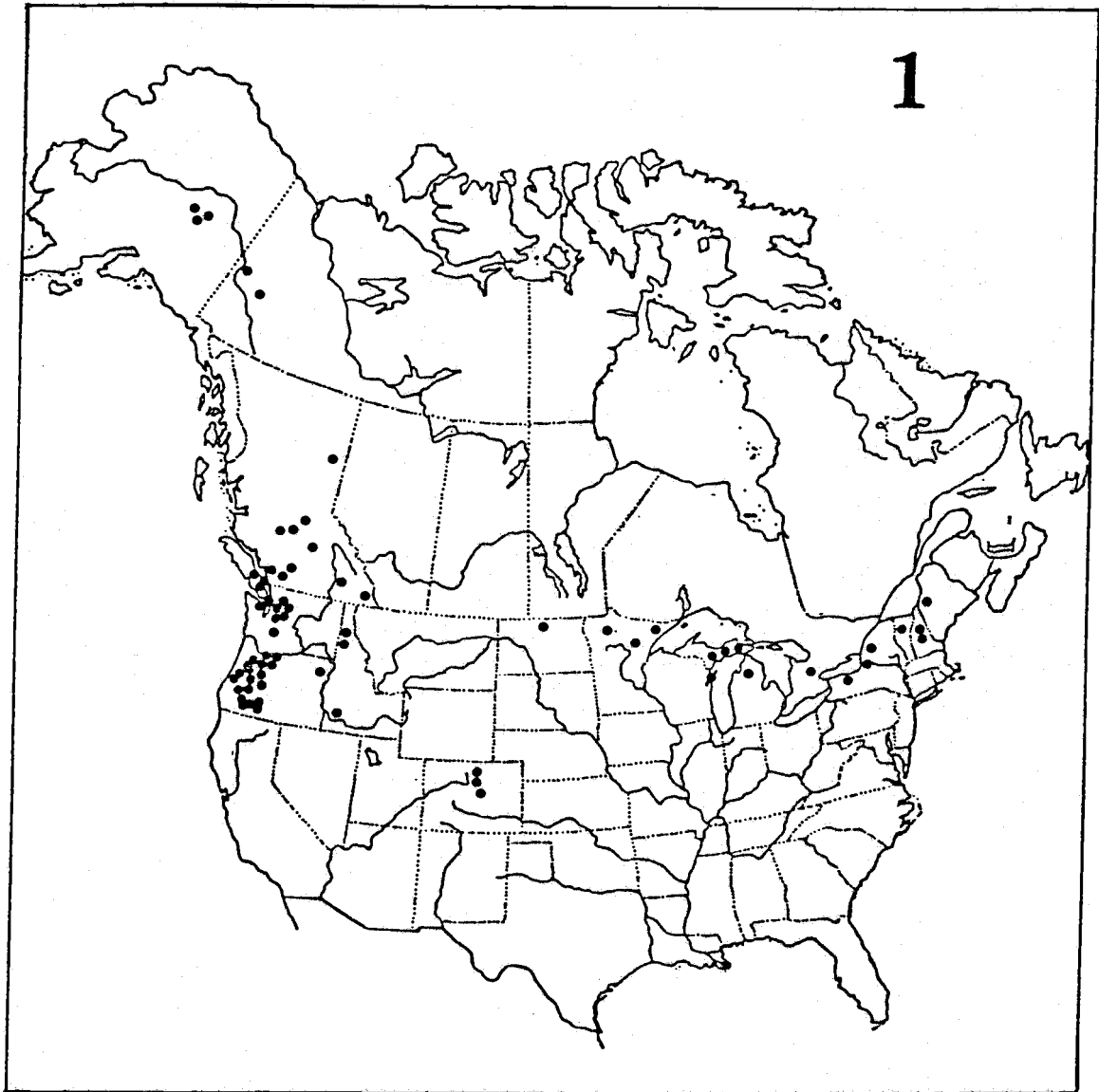
1) the peritremal disc is shorter and broader (cf. figs. 1 and 2, to 3). 2) male vesica with spiculi (Uhlerella species have a simple, sac-like vesica. 3) apex of shaft of left clasper with serrations (fig. 25). 4) middle and hind tibiae with spines.

This species is also distinguished by a common, brachypterous morphotype (Uhlerella only semibrachypterous). Also, there are two color morphs, a melanic, and a pallid form.

Downes (1957) first recorded this species as an introduction into British Columbia (Canada) from Europe. This species appears to be expanding its range rapidly, as I have found it as far south as Humboldt Co., California (Map 9). Its host plant, Digitalis purpurea L., (Scrophulariaceae), is also an introduction from Europe, and is common in disturbed habitats such as roadsides.

MAP III. 1.

D. (Uhlerella) discrepans.

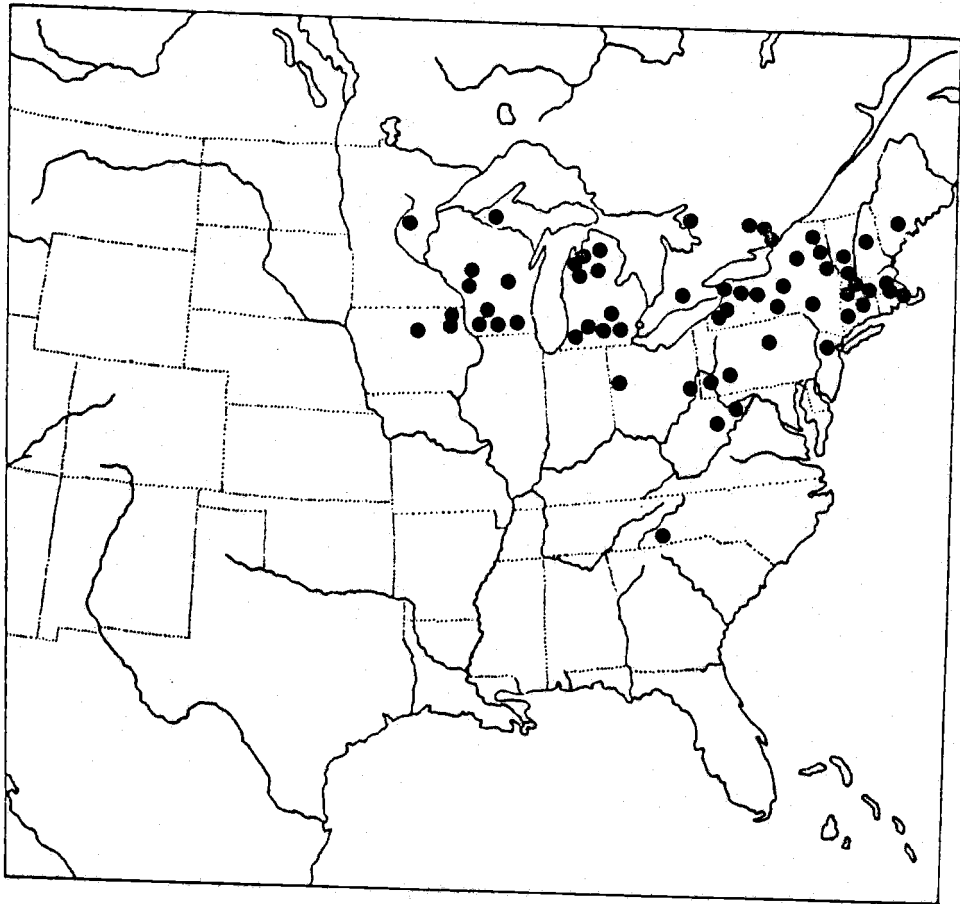


MAP III. 1.

MAP III. 2.

D. (Uhlerella) famelicus.

2

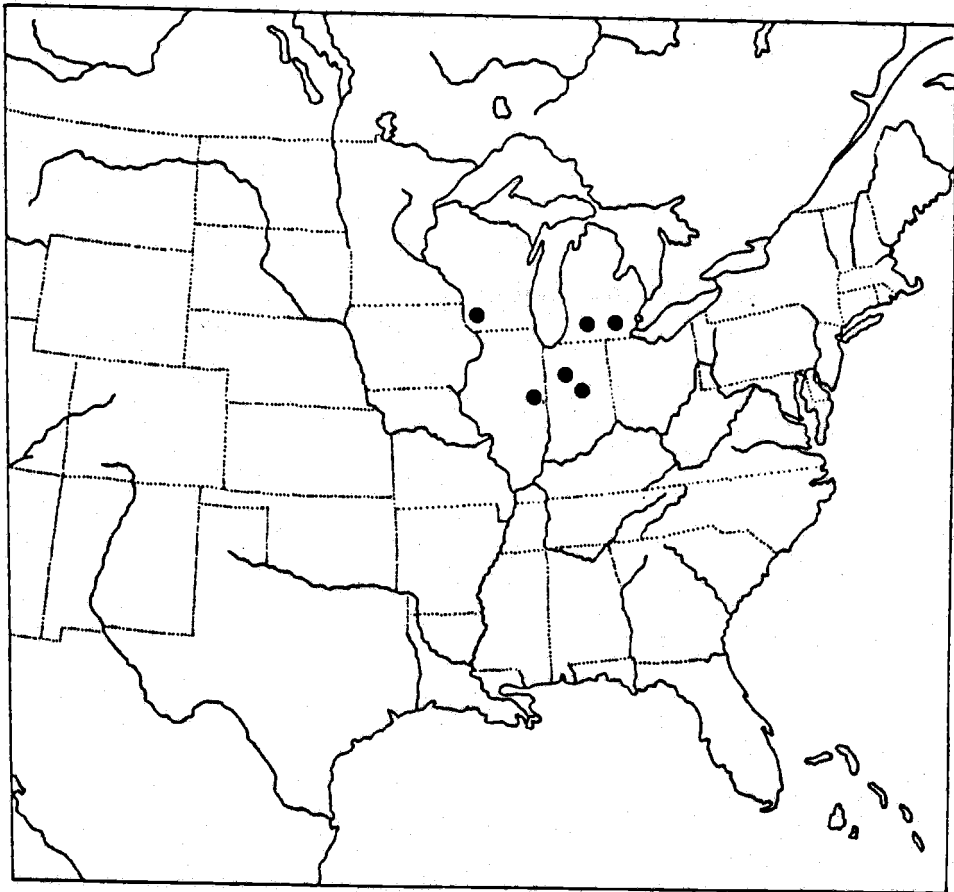


MAP III. 2.

MAP III. 3.

D. (Uhlerella) gracilentus.

3



MAP III. 3.

MAP III. 4.

D. (Uhlerella) hesperus.

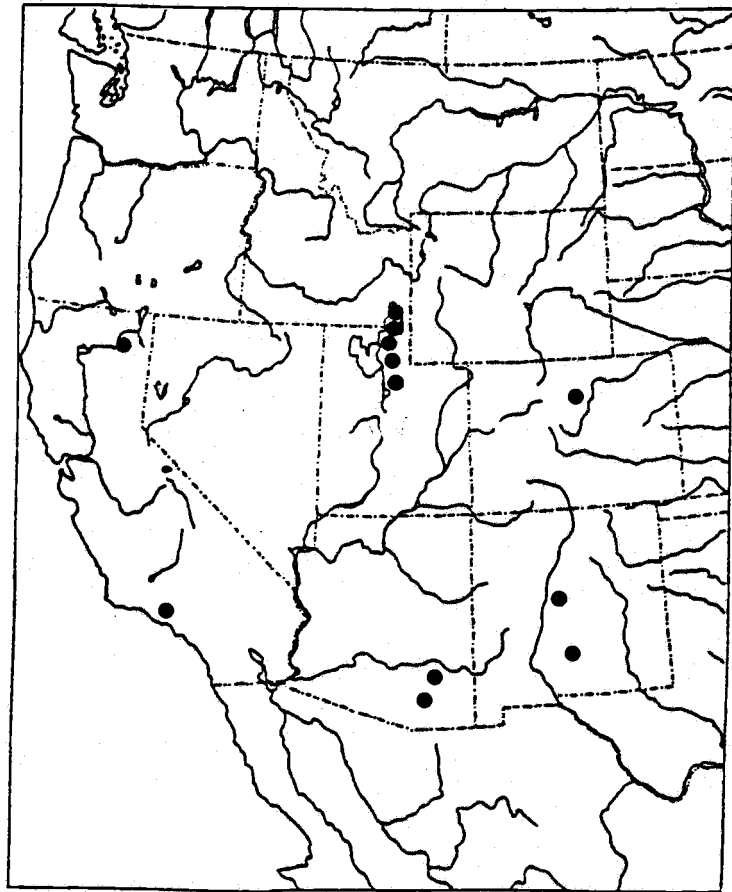


MAP III. 4.

MAP III. 5.

D. (Uhlerella) nigracorium.

5

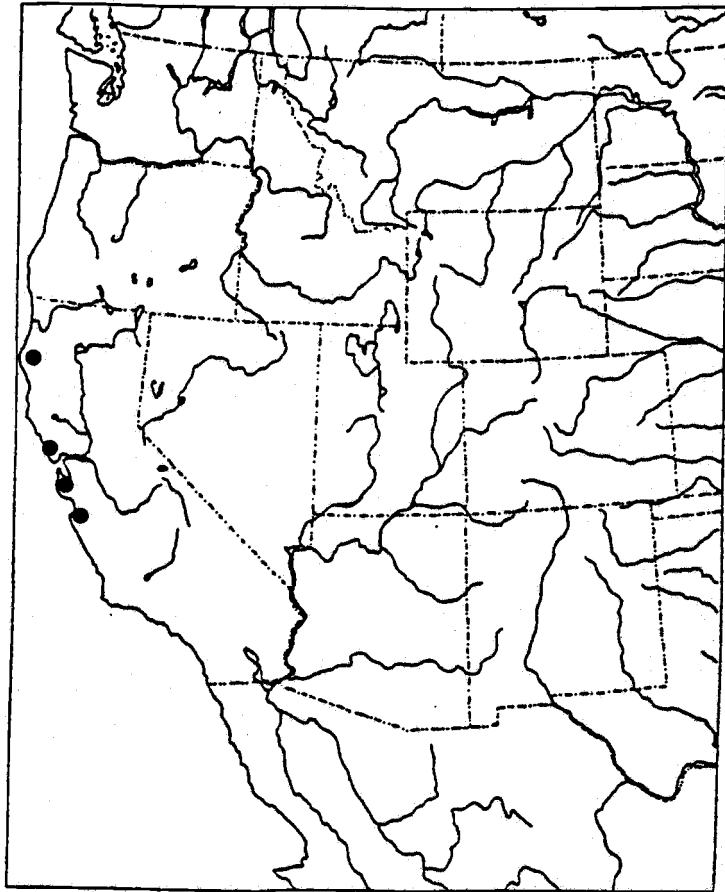


MAP III. 5.

MAP III. 6.

D. (Uhlerella) occidentalis

6

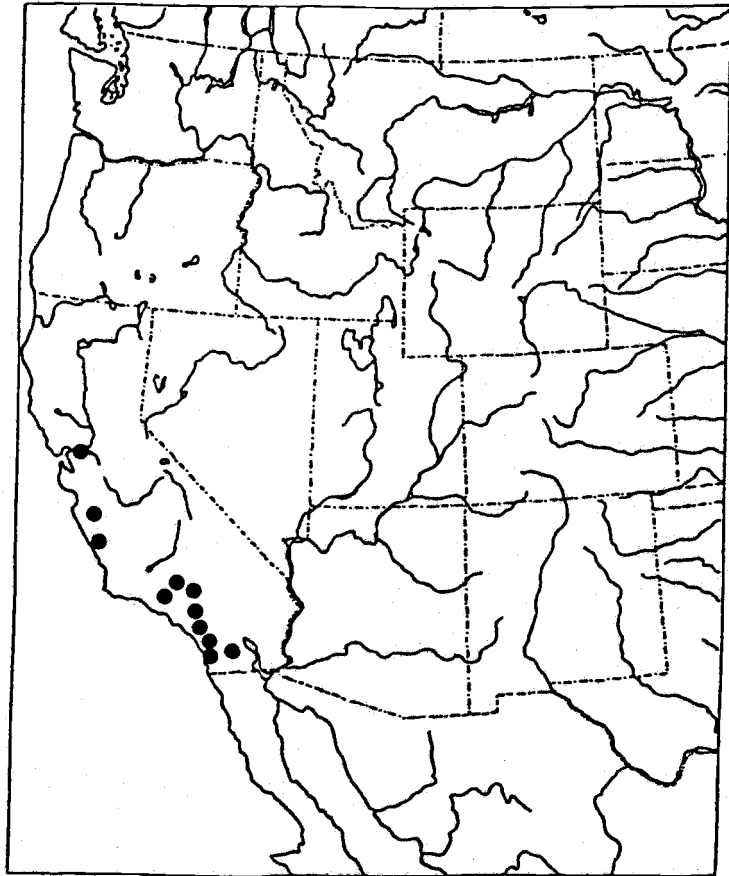


MAP III. 6.

MAP III. 7.

D. (Uhlerella) paddocki.

7

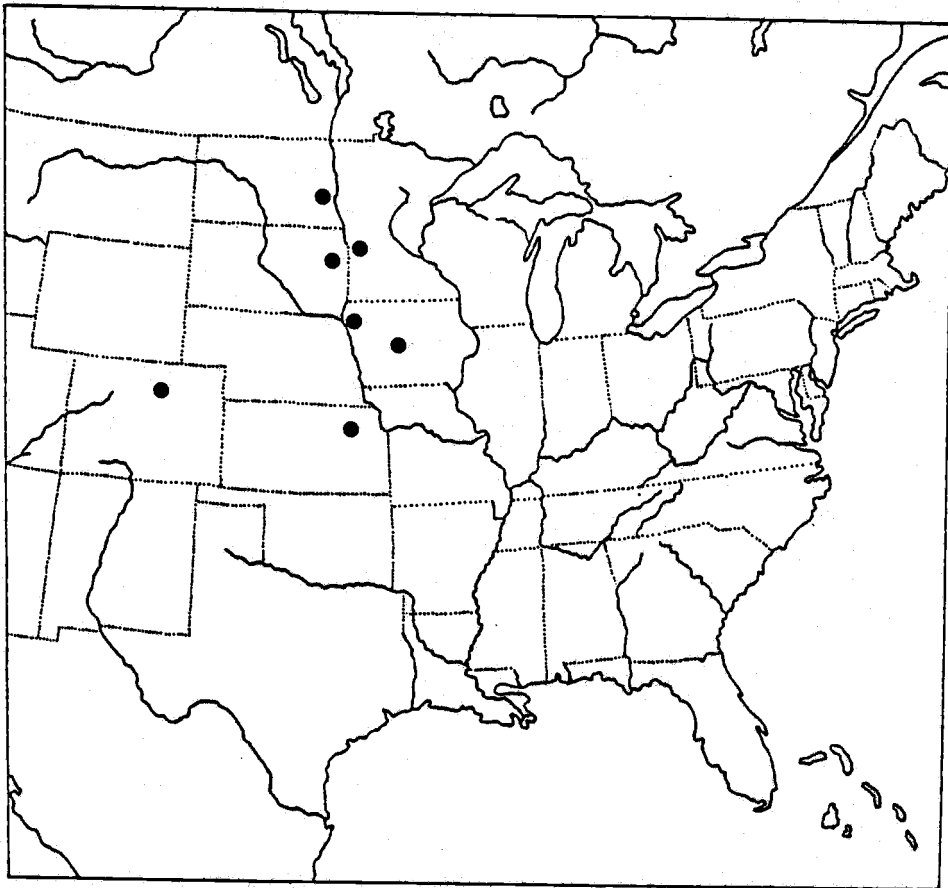


MAP III. 7.

MAP III. 8.

D. (Uhlerella) vestitus.

8

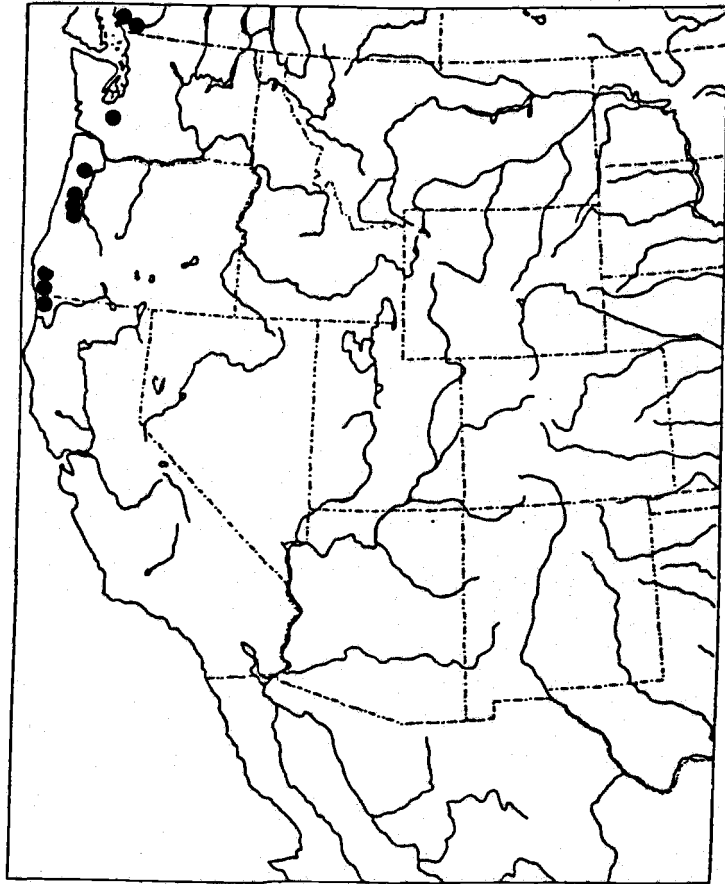


MAP III. 8.

MAP III. 9.

D. (Idolocoris) pallicornis.

9



MAP III. 9.

FIGURES III. 1 - III. 25. Diagnostic characters of Dicyphus (Uhlerella) species and D. (Idolocoris) pallicornis.

Figures: 1, 2, and 3, thoracic pleura, 40x.

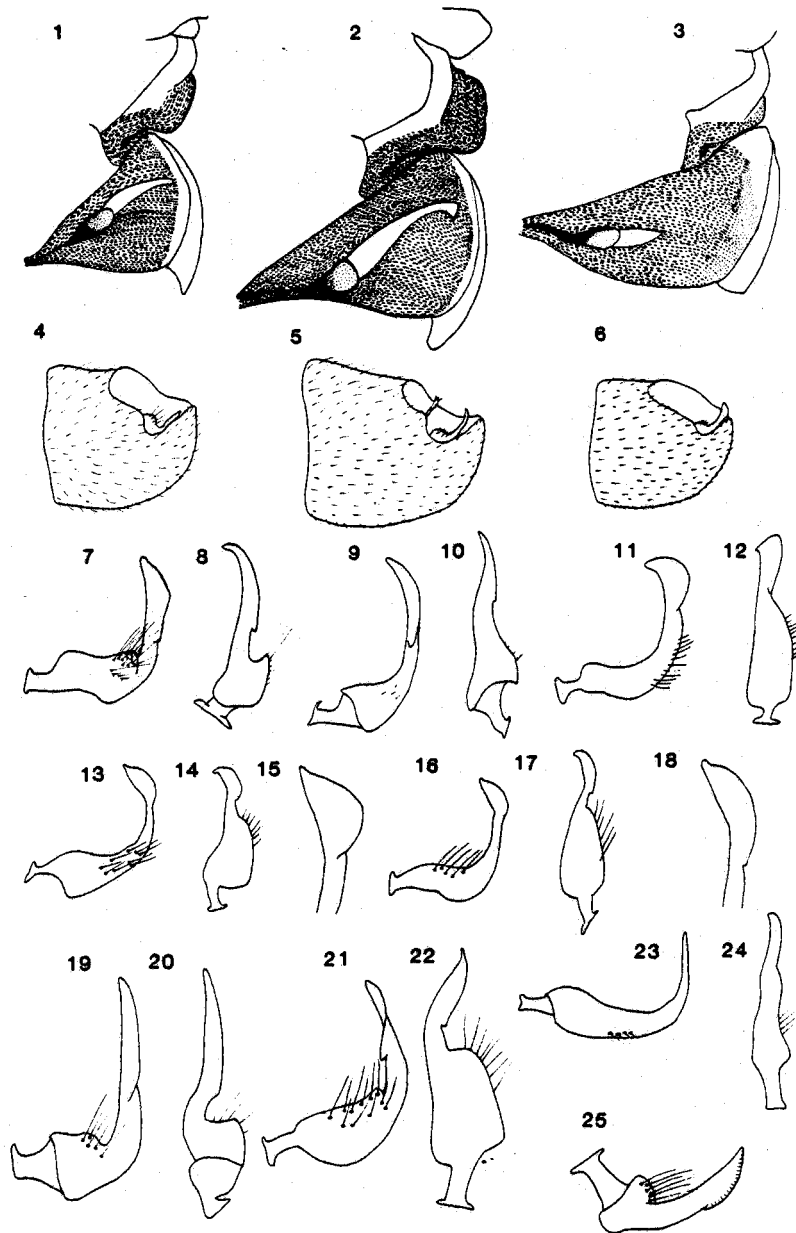
Figures: 4, 5, and 6, sinistrolateral view of pygohpore, 25x.

Figures: 7, 9, 11, 13, 16, 19, 21, and 25, dorsal view of left clasper, 40x.

Figures: 8, 10, 12, 14, 17, 20, and 24, internal, lateral view of left clasper, 40x.

Figures: 15 and 18, apex of left clasper, dorsal view, 78x.

1. D. (Uhlerella) discrepans.
2. D. (Uhlerella) paddocki.
3. D. (Idolocoris) pallicornis.
4. D. (Uhlerella) discrepans.
5. D. (Uhlerella) vestitus.
6. D. (Idolocoris) pallicornis.
- 7, 8. D. (Uhlerella) discrepans.
- 9, 10. D. (Uhlerella) famelicus.
- 11, 12. D. (Uhlerella) gracilentus.
- 13, 14, 15. D. (Uhlerella) hesperus.
- 16, 17, 18. D. (Uhlerella) nigracorium.
- 19, 20. D. (Uhlerella) occidentalis.
- 21, 22. D. (Uhlerella) paddocki.
- 23, 24. D. (Uhlerella) vestitus.
25. D. (Idolocoris) pallicornis.



FIGURES III. 1 - III. 25

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