REVISION OF THE NEW WORLD ENICOCEPHALOMORPHA (HETEROPTERA)

PEDRO W. WYGODZINSKY and KATHLEEN SCHMIDT

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
NUMBER 200 NEW YORK : 1991

Recent issues of the *Bulletin* may be purchased from the Museum. Lists of back issues of the *Bulletin, Novitates,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, New York 10024.

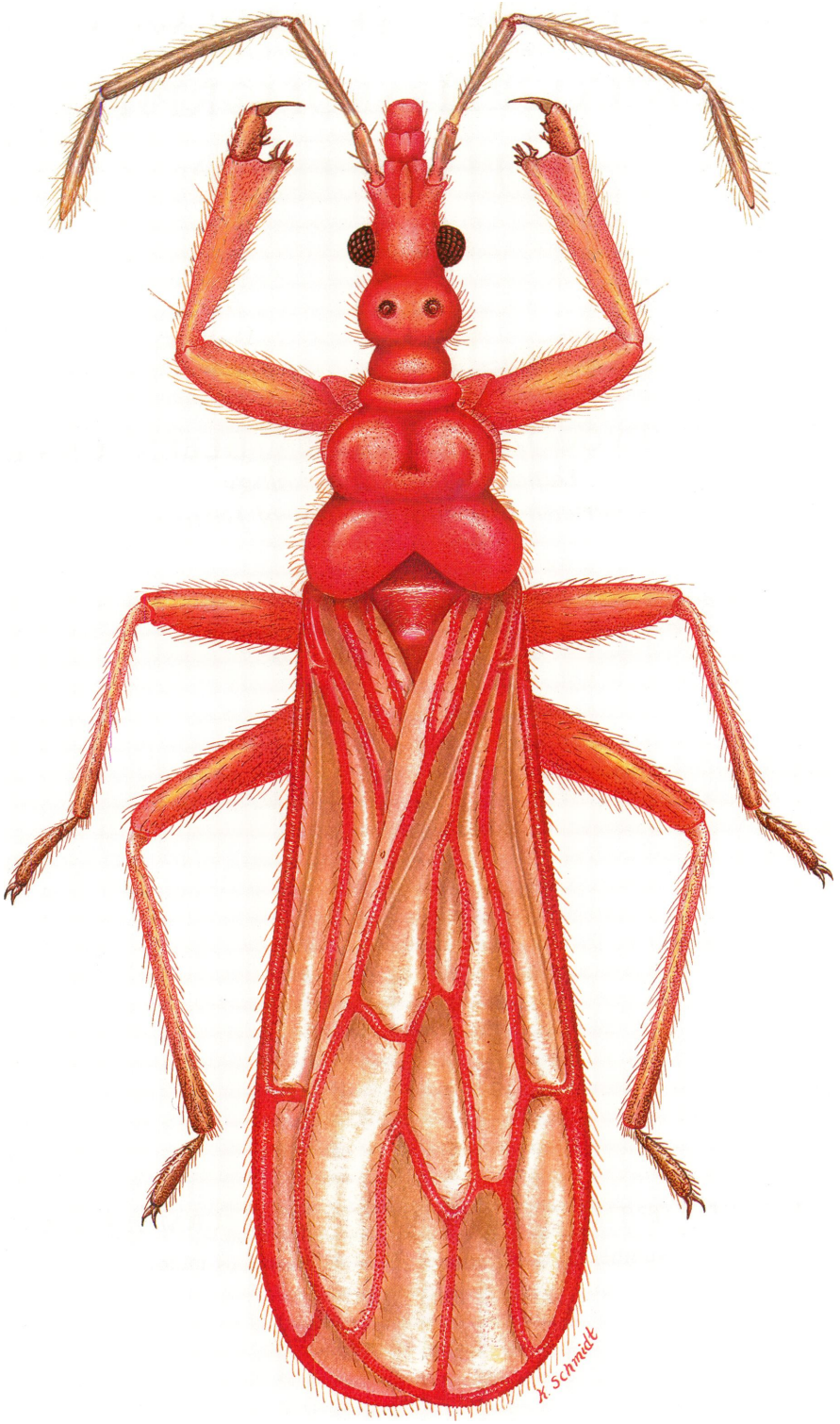
REVISION OF THE NEW WORLD ENICOCEPHALOMORPHA (HETEROPTERA)

PEDRO W. WYGODZINSKY and KATHLEEN SCHMIDT
Department of Entomology
American Museum of Natural History

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 200, 265 pages, 174 illustrations, 14 tables
Issued March 12, 1991
Price: $20.60 a copy

Copyright © American Museum of Natural History 1991

ISSN 0003-0090


K. Schmidt

CONTENTS

Preface 4
Abstract 5
Introduction 5
Acknowledgments 5
Abbreviations 6
Biology 7
Somatic Structures and Diagnostic Characters 13
Generalities 13
Sexual Dimorphism 13
Structures of Taxonomic Significance 15
Head 15
Antennae 16
Prothorax 16
Wing Coupling Mechanisms 17
Identities of some Pterothoracic Segments 19
Cuticular Structures of Thorax and Abdomen 22
Legs 22
Genitalia, Homologies, and Phylogeny of New World Taxa 30
Type Fixations 36
Key to Genera of the New World 36
Systematics 38
Aenictopecheinae 38
Gamostolini 38
Boreostolus Wygodzinsky and Štys 38
Gamostolus Bergroth 46
Tornocrusus Kritsky 51
Enicocephalinae 85
Systelloderini 85
Systelloderes Blanchard 85
Enicocephalini 87
Brevidorsus Kritsky 87
Chiricocoris, new genus 95
Enicocephalus Westwood 103
Hymenocoris Uhler 142
Lysenicocephalus, new genus 160
Neoncylocotis, new genus 164
Urnacephala, new genus 194
Xenicocephalus, new genus 200
Alienatinae 207
Alienates Barber 207
References 240
Appendix 244
Index of Scientific Names 261
Subject Index 264

Preface

This project was conceived in 1961 by the late Robert L. Usinger. The original plan was for Professor Usinger to provide habitus drawings and specific descriptions, as well as adding various other parts of the paper. Pedro Wygodzinsky was to contribute sections on morphology, phylogeny, generic descriptions, and keys. However, when Usinger's health began to decline in early 1968, he turned all of his notes and specimens over to Wygodzinsky and suggested that the paper be written by him alone. Dr. Wygodzinsky subsequently did considerable work on the manuscript, including portions of the introduction, generic descriptions, keys to genera and some species, morphology, and many drawings. Other obligations delayed work on the paper until 1979, when Dr. Wygodzinsky introduced me to the enicocephalids. He later suggested that I take responsibility for producing the specific descriptions and adding illustrations to complement those which were already finished.

The work progressed for the next four years in an atmosphere of mutual inspiration and criticism. I became increasingly interested in the group and during this time began the scanning electron microscope study. In the summer of 1983, sadly, Wygodzinsky became ill and could no longer work. I felt his loss acutely and gradually realized that the manuscript had to be finished soon or it might never see publication. Too much time and effort had gone into the project to let it languish. I was supported in every conceivable way in my attempt to complete the study by Dr. R. T. Schuh, Entomology Department Chairman at that time.

Additional complications arose when I resigned my position as Scientific Assistant at the American Museum of Natural History late in 1984, and when Dr. Wygodzinsky died in 1987. By then I had revised all sections of the paper and incorporated information from the SEM studies.

It became evident then that the greatest obstacle to completion of the work was the multitude of undescribed species of *Systelloderes*. After much thought, I finally decided to eliminate treatment of *Systelloderes* on the specific level, a possibility that Dr. Wygodzinsky had discussed frequently. *Systelloderes* is by far the largest genus in the Western Hemisphere. Dr. Wygodzinsky and I had delineated over 40 new and previously described taxa, and suspected that dozens, if not hundreds, of additional species were still undiscovered, especially in South America. On a worldwide basis, *Systelloderes* is probably not monophyletic. Štys (1970a) has tentatively divided it into three groups: the *moschatus* group from the Americas, the Ethiopian region, the Australian region (except New Zealand), and the Asiatic Archipelago; the *maclachlani* group from New Zealand; and the *uvarovi* group from the Ethiopian region and the Middle East.

The scanning electron microscope study has shown that there is a good morphological basis on which to separate *Systelloderes* (now tribe Systelloderini) from the rest of the New World Enicocephalinae. I believe that a genus of this nature should be the subject of a separate monograph and that its omission will not seriously impair the value of the present contribution. I have included in the Systelloderini section of the present paper a synonymy of the genus *Systelloderes* in the New World, a species list, and scanning electron micrographs of two species for comparative purposes.

There are certain inconsistencies in this work which could not be avoided, given its long gestation. For example, it was not always possible to determine the exact specimen from which drawings had been made, especially in older material or borrowed specimens which Dr. Wygodzinsky had returned. When this information was available, I have provided it.

Furthermore, the treatment of morphology is not exhaustive, but rather organized to present new findings and to integrate them to the degree possible into information previously available for the group.

The descriptions of several new genera suffer from lack of material, the worst case being that of *Xenicocephalus*. Unfortunately, the only adult specimen of this genus is missing its head, pronotum, and forelegs. The

nymphs, however, are so large and distinctive that they are unlikely to be confused with any other taxon, and I have chosen to describe the genus despite this obvious drawback. Since I have recently caught nymphs of *Xenicocephalus* in Guyana, and some have been found elsewhere, I am hopeful that adult material will soon become available and that a more complete description can be made.

Finally, Dr. Wygodzinsky was not able to review and update some of his findings or comment on the final version of this work. He might well disagree with some of the conclusions presented here. I have done my best to present his data and interpretations fairly, and as clearly as possible. When it was not obvious to me what Dr. Wygodzinsky thought about a particular subject, or when we disagreed, I have presented evidence to support my own conclusions. I feel that this is justified, given the peculiar circumstances surrounding the completion of the project. I only hope that it will measure up to Dr. Wygodzinsky's high standards and that he would feel that our knowledge of the Encicocephalidae has been increased in some small way.

Kathleen A. Schmidt
April 13, 1990

ABSTRACT

The taxonomy of the New World Encicocephalidae is treated in detail at the generic and specific level, with the exception of *Systelloderes* Blanchard, for which only the genus is diagnosed. The tribe Systelloderini is resurrected to contain the genus *Systelloderes* within the Encicocephalinae. The new genera *Chiricocoris*, *Lysenicocephalus*, *Neoncylocotis*, *Urnacephala*, and *Xenicocephalus* are described. Thirty-eight new species are described in 9 genera. *Enicocephalus marimutti* Kritsky and *E. yvonneae* Kritsky are treated as junior synonyms of *E. cubanus* Barber; *E. emarginatus* Champion is treated as a junior synonym of *E. pilosus* Champion; *Oncylocotis braziliensis* Kritsky is treated as a junior synonym of *Neoncylocotis stannardi* (Kritsky). Several new combinations are created, particularly for species transfered to the genus *Neoncylocotis*. Keys are provided for all genera except *Xenicocephalus*, and for all species except those of *Sytelloderes*. General reviews are provided for the following subject areas: biology; somatic structures and diagnostic characters; and genitalia, homologies, and the phylogeny of the New World taxa. Scanning electron microscopy is used intensively for the study of morphological structure, and the results in the form of micrographs are presented in conjunction with numerous line drawings.

INTRODUCTION

Faunistic studies of the Enicocephalidae have been done for New Zealand (Woodward, 1956), Micronesia (Usinger and Wygodzinsky, 1960), Africa and Madagascar (Villiers, 1969), and the Palaearctic Region (Štys, 1970b). In addition Štys has presented a remarkable body of work over the last two decades updating some former studies and detailing the morphological, taxonomic, and biogeographical significance of groups of the South Pacific, Oriental, African, and Middle Eastern regions. Although there are several small revisions of New World genera (Kritsky, 1977b, 1978a, 1978c, 1979) and also Jeannel's (1942) monograph dealing in part with the geographical area, no comprehensive surveys exist for the New World alone. The purpose of this monograph is to fill that gap in our knowledge.

ACKNOWLEDGMENTS

We thank the following individuals and institutions for lending or donating specimens in their care. Institutional abbreviations used in the text are listed below.

AMNH	American Museum of Natural History, V. Roth and W. J. Gertsch (Southwestern Research Station)
BM	British Museum of Natural History, W. J. Knight, W. R. Dolling
CAS	California Academy of Sciences, P. Arnaud, E. S. Ross, W. Pulawski
CIS	California Insect Survey, University of California, Berkeley, J. Chemsak
La Plata	Museo de la Plata, La Plata, R. Ronderos
FMNH	Field Museum of Natural History, Chicago, R. Dybas and G. Solem

HDZ	Hope Department of Zoology, Oxford University, I. Lansbury
HNHM	Hungarian Natural History Museum, Budapest, T. Vasarhelyi
INHS	Illinois Natural History Survey, D. J. Voegtlin
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, A. Bachmann, M. J. Viana
MNHN	Muséum National d'Histoire Naturelle, Paris, J. Carayon, A. Villiers
MNR	Museu Nacional de Historia Natural, Rio de Janeiro, J. C. M. Carvalho
MZSP	Museu de Zoologia, Sao Paulo
OSU	Oregon State University, J. D. Lattin, A. Moldenke, G. M. Stonedahl
UAR	University of Arizona, Tucson, F. G. Werner, Jr.
UCB	University of California, Berkeley, J. A. Powell, E. I. Schlinger
UCD	University of California, Davis, F. D. Parker, R. O. Schuster
UCR	University of California, Riverside, S. Frommer
UCONN	University of Connecticut, Storrs, N. T. Davis, J. A. Slater
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor, T. Moore
USNM	National Museum of Natural History, Washington, D. C., R. C. Froeschner, J. L. Herring, G. Hevel, P. Spangler

We are grateful to the following individuals for collecting and donating material for our use, and for providing observations on the biology and behavior of encicocephalids: R. T. Allen, M. Alvarenga, P. D. Ashlock, R. Baranowski, P. F. Bellinger, R. A. Belmont, W. L. and D. E. Brown, G. M. Buxton, G. W. Byers, J. Cassis, M. A. Cazier, T. Cekalovic, H. V. Daly, P. J. Darlington, Jr., W. A. Drew, K. M. Fender, W. Ferguson, A. Fiske, S. Frommer, J. A. Grant, C. Green, L. H. Herman, R. F. Hussey, M. Ivie, W. and J. Ivie, I. M. Kerzhner, N. L. H. Krauss, J. R. La Bonte, J. F. Lawrence, K. Lenko, J. Lima, C. Lindroth, J. MacNeill, J. Maldonado C., B. Malkin, G. B. Monteith, W. B. Muchmore, A. F. Newton, Jr., G. Parsons, S. and J. Peck, L. Peña, G. Peters, F. Plaumann, J. T. Polhemus, J. A. Powell, J. E. Prine, E. S. Ross, R. T. Schuh, P. Spangler, G. M. Stonedahl, H. Sturm, T. W. Taylor, M. Thayer, H. and M. Townes, R. Vierhus, M. S. Wasbauer, W. Weyrauch.

We thank Simon's Rock of Bard College, including (former) Dean J. Paskus, Dean B. Rogers, Dr. D. Roeder, and Dr. R. E. Schmidt for providing space and computer facilities for the junior author during the final synthesis of the manuscript.

We are most grateful to Drs. Pavel Štys and J. A. Slater for review of the manuscript and for many valuable suggestions along the way. We very much appreciate Dr. Štys's referral of specimens to us and his detailed correspondence concerning taxonomy and morphology of the world enicocephalid fauna.

We especially thank Dr. R. T. Schuh (AMNH), who graciously facilitated the production of this work on many levels, from making museum facilities more accessible to the junior author, to reviewing, editing, and final compilation of the manuscript. Without his knowledge, invaluable suggestions, and eagerness to help with the most minute tasks, the completion of this work would not have been possible.

We thank Lilian Marzano and Brenda Massie for typing and correcting much of the manuscript. We also thank Michael Klemens of the American Museum for his assistance during the preparation of the manuscript.

And finally, the junior author thanks her husband, Dr. Robert E. Schmidt, for his selfless support in this endeavor, his innumerable readings of the manuscript, and financial and emotional support. His enthusiasm and quick eye are much appreciated.

Abbreviations

Ae - aedeagus (= phallus)
An - anal vein
$ascl_{2,3}$ - anterior supracoxal lobe (2nd or 3rd thoracic segment)
C - costa
cf - costal fracture
clf - claval fracture
Cu - cubitus
cx_{1-3} - coxae 1–3
f_1 - fibula of 1st valvula
f_2 - fibula of 2nd valvula
f - cubital furrow
Fl - floor beneath proctiger
fw - forewing
fwb - forewing base
fwcg - forewing coupling groove
G - guide
GO - gonoporal opening
gon - gonangulum

Gyn - gynatrium
h - hamus
hw - hind wing
hwb - hind wingbase
hwcg - hind wing coupling groove
IDP - infradistal plate
ima - internal muscle attachment
IX - ninth segment (or tergum where appropriate)
M - media
m-cu - medio-cubital crossvein
macrop. - macropterous
mf - medial fracture
microp. - micropterous
msc - mesosternal complex
msepim - mesepimeron
msepis - mesepisternum
msp - mesothoracic spiracle
mtepim - metepimeron
mtepis - metepisternum
mtsc - metasternal complex
mtsp - metathoracic spiracle
P - pronotum
Pa - paramere
Pab - paramere, basal part
Pcu - post cubitus
pepim - proepimeron
pepis - proepisternum
Ph - phallus
PP - proximal plate
PPds - dorsal strut of proximal plate
Pr - proctiger
$pscl_{2,3}$ - posterior supracoxal lobe (2nd or 3rd thoracic segment)
Py - or Py(IX) pygophore (ring formed by ninth tergum, laterotergites and sternum)
R - radius
r-m - radio-medial crossvein
Rs - radial sector
rSDP -remnant of supradistal plate
Sc - subcosta
scu - scutellum
sga - scent gland auricle
Sp - spiracle
SPa - setae on paramere
T - teratological portion of forewing
Tabm - median tab
TrS - trichoid sensillae
Va_1 - first valvula
Va_2 - second valvula
Vf_1 - first valvifer
Vf_2 - second valvifer
VG - ventral gland orifices
VIII - eighth segment (or tergum, where appropriate)
Wc - wing coupling mechanism
X (or T-10) - Tenth tergum
XI (or T-11) - Eleventh tergum

BIOLOGY

Published information on the biology of the Enicocephalidae is generally scant and has been pieced together from collecting data and scattered personal observations. The most extensive summaries of existing information are Usinger (1932, 1945), Jeannel (1942), Carayon (1950, 1951) Usinger and Wygodzinsky (1960) and Štys (1981c) [summary of swarming data]. Less comprehensive, although not necessarily less detailed references to their biology exist in Kirkaldy (1901), Bergroth (1903), Bruner (1924b) [general reviews and allusion to swarms producing an odor], Usinger (1939) Villiers (1960) [associations with ants, and more], China (1963) [summary of aenictopecheine ecology and data], Schuh (1970), Kritsky (1976) [swarming in *Systelloderes* spp., and more], Villiers (1961) [habitats and biology of some African species], Kritsky (1977a) [morphology and behavior], Štys (1980) [habitats and habits of *Austrostolus monteithi*], Hickman and Hickman (1981) [detailed developmental biology of *Oncylocotis tasmanicus*], and Štys (1981a) [morphology and feeding strategies]. Many more smaller references are scattered throughout the literature, often under material examined sections of species descriptions. No exhaustive compilation of biological data exists, nor do we intend to undertake that task here. We will present a brief discussion of known biology along with our own new observations of new world taxa. Biological data for these taxa are summarized from our label data and the literature in table 1.

Nymphs and adults of the Enicocephalidae are basically soil dwellers. Wherever sufficient moisture is present, they can be found in superficial layers of soil or in other places where detritus accumulates. They have been reported numerous times from leaf litter, under rocks, under rotten tree stumps resting on the soil, under bark, and at the bases of leaf sheaths.

We have collected *Enicocephalus tupi* in

TABLE 1

Summary of Biological Data from Labels and the Literature

(ap = apterous, br = brachypterous, ma = macropterous, mi = micropterous, cad = caducous, unk = unknown)

Genus	From swarms?	At lights?	Wing morphs	Altitude range (m)	Summarized habitat data
Alienates	—	yes (♂)	♂ ma ♀ ap	92–1906	Found in leaf litter and berlese samples from: tropical evergreen forests, cloud forests, dry limestone forests, dead stumps, moss and liverwort mats, pack rat nests. Also in dry tree holes, kapok buttresses, and under agave.
Boreostolus	—	—	♂ ma and mi ♀ ma + br + mi	719–2188	Found by hand-searching under stones at edges of streams, often in inundation zone.
Brevidorsus	—	yes (♂)	♂ ma ♀ unk.	—	Caught at light only.
Chiricocoris	—	—	♂ unk. ♀ ma	1530–1750	Found in litter of forest floor, deep ravine, and wood chips at base of cut stump.
Enicocephalus	yes (sex unk.)	yes (♂ + ♀?)	♂ ma ♀ ma + cad	769–3125	Found in wet mountain and insular forests; under dried leaves in litter, rocks in stream valley, and bark; and in suspended soil between palm fronds and trunk.
Gamostolus	yes (♂ + ♀)	—	♂ ma ♀ ma	94–1094	Found hand searching under stones, resting on surface of small pool (near swarm), in trap at tree line of *Nothofagus* forest.
Hymenocoris	yes (♂)	yes (♂)	♂ ma ♀ ap	938–1850	Found under rocks in soil (some deep), in bee tunnel, incidentally in swimming pools, malaise trap, and spider web.
Lysenicocephalus	—	yes (♂)	♂ ma ♀ unk.	—	Caught at light only.
Neoncylocotis	—	—	♂ ma ♀ ma + cad	8–3300	Found under stones (very little habitat data available).
Systelloderes	yes (♂ + ♀)	yes (♂ + ♀)	♂ ma + br + mi ♀ ma + br + mi	141–2813	Found in berlese samples from forest leaf litter, old sawdust pile. Also under bark of trees, under wet cow droppings, in suspended soil at leaf bases, under rocks along stream, around corn roots, under moss.
Tornocrusus	yes (sex unk.)	—	♂ ma ♀ ma + br	850–3400	Found in wet forests and rain forests. Also in suspended soil between dead leaves and trunk of Espelitia (Compositae).
Urnacephala	—	yes (♂)	♂ ma ♀ unk.	—	Caught at light only.
Xenicocephalus	—	—	♂ unk. ♀ ma	lowland–2000	Caught in pitfall traps in lowland forest and also from montane forest.

"suspended soil" formed between the bases of palm fronds and trunks of trees. Sturm (in litt.) found numerous specimens of *Tornocrusus sturmi* in "suspended soil" between dead leaves of *Espeletia* sp. (Compositae) still adhering to the trunk (fig. 1A) and we have collected *Systelloderes* in identical conditions. Species of *Alienates* have been found in pack rat nests (*Neotoma floridana*), and under mats of moss and liverworts. *Hymenocoris formicinus* has been found in a bee tunnel.

A detailed description of the habitat of *Boreostolus americanus* was provided by Dr. Gary Stonedahl, who spent several hours collecting it. He reported that specimens can be found along stream beds under fairly well-embedded rocks, four inches to one foot in diameter. Preferred substrate is pebbles or pea-size gravel mixed with sand that is moist but never wet. The rocks under which he found specimens were not too near the river at the collection time, but he felt that they would be in the inundation zone at times of high water (also reported for *B. sikhotalinensis* in the U.S.S.R.). He spent approximately 20 minutes turning over rocks between each catch, and never found two adults under the same rock. However, they coexist with small groups of *Systelloderes* (probably *grandes*). He hypothesized that they eat Collembola, since the latter were abundant in the same habitat, but he did not observe feeding. Kerzhner (1988b) suggested that *B. sikhotalinensis* feeds on *Cryptostemma japonicum* Miyamoto.

We do not know how deep enicocephalids will penetrate into the soil. The fact that it is sometimes very difficult or even impossible to find even a few specimens where thousands are known to occur (Usinger, 1939; Schuh, 1970), suggests that they will penetrate the soil to considerable depths. This can be further illustrated by the unsuccessful efforts of one of our collectors, Richard Vierhus, to find females of *Hymenocoris formicinus*, which are apterous and known to be soil dwellers. He was most fortunate in being able to collect a large series of males from the vicinity of his house in Los Gatos, Santa Clara County, California. More than 128 specimens were obtained as they fell into his swimming pool between August 27 and December 20, 1967. Vierhus describes the habitat as chaparral-oak woodland, receiving 17–30 inches of precipitation per year, mostly in the spring. The soil is porous and composed of mudstone-clay. It becomes very dry in the summer months. A nearby ravine is choked by vegetation consisting of poison oak, valley oak, scrub oak, coast live oak, California laurel, coyote bush (*Baccharis pilularis*), chamise, and thistle, with a layer of litter beneath.

Despite extensive efforts, and the proven existence of the species in that area, Vierhus was never able to find females of *H. formicinus*. Males flew from the end of June through the end of December, roughly the dry season. This agrees with information summarized from other label data (table 2). Females in other localities were found from February through May.

It is probable that females surface during the wetter months to mate. They can store sperm for at least two months, as specimens that we kept in the laboratory laid fertile eggs for that period with no observed mating. Hickman and Hickman (1981) reported that females of *Oncylocotis tasmanicus* would mate one to several times and subsequently lay fertile eggs for up to four months. We were able to observe sperm in the spermatheca of one female of *H. formicinus* (fig. 2).

Though most enicocephalids are presumably free-living, there is evidence of association of some species with ants. Usinger (1945) cited the finding of *Systelloderes angustatus* associated with a variety of *Formica rufibarbis* in Mexico. Lenko (in litt.) found, on repeated occasions, nymphs of all instars and adults of *Enicocephalus lenkoi* in nests of *Camponotus rufipes* in Southern Brazil. Villiers (1961) described *Compsoderes stuckenbergi* from a large colony of *Pheidole foreli* in Africa.

The Enicocephalidae are the only family of Heteroptera in which swarming occurs. Swarms are apparently formed for the purpose of mating and there are at least two observations of individuals *in copulo* (Berg, 1893; Schuh, 1970). The sex ratio of the swarm varies according to the taxa involved, although most swarms are composed predominately of males (Štys, 1981c). They tend to form in sunny cleared areas near edges of forests or in open glades, often in the late

Fig. 1. **A**. Suspended soil in leaf axils provides a habitat for many enicocephalids; in this Colombian *Espeletia* sp., numerous specimens of *Tornocrusus sturmi* were found. **B**. A female of *Hymenocoris formicinus* feeds on a symphylid (Courtesy of E. S. Ross).

afternoon (Blanchard, 1852; Knab, 1909; Johannsen, 1909; and others), although Schuh (1970) and Polhemus (1988) reported them under the forest canopy in midmorning. The swarm occurs at a height of 1–6 m and probably forms around a marker or station (Krit-

TABLE 2
Summary of Flight and Appearance Dates of Males and Females of *Hymenocoris formicinus* (from labels)

	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
Number of males	0	0	0	0	1	3	4	4	2	15	10	1
Number of females	0	2	3	0	2	0	0	0	0	0	0	0

sky, 1977a). Several authors have reported a strong odor associated with the swarms (Berg, 1893; Kirkaldy, 1901; and Bruner, 1924b).

Swarms may contain specimens of only a single species, such as a large swarm of *Gamostolus subantarcticus* observed by C. Olrog (in litt.) on Herschel Island off southern Chiloé, but very often several species are found together. Usinger (1945) mentioned having found two species of *Systelloderes* in a single swarm in Mexico. The senior author found at least three different species of *Systelloderes* in a swarm in Tucuman, in northern Argentina, and huge swarms sampled by M. Cazier in Arizona and examined by us, contained consistently two species of *Systelloderes*. W. Ferguson (in litt.), Vierhus, and others have observed single males of *Hymenocoris* on the wing during the daytime in California, but swarms of this species have been reported by Michelbacher and White (Usinger, 1939).

Macropterous forms of many genera fly to lights; indeed, species of *Brevidorsus*, *Lysenicocephalus*, and *Urnacephala* are known only from males caught in this way. Label and literature data (table 1) reveal that males are most frequently caught at lights, although both sexes of *Systelloderes* are light-attracted. In the genera *Alienates* and *Hymenocoris*, females are apterous, and would not be expected to appear at lights nor would they be able to swarm. This is probably true of *Brevidorsus*, *Lysenicocephalus*, and *Urnacephala* species as well.

Circumstantial evidence and numerous unsubstantiated personal communications lead us to believe that there are large gaps of information in table 1. It is probable that macropterous specimens of one or both sexes of the undocumented genera in the table will at some point be found to swarm and fly to lights. We concur with Štys's hypothesis (1981c) that all Enicocephalidae capable of flight probably do swarm. Sexually dimorphic wings, the existence of scent structures in one or both sexes, sex ratios in swarms, and other factors undoubtedly correlate with differences between taxa in mating strategy and behavior. However, paucity of data and the enigmatic nature of swarms make this type of study difficult at best.

Some enicocephalids have the unusual ability among Heteroptera of being able to shed their wings (some species of Gerridae and Aradidae do this also). In a few species of *Enicocephalus* and a very few species of *Neoncylocotis*, as well as in some of the Old World *Oncylocotis* and probably most *Nesenicocephalus*, the female will shed both fore and hind wings. The senior author observed this phenomenon in several species of *Enicocephalus*. Seconds after a female collected under bark was placed in a jar, all four wings were found to be shed. It can be presumed that after copulation, which may take place on or above the surface, females will retreat into the soil and that, as in termites, wings will be a hindrance in subterranean life.

Enicocephalids are reported to be entomophagous and omnivorous (Carayon, 1951); we can confirm these observations. Specimens of *Enicocephalus tupi* kept in captivity fed on living and freshly killed larvae of Diptera, freshly killed adult flies, and other small softbodied insects. Females of *Hymenocoris formicinus* were kept alive for two months on a varied diet of small softbodied insects and arthropods (including millipedes), alive or freshly killed. During this time, the specimens laid numerous eggs. E. S. Ross (in litt.) observed females of this species feeding on symphylids and campodeids. We have the privilege of reproducing one of Dr. Ross's photographs, which illustrates the above (fig. 1B). Drake and Harris (1927) reported *Systelloderes iowensis* feeding on emerging adults

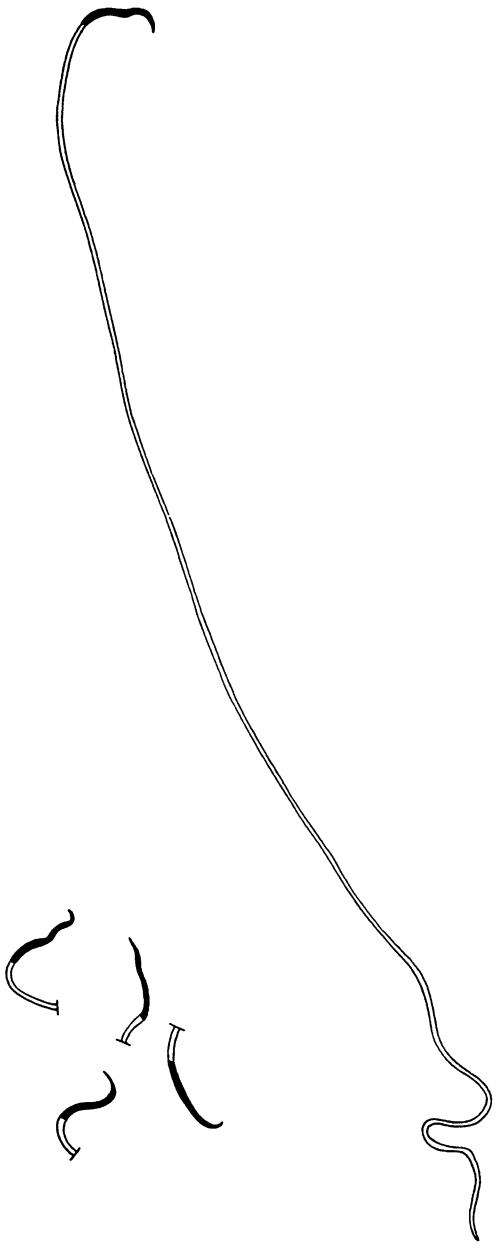


Fig. 2. Sperm observed in spermatheca of female of *Hymenocoris formicinus*.

of the Hessian fly, *Mayetiola destructor*, as they were collected in "concentration cages." Hickman and Hickman (1981) maintained numerous individuals of *Oncylocotis tasmanicus* on larvae and pupae of ants, especially *Pheidole tasmaniensis*, and eggs or newly hatched young of the spider *Trachycosmus sculptilis*.

In the three genera known from males only, *Urnacephala*, *Brevidorsus*, and *Lysenicocephalus*, circumstantial evidence suggests that males may not feed as adults. This may be true for *Hymenocoris* males as well. Gross microscopic examination of the gut through the transparent walls of 51 males of *H. formicinus* showed them to be essentially empty: no contents in 17 specimens, extremely minute amounts of well-digested material in 32, and very small lumps of black material in only 2. Vierhus (in litt.) repeatedly offered males food (Collembola), but they would never accept it.

Oviposition in captivity was observed in *Hymenocoris formicinus*. Three females, collected near San Francisco in March 1961, were kept in individual containers from March 26 through May 23. The substrate in the containers was a mixture of activated charcoal powder and plaster of Paris. This was kept damp, but not visibly wet. The enicocephalids were fed on crushed flies, fly larvae, and other small arthropods. They laid 77, 91, and 92 eggs, respectively (fig. 3). A fourth female was kept from April 17 through May 15, and laid a total of 26 eggs between May 10 and 15. Notably, she laid 11 in one day (May 15).

Eggs laid on May 19 showed eye spots on June 7 and hatched between June 13 and June 14, at room temperature (20°C); development took from 25 to 26 days. The senior author confirmed the observation given by Carayon (1950) regarding the growth in volume of eggs during development of the embryo. Average measurements for freshly laid eggs of *Hymenocoris formicinus* were 0.60 mm × 0.39 mm; the average measurements for eggs containing a fully developed embryo were 0.79 × 0.44 mm. The eggs were whitish, and agreed in their general features with those of the African species described by Carayon. Observation of the chorion with phase contrast under high power revealed the presence of minute, more or less circular protuberances. The eggs had no caps. The day before hatching, faint outlines of legs, antennae, etc., could be observed within. After hatching, the eggs collapsed completely.

The first instar nymphs were quite active,

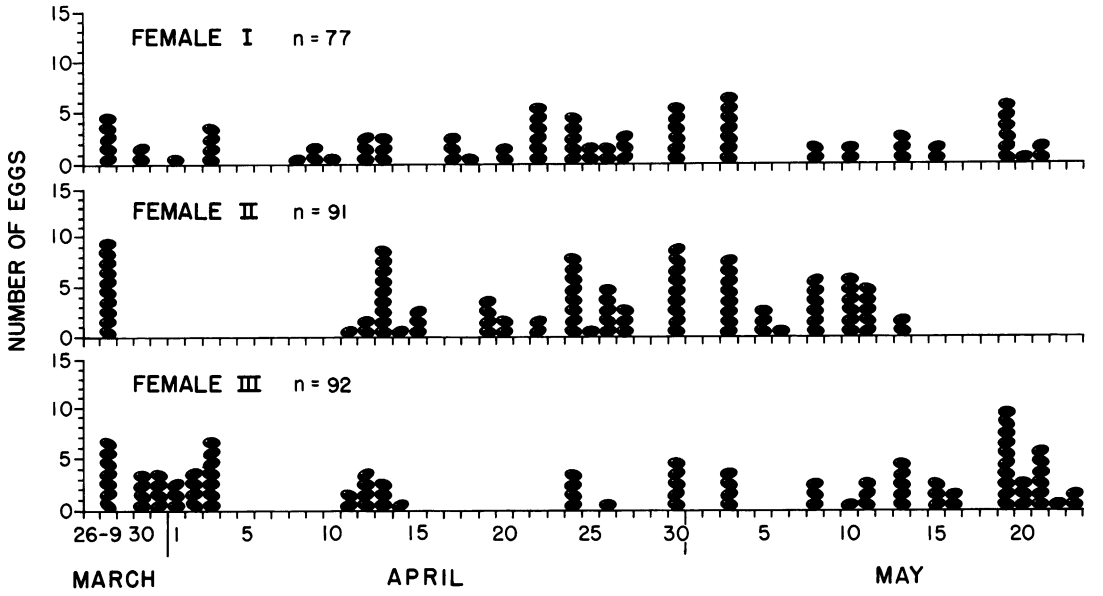


Fig. 3. Egg output of three females of *Hymenocoris formicinus* kept alive over a two month period.

running around and extending their rostra. Their forelegs were well-formed and apparently bore all the specialized spines. Their general color was whitish; in the forepart of the alimentary system, a yolk blotch could be seen.

SOMATIC STRUCTURES AND DIAGNOSTIC CHARACTERS

Good summaries of enicocephalid morphology are provided by Usinger (1932), Jeannel (1942), and Villiers (1958). In the sections below we discuss only new interpretations of morphology revealed through use of the scanning electron microscope, and those characters we believe to be of particular taxonomic significance.

Generalities. Three subfamilies are known from the New World. The phyletic line including the subfamily Aenictopecheinae has an indistinctly subdivided pronotum, a costal fracture in the forewing, mobile parameres, a phallus, lacks male genital plates, and has a distinctive linear arrangement of the foretibial spines in two groups separated by a deep notch. The phyletic line including the Enicocephalinae has a distinctly three-lobed pronotum, lacks a costal fracture, lacks a phallus, has immobile parameres, lacks male genital plates, and has a clustering of the foretibial spines in one group. The Alienatinae, sister group of the Enicocephalinae, contains extremely small and delicate insects with two or indistinctly three-lobed pronota, very reduced external genitalia, one-segmented tarsi, and extreme sexual dimorphism; females are eyeless and wingless and males have a simplified pattern of wing venation.

Morphological and structural nomenclature varies somewhat in the above three subfamilies and is covered in the following discussions of body regions. Our measurement methodology is illustrated in figure 4.

Sexual Dimorphism. Secondary (nongenitalic) sexual dimorphism occurs throughout the Enicocephalidae. In most species, females are larger than males and have smaller eyes and stouter proportions, especially of head and legs.

More drastic sexual dimorphisms also occur throughout the family and can be associated with wing polymorphism. Micropterous and apterous forms exhibit loss of ocelli, reduction in eye size, and modification of pronotal shape. In the New World taxa there

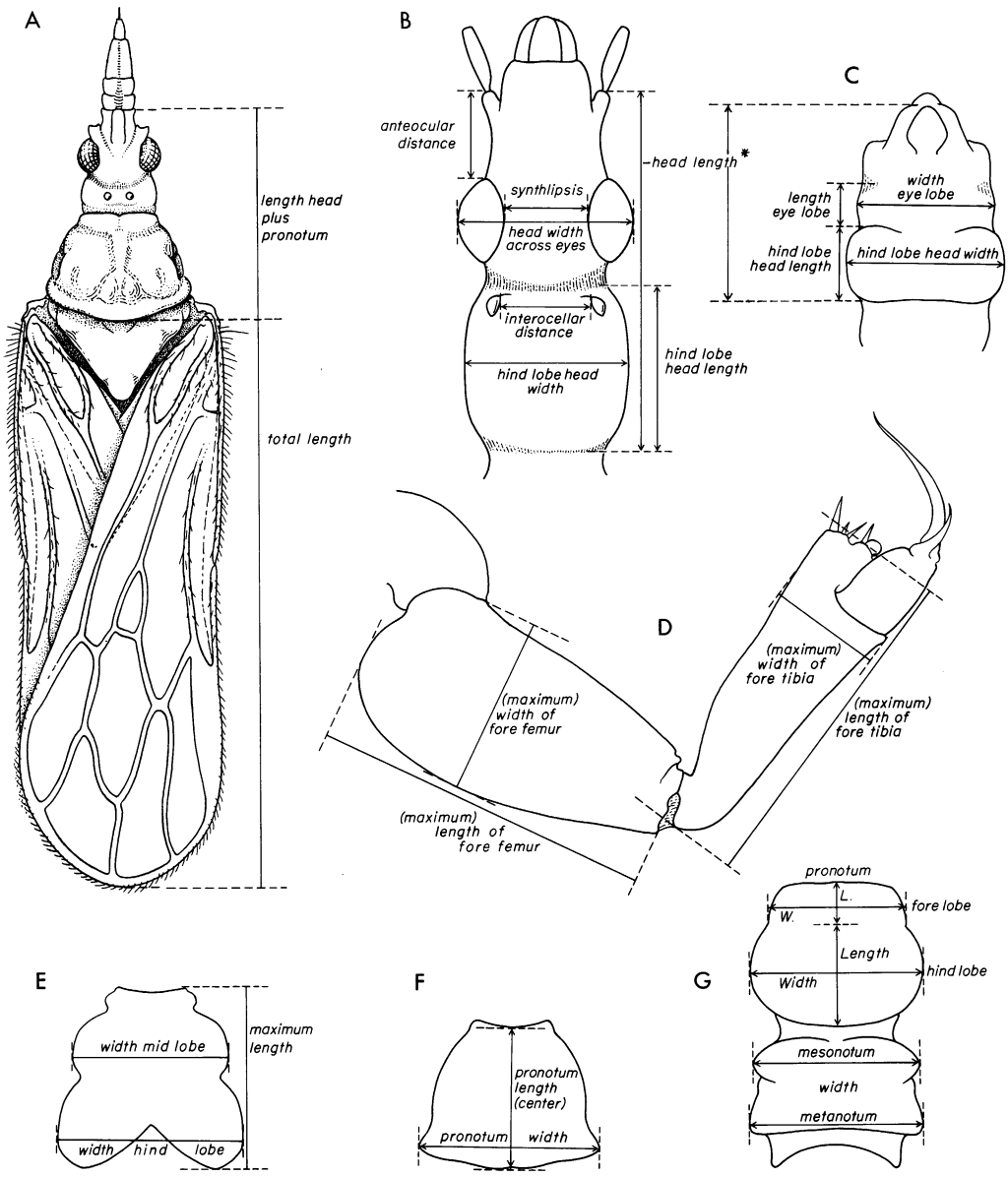


Fig. 4. Measurement methodology. **A**. Total length measured from tip of tylus to tip of wing or abdomen, whichever is longest. **B**. Head measurements.* **C**. Head measurements of *Alienates* ♀.* **D**. Leg measurements, maximum length and width taken parallel and perpendicular, respectively, to long axis of article. **E–G**. Pronotum measurements. **E**. Enicocephalinae and ♂ *Alienates*. **F**. Aenictopecheinae. **G**. *Alienates* ♀ (*Hymenocoris* similar).

* In all cases except *Alienates* females, head length was measured from antenniferous tubercles to sulcus posterior to hind lobe. Although it would make more sense to measure from the tip of the tylus, this is not always easy to see, and also, the project was begun using the antenniferous tubercle measurement.

is a wide range of wing sizes. They vary from the plesiomorphic condition of exclusively macropterous forms in both sexes (*Gamostolus* and some enicocephaline genera), through dimorphic or continuously pterygopolymorphic forms in one or both sexes (*Boreostolus*, some *Tornocrusus*, and some *Systelloderes*), to the condition in which males are exclusively macropterous and females are exclusively apterous (*Hymenocoris* and *Alienates*). There are no groups in the New World in which males are apterous.

In groups where wing morphs are *different* in both males and females, sexual dimorphism is very pronounced. Where wing morphs are the same in both sexes, dimorphism is less pronounced. This principle is well-illustrated in *Boreostolus*, in which most sex and wing morph combinations are known, except aptery. Male and female macropters differ from one another only slightly in eye size and proportions, in accordance with the basic sexual dimorphism seen in other groups. Micropterous forms of both sexes have much smaller eyes and modified pronota. As a general rule, males and females of the same wing morph are much more similar to one another than they are to the corresponding sex of the other wing morph. Wing polymorphism is more complicated on a worldwide basis (see Štys, 1982a), showing existence of micropterous and apterous forms of both sexes in diverse evolutionary lines.

It is clear that there is great selective pressure toward microptery and aptery in these insects, and that it occurs more frequently in females than in males. The drastic sexual differences such as those seen in *Hymenocoris* and *Alienates* could conceivably be derived from an ancestral stock which was pterygopolymorphic in both sexes, followed by the elimination of micropterous males and macropterous females.

STRUCTURES OF TAXONOMIC SIGNIFICANCE

Head. We have found several head proportions to be taxonomically valuable, although they should be used in conjunction with other characters, and certain cautions should be observed. For example, changes in the head, such as smaller eyes in females and short-winged morphs, and reduction or loss of ocelli, are associated with sexual dimorphism and wing polymorphism (see discussion above). When looking at head proportions, therefore, it is necessary to compare specimens of identical sex and wing length. Both cross-sexual and cross-pterygomorphic comparisons between taxa are nearly always misleading.

In all genera in which both sexes are known, males have larger eyes than females. This difference varies from slight in *Gamostolus* and *Tornocrusus* to extreme in *Hymenocoris* and *Alienates*, females of the last lacking eyes altogether. Throughout the New World Enicocephalidae, two head proportions consistently correlate with sexual dimorphism:

Eye Length/Anteocular Distance

Eye Width/Synthlipsis

In addition, the following proportions are correlated with sexual dimorphism in some, but not all, species:

Head Length/Pronotum Length

Head Length/Head Width Across Eyes

Hind Lobe Head Length/Hind Lobe Head Width

Once the effects of sex and wing polymorphism have been considered, head proportions become useful in delineating species. We have used eye size, for example, as a major character in separating species of *Hymenocoris*, some *Enicocephalus*, and delineating groups of *Urnacephala*. Other head proportions have been useful in *Lysenicocephalus* and elsewhere throughout the family, and we suspect that proportions will play a crucial role in the alpha taxonomy of *Systelloderes*.

Other head measurements of taxonomic importance include the size of the ocelli, the distance between them, and the distance from the ocelli to the lateral border of the head.

In *Alienates*, we evaluated the use of gular shape and shape of the hind lobe of the head as taxonomic characters, with mixed results (see Discussion under *A. insularis*). We concluded that gular shape was not a reliable specific character and that shape of the hind lobe of the head should be used with caution.

TABLE 3
Ground Plan of Antennal Proportions for New World Genera[a]

Genus	Males	Females	Ground plan
Alienates	1:2:1.7:3	1:1.3:1.1:2.4	IV longest (IV > II > III)
Boreostolus	1:2.9:3:2.3	1:2.8:2.8:2.3	II and III subequal (>IV)
Brevidorsus	1:3.4:2.9:2.9	—	II longest, III and IV subequal
Chiricocoris	—	1:1.9:2.6:2.1	III longest, II and IV subequal
Enicocephalus	1:2:3:2.6	1:2:2.5:2.3	III longest (III > IV > II)
Gamostolus	1:2:2.2:1.8	1:2:2.2:1.7	III longest (III > II > IV)
Hymenocoris	1:3.6:3.3:2.6	1:2.7:2.6:2.1	II longest (II > III > IV)
Lysenicocephalus	1:2.6:2.8:?	—	II and III subequal
Neoncylocotis	1:2:2.4:2	1:2.3:2.3:2	♂—III longest, II and IV subequal ♀—II and III subequal (>IV)
Systelloderes[b]	1:2:2.1:1.8	1:2.2:2.3:1.9	II and III subequal (>IV)
Tornocrusus	1:1.7:1.8:1.7	1:1.6:1.8:1.5	III longest, II and IV subequal
Urnacephala	1:3:2:2	—	II longest, III and IV subequal
Xenicocephalus[c]	1:2.9:2.3:2.7	—	II and IV subequal (>III)

[a] Calculated by averaging the means of each species as found in measurement tables.
[b] From 34 different species, including 15 females and 19 males.
[c] From nymph.

Antennae. In each genus the proportions of the antennal segments follow a basic groundplan, shown in table 3. These numbers are averages of proportions of the species in each genus, and individual species can vary significantly from them, even occasionally contradicting the basic pattern. This happens, for example, in the case of *Enicocephalus ningulus* in which the fourth antennal segment is the longest, unlike the averages. However, in the vast majority of cases, species conform very well to the basic plan. Sexual dimorphism is slightly evident in the differences in proportions between males and females, but in only one case are they strikingly different. Males of *Neoncylocotis* have segment III longest with II and IV subequal, while females have II and III subequal with IV shorter.

TABLE 4
Summary of Condition of Foreacetabula in New World Genera

Genus	Males	Females
Alienates	O	O
Boreostolus	O	O
Brevidorsus	O	?
Chiricocoris	?	[]
Enicocephalus	O	O
Gamostolus	O	O
Hymenocoris	O	[]
Lysenicocephalus	O	?
Neoncylocotis	O	O
Systelloderes	O	O
Tornocrusus	O	O
Urnacephala	O	?
Xenicocephalus	?	?

[] = closed.
O = opened.

Prothorax. Most of the important taxonomic characters of the thorax are found in the structure and proportions of the pronotum. In the Enicocephalinae, the pronotum is divided into three lobes by two transverse constrictions (fig. 4E). These constrictions are incomplete in the Aenictopecheinae (fig. 4A), and the posterior one has almost completely disappeared in the Alienatinae, being absent altogether in the apterous females (fig. 4G) and represented by a sinuosity in the lateral outline of the males (fig. 153A). The degree of differentiation of the lobes, the ornamentation, and the opened or closed condition of the foreacetabula (table 4) are all characters used at the generic level or higher.

Pronotal proportions are most useful at a specific level. Here, as with head proportions, care must be taken not to make cross-sexual or cross-pterygomorphic comparisons. There are two proportions in which sexual and pterygopolymorphic differences sometimes appear:

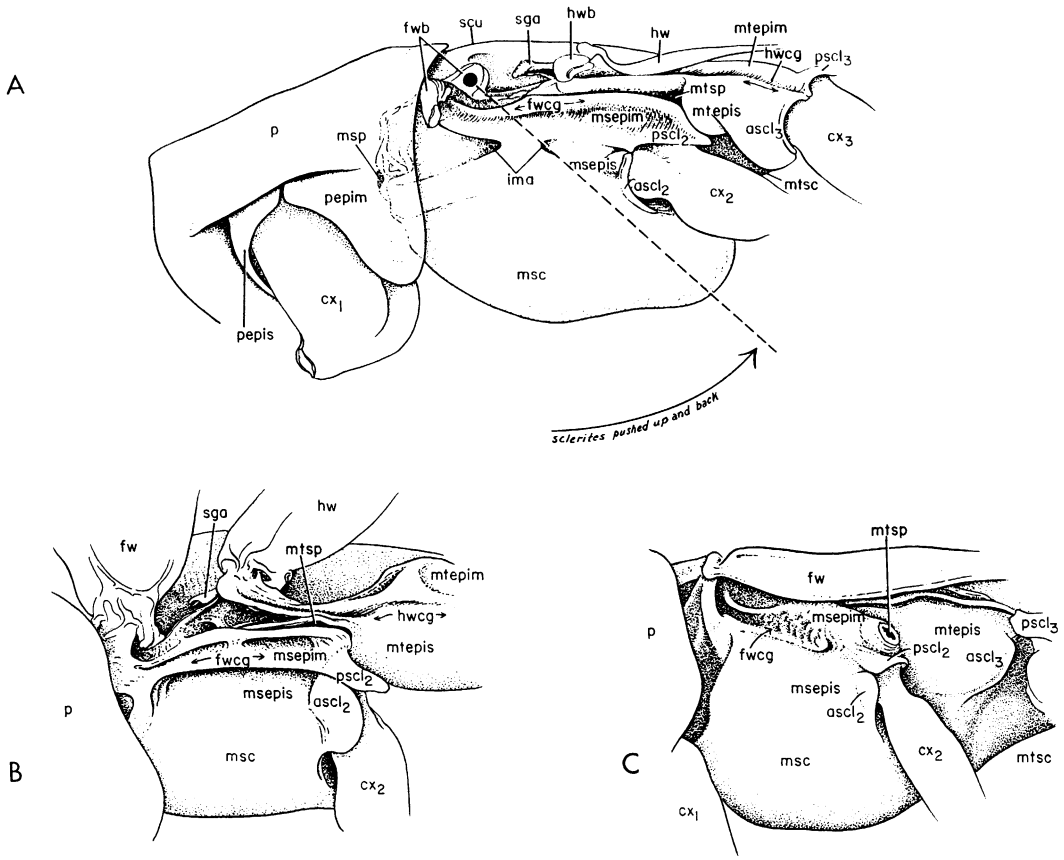


Fig. 5. Lateral view of thorax. **A**. *Gamostolus subantarcticus*. **B**. *Hymenocoris formicinus*. **C**. *Alienates millsi*. ascl, anterior supracoxal lobe; cx, coxa; fw, forewing; fwb, forewing base; fwcg, forewing coupling groove; hw, hindwing; hwb, hindwing base; hwcg, hindwing coupling groove; ima, internal muscle attachment area; msc, mesosternal complex; msepim, mesepimeron; msepis, mesepisternum; msp, mesothoracic spiracle; mtepim, metepimeron; mtepis, metepisternum; mtsc, metasternal complex; mtsp, metathoracic spiracle; p, pronotum; pepim, proepimeron; pepis, proepisternum; pscl, posterior supracoxal lobe; scu, scutellum; sga, scent gland auricle.

Width of Mid/Hind Lobe of Pronotum
Maximum Length/Maximum Width of Pronotum

These proportions differ most between the sexes in *Enicocephalus* and *Neoncylocotis* but show up as slight differences in other genera. The wing polymorphism factor is well-demonstrated in the genus *Boreostolus*, in which we could not make valid comparisons between the macropterous male holotype from Colorado and our West Coast material because we lacked macropterous males from the latter localities (see Discussion, *B. americanus*).

Wing Coupling Mechanisms. There are two kinds of coupling mechanisms associated with the wings of enicocephalids: fore-hind wing coupling mechanisms and wing-body coupling structures. The forewing-hind wing coupling mechanisms have been most extensively explored by Wygodzinsky and Štys (1982). In the present paper we have studied these wing coupling mechanisms with the scanning electron microscope. We have photographed the device itself and also the corresponding edge of the hind wing in 11 genera (not including *Lysenicocephalus* and *Xenicocephalus*). Scanning micrographs are included with each genus, and figure 7 compares the 11 genera. We looked at three

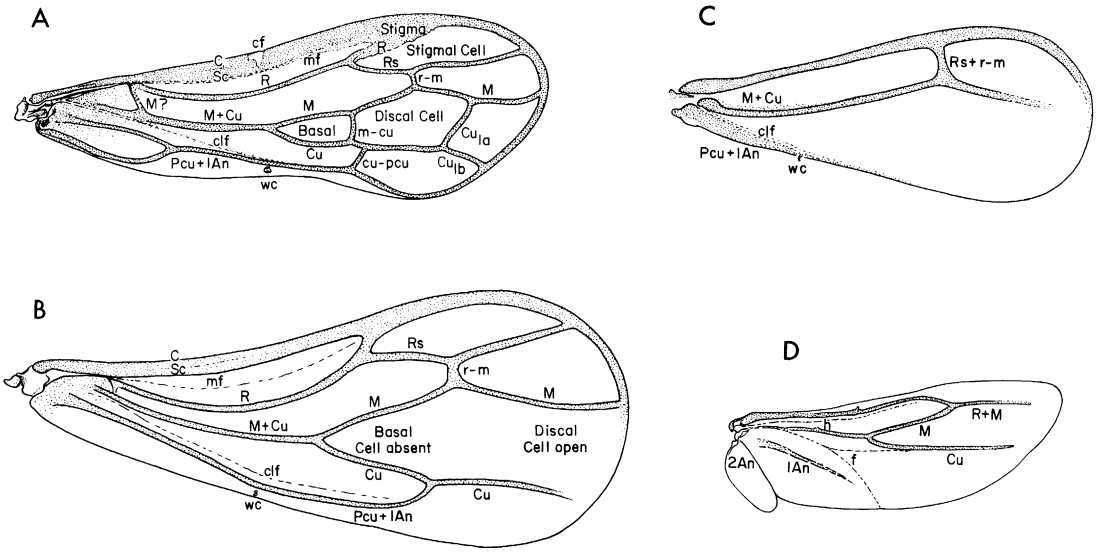


Fig. 6. Enicocephalid wing venation and terminology. **A–C**. forewings. **A**. *Gamostolus subantarcticus* (based on Štys, 1980). **B**. *Brevidorsus arizonensis*. **C**. *Alienates insularis*. **D**. *Tornocrusus penai*, hind wing. An, anal; C, costa; cf, costal fracture; clf, claval fracture; Cu, cubitus; f, cubital furrows; h, hamus; M, media; m-cu, medio-cubital crossvein; mf, medial fracture; Pcu, postcubitus; R, radius; r-m, radio-medial crossvein; Rs, radial sector; Sc, subcosta; wc, wing coupling mechanism.

characters of the wing coupling mechanism: its distance from the wing base, the length and the ornamentation[1] of its posterior arm (closest to wing edge, figs. 7H, 104E), and the corresponding edge of the hind wing (fig. 104F). The results are summarized in table 5.

These characters suggest several trends, although they are by no means unambiguous. The wing coupling device is located farthest from the wing base (45–47% of wing length) in the three Aenictopecheine genera; in *Alienates* it is located closest (27% of wing length). All other genera fall somewhere in between, with *Systelloderes* and *Xenicocephalus* most similar to the Aenictopecheinae.

[1] After seeing the wing coupling mechanisms under the SEM, we realized that we had been consistently interpreting the ornamentation of the posterior arm as shorter, more peglike than it really is. Compare the *E. ningulus* SEM (fig. 73E) with its light microscope drawing (fig. 85I). For the latter, the wing lies flat on a slide, thus orienting the papillae downward and making them appear in cross section like small circles. Even though many of the light microscope drawings of this device are similarly misleading, we include them because this is the way they will be most frequently observed.

In most genera, the posterior arm of the wing coupling mechanism is only slightly longer than the anterior arm (fig. 7). In *Neoncylocotis* and *Enicocephalus* it becomes progressively lengthened, until in *Alienates* it is very elongate and extends way beyond the wing edge (figs. 7K, 153E). We concur with Wygodzinsky and Štys (1982), that the lengthened, hyperextended condition of the posterior arm is derived, since the nonextended condition is more similar to that found in other Heteroptera. Looking at the SEMs, it is tempting to speculate that the wing coupling mechanism formed from an aggregation and subsequent elongation of the microtrichiae normally present on the wing surface. If this hypothesis is correct, it would also support the contention that the hyperextended condition is apomorphic.

The ornamentation of both the hind wing edge and the posterior arm of the wing coupling mechanism present a mosaiclike distribution of characters that is difficult to analyze. All anterior arms terminate in long, pointed microtrichiae. Posterior arms bear apical projections varying from short, blunt pegs in *Systelloderes* (fig. 58E), to slightly

TABLE 5
Summary of Information on Forewing Coupling Devices and Corresponding Hind Wing Edges in New World Genera

Genus	Distance from wing base % of wing length (range)	Length of posterior arm	Ornamentation of posterior arm	Ornamentation of hind wing edge
Alienates	27% (24–31)	Very long	Long, pointed	Plain
Boreostolus	45% (—)	Short	Long, pointed-rounded	Foliaceous
Brevidorsus	41% (—)	Short	Long, pointed	Foliaceous
Chiricocoris	41% (—)	Short	Long, pointed	Plain
Enicocephalus	39% (30–46)	Long	Medium, pointed	Foliaceous
Gamostolus	47% (—)	Short	Medium, rounded	Foliaceous
Hymenocoris	36% (32–40)	Short	Medium, pointed-rounded	Foliaceous
Lysenicocephalus	—	—	—	—
Neoncylocotis	39% (36–41)	Medium	Short, pointed	Plain
Systelloderes	44% (42–45)[a]	Short	Short, rounded	Foliaceous
Tornocrusus	46% (43–48)	Short	Medium, rounded	Plain
Urnacephala	35% (33–39)	Short	Medium, pointed	Plain
Xenicocephalus	42% (—)	—	—	—

[a] Based on two species only.

longer rounded papillae in *Hymenocoris*, *Gamostolus*, and *Tornocrusus* (figs. 104E, 32E, 41B), to short or long pointed microtrichiae in the other genera (fig. 66F). Hind wing edges are plain in *Tornocrusus*, *Chiricocoris*, *Urnacephala*, *Neoncylocotis*, and *Alienates* (fig. 41C), and foliaceous in *Hymenocoris* (fig. 104F) and *Brevidorsus* (fig. 63F). The intrageneric and even intraspecific variation of these last two characters has yet to be determined. For example, our SEM of the wing coupling device of *Systelloderes culicis* disagrees in details with the description by Wygodzinsky and Štys (1982); its anterior arm has more than a single row of teeth (fig. 58E). We do not know how length, number, and shape, etc., of these microtrichiae vary and it is probably premature to attempt more than a gross analysis of these characters.

The wing-body coupling structures are dealt with below in our discussion of lateral thoracic segments.

Identities of some Pterothoracic Segments. In order to establish the homologies of the lateral thoracic sclerites with certainty, a detailed study of nymphal development would be necessary. Although such an endeavor is beyond the scope of this paper, we have formed some hypotheses based on close examination of adults of the three subfamilies.

The structure of the prothorax is relatively uncomplicated, but that of the meso- and metathorax is more complex and may have important taxonomic ramifications. We have paid particular attention to three structures: the true metathoracic scent gland orifices, first described here; the wing-body coupling groove; and the metathoracic spiracle.

The first two structures are most easily seen in the Aenictopecheine genera, while the metathoracic spiracle is most easily visible in *Alienates* males (fig. 153C). All of these structures are present, although not always well developed, in all macropterous specimens of each genus; the external scent gland structure and wing coupling groove are absent from the apterous *Hymenocoris* and *Alienates* females. These latter would be expected to produce some form of sexual attractant and the possibility of scent dispersal structures should be more fully investigated (P. Štys, personal commun.).

The peculiar position of the lateral thoracic sclerites can best be understood by imagining that the segments have been crowded together, as if they had been pushed up and back by a line pivoting around a point near the forewing base (fig. 5A). This may relate in some way to the unusually expanded condition of the mesosternum and its related sclerites. The final result is a more dorsal location of the metathoracic scent gland, spiracle, and mesepimeron than is seen in most other Heteroptera, and a nearly horizontal

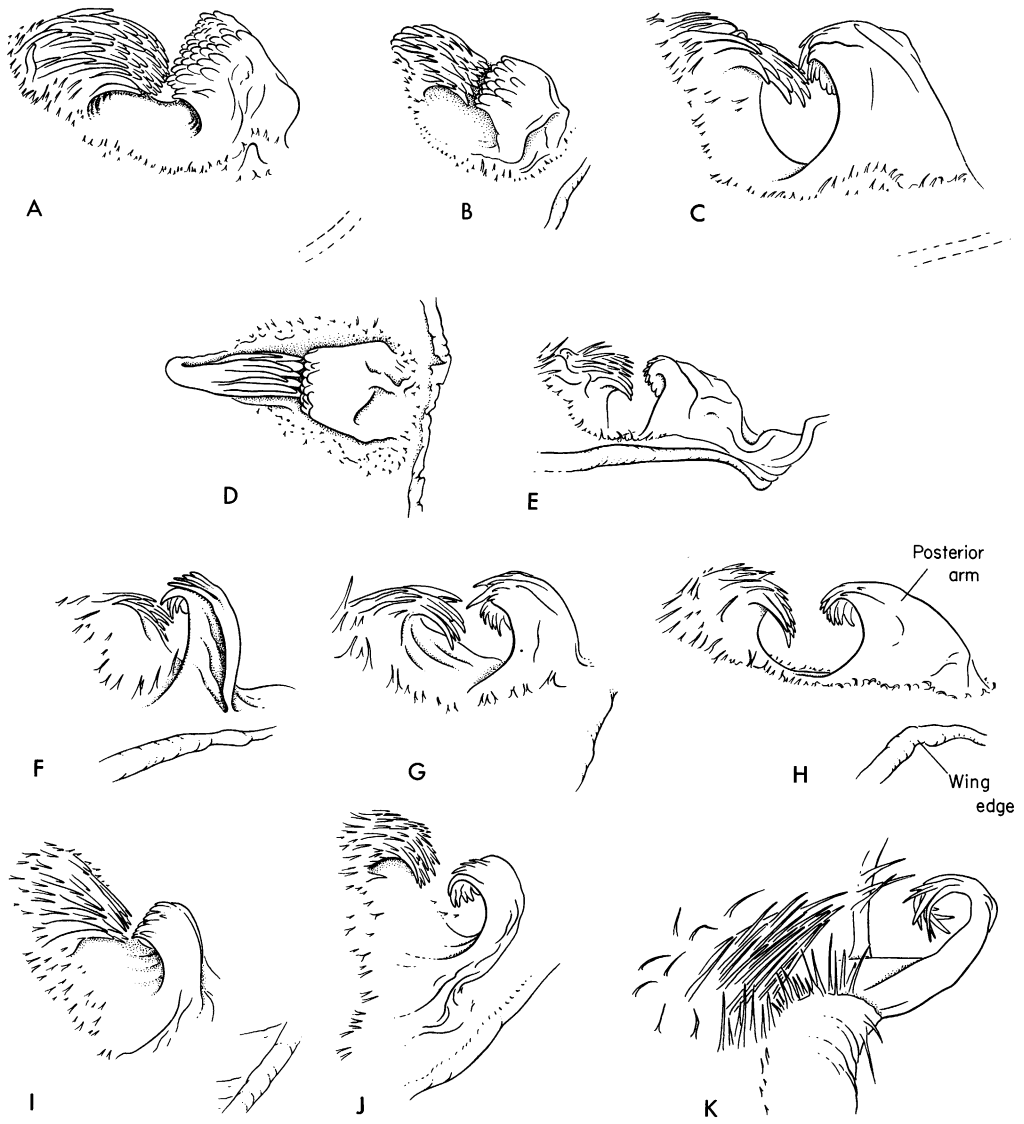


Fig. 7. Wing coupling mechanisms on forewings of Enicocephalidae. **A**. *Gamostolus subantarcticus*. **B**. *Tornocrusus penai*. **C**. *Boreostolus americanus*. **D**. *Systelloderes culicis*. **E**. *Hymenocoris formicinus*. **F**. *Brevidorsus arizonensis*. **G**. *Urnacephala californica*. **H**. *Chiricocoris dybasi*. **I**. *Neoncylocotis albovenosus*. **J**. *Enicocephalus ningulus*. **K**. *Alienates millsi*.

rather than vertical orientation of the meso-metathoracic junction.

There is much confusion in the literature concerning scent glands of Enicocephalidae, and, unfortunately, our results do not provide answers to all questions. However, we have discovered the previously unrecognized metathoracic scent glands proper, known throughout the Heteroptera and discussed at length for other families by Carayon (1962). The paired orifices are located dorsally, laterad of the scutellum. They are normally hidden under the closed forewings and this is undoubtedly why they have gone unnoticed for so long. They are most highly developed in macropterous specimens of *Ga-*

mostolus (fig. 30F), *Tornocrusus*, and *Boreostolus*, somewhat reduced in the Enicocephalinae (fig. 104B), a minute nearly unrecognizable twisted channel in male *Alienates*, and altogether absent in apterous forms. Their location just under the forewing base would undoubtedly allow the scent to be dispersed quite effectively in the draft created by the moving wing. The microstructure of the evaporative areas of the scent gland auricles needs to be investigated in greater depth.

The taxonomic ramifications of the presence of such well-developed and widely separated scent gland orifices creates a discrepancy with Carayon's (1971) information on enicocephalid scent glands. He reported them as having what he considered to be the primitive omphalian type system, with a median internal sac and either an unpaired median opening or two closely spaced and simple orifices. After several dissections of already preserved material, we were not able to see much of the internal structure of the scent glands, other than a duct on each side leading out to the auricles in *Gamostolus subantarcticus*. The presence of such widely separated orifices strongly suggests that Enicocephalidae have the diastomian system. Since this is the condition encountered in the majority of other Heteroptera, and since developmental progress tends to go from paired lateral toward single median structures, it may mean that the diastomian system is plesiomorphic.

The metathoracic scent glands proper are not to be confused with the paired ventral glands at the thoracico-abdominal junction, the orifices of which appear in all three Aenictopecheine genera, and they have also been found in three Reduviid subfamilies, Phymatinae, Elasmodeminae, and Holoptilinae (Carayon, 1962). They show best in SEMs of *Gamostolus subantarcticus* (figs. 31A, C–E), but also appear in *Tornocrusus sturmi* (figs. 41D, E) and *Boreostolus americanus* (figs. 20D–F). A cursory light microscope study of these structures reveals bicornate sclerotized invaginations within the orifices (fig. 35A). These probably act as egresses for glandular secretions, although further histological studies would have to be done to establish this. We did not look for these glands in the Enicocephalinae and the Alienatinae. Scanning electron microscope observations of *B. americanus* do not substantiate the previous claim of Wygodzinsky and Štys (1970) that there is a median ventral scent gland orifice at the base of the abdomen of this species, nor in the other two Aenictopecheine genera (figs. 20D, 31A, D, 41D).

The meso- and metathoracic segments exhibit varying degrees of fusion with one another. As a general rule, the second and third anterior supracoxal lobes (of Štys, 1981b) form the receptacles for the second and third coxae, respectively. The separation of these lobes from the more anterior episterna and epimera are evident in some genera (*Hymenocoris*, fig. 5B) and not in others (*Gamostolus*, fig. 5A).

The fore and hind wing-to-body coupling grooves are also variously developed. The forewing coupling groove is most obvious in the Aenictopecheine genera, forming a wide groove extending from the forewing base back to form the upper edge of the mesocoxal cavity (see *Gamostolus subantarcticus*, fig. 30E). The costal edge of the forewing lies in the groove while the wing is at rest. The groove is less extensive in brachypterous specimens of *Boreostolus* (fig. 19B), along with a noticeably shorter and less expanded mesosternal complex. This undoubtedly relates to the reduction in function of the forewings and their associated flight muscles. The groove in the Enicocephalinae is variously developed, ranging from short and wide in *Enicocephalus* and *Neoncylocotis* to long and very narrow in *Systelloderes* and *Urnacephala*. In *Alienates* males it is well-defined anteriorly but fades out posteriorly.

The hind wing-to-body coupling groove to accommodate the costal edge of the hind wing is formed by the metepimeron, or the fused metepimeron and third posterior supracoxal lobe. It is variously developed among the genera (*Enicocephalus*, fig. 74B; *Gamostolus*, fig. 30E; and *Hymenocoris*, fig. 104B).

The Aenictopecheinae have 10 pairs of spiracles, the first on the anterior portion of the mesothorax, hidden under the pronotum, the second between the mesepimeron and metepisternum, and the rest on segments I–VIII of the abdomen. We could not determine whether the first pair of thoracic spiracles is present in the Enicocephalinae and Alienatinae. The abdomen in these two sub-

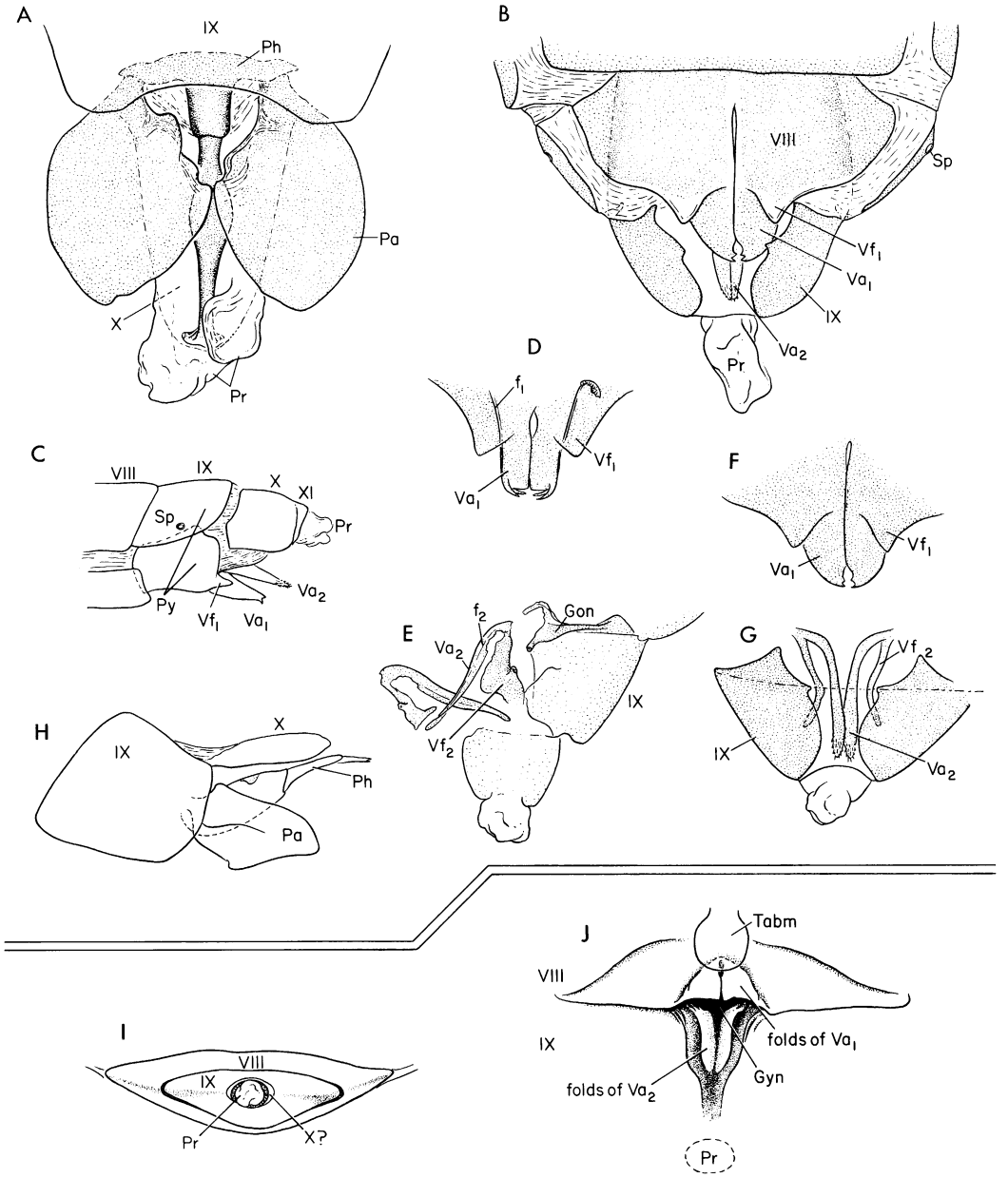


Fig. 8. **A–H**. Genitalia of Aenictopecheinae. **I** and **J**. Female genitalia of Enicocephalinae. **A**. *Tornocrusus penai*, ♂ genitalia, ventral view. **B**. *Gamostolus subantarcticus*, ♀ genitalia, ventral view. **C**. same, lateral view. **D**. *T. sturmi*, ♀ reproductive structures associated with segment VIII. **E**. same, damaged section on slide, structures associated with segment IX. **F**. *G. subantarticus*, ♀, segment VIII genital structures. **G**. same, segment IX genital structures. **H**. *T. occidentalis*, ♂, lateral view. **I**. Posterior view of *Neoncylocotis albovenosus*, ♀. **J**. *Systelloderes culicis* ♀, segments VIII & IX, ventral, reconstructed from SEM (fig. 60F). (For key, see abbreviation list).

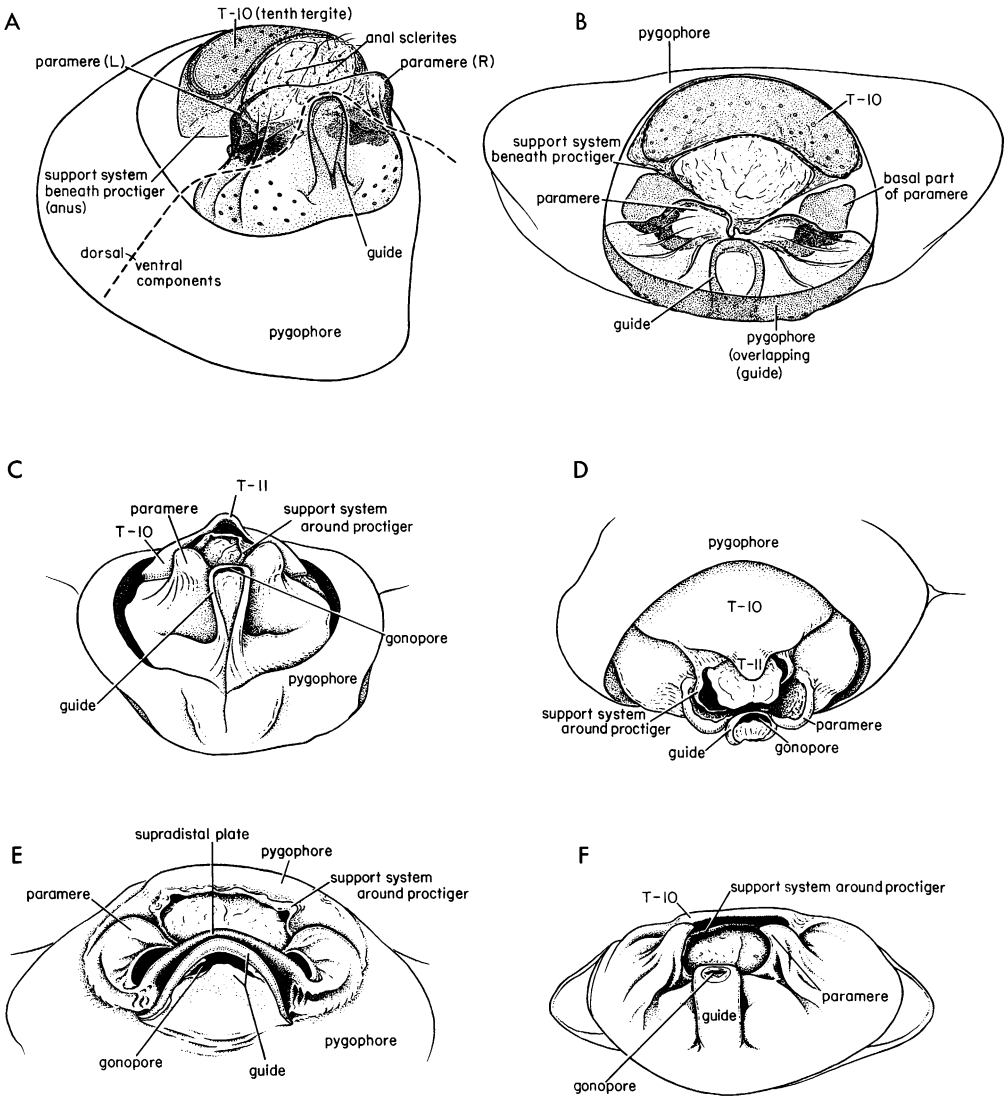


Fig. 9. Male genitalia of Enicocephalini, Systelloderini, and Alienatinae. **A**. *Hymenocoris formicinus* (from slide), ventrolateral, slightly posterior view, showing division between dorsal and ventral components. **B**. Posterior view of same. **C**. *Urnacephala californica* (from SEM), posteroventral view. **D**. Posterodorsal view of same. **E**. *Systelloderes culicis* (from SEM), posterior view, showing supradistal plate. **F**. *Alienates millsi*, posterior view.

families usually lacks the spiracles on segment I, but the metathoracic spiracle (number 2) is always present.

The position of the metathoracic spiracle is illustrated by *Alienates* (figs. 5C, 153C). It is located at the extreme posterolateral edge of the mesothorax. In the other genera it is in a similar location, although it tends to be hidden in a triangular pocket in the deep groove between the meso- and metathorax (figs. 5A, B). Examination of slides of several genera reveals tracheae converging on this area in each case, and there can be little doubt that the opening is a spiracle. The apparent lateral holes visible in the aenictopecheine genera (fig. 5A) are areas of muscle attachment rather than spiracles.

Cuticular Structures of Thorax and Abdo-

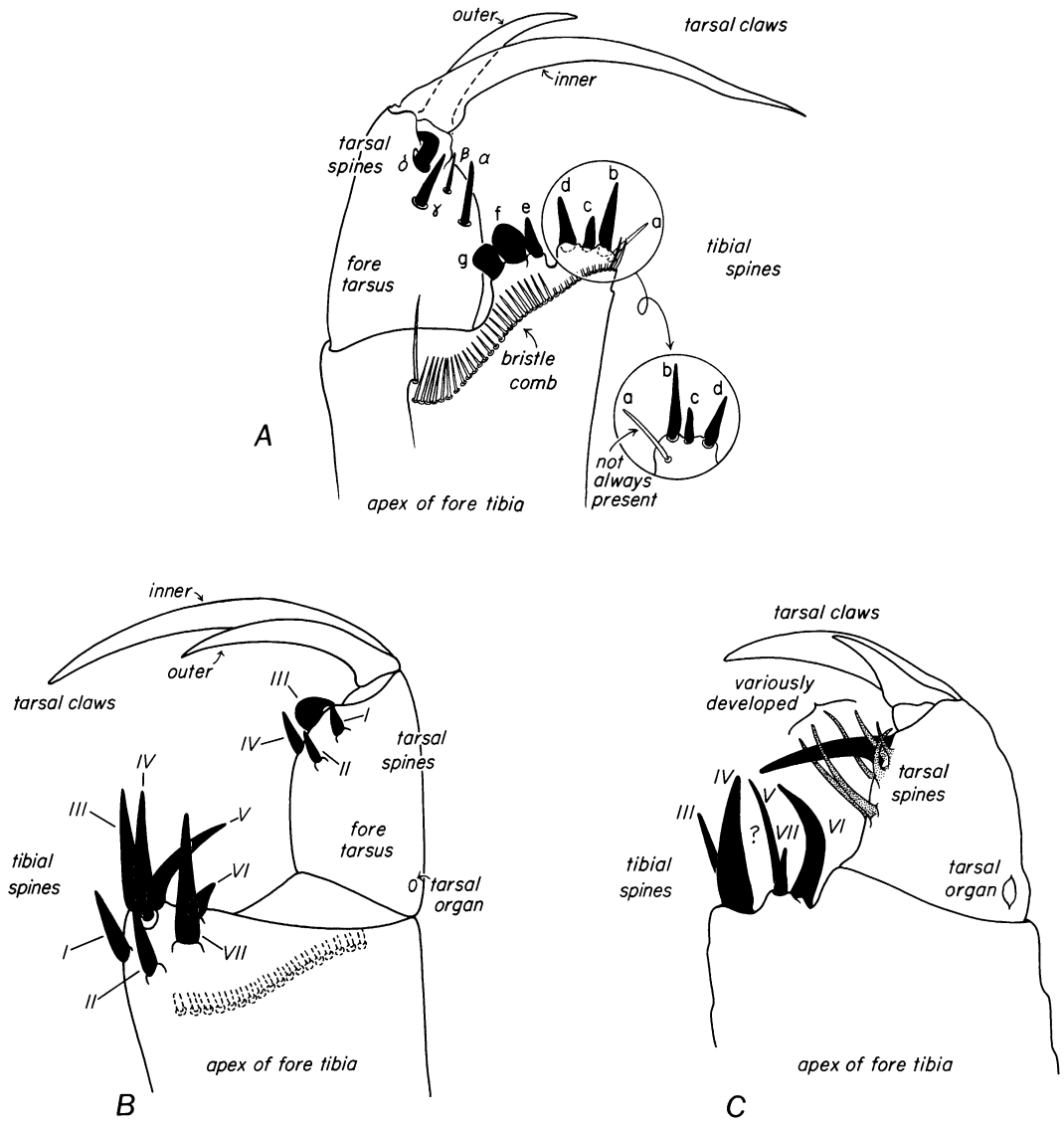


Fig. 10. Apices of generalized forelegs of the three New World subfamilies. **A**. Aenictopecheinae, inner view. **B**. Enicocephalinae, outer view. **C**. Alienatinae, female, outer view. Homologies of spines uncertain. (The bristle comb is always on the "inner" surface of the foreleg; the shorter of the two tarsal claws, if they are not equal, is always on the outer surface in New World taxa.)

men: The SEM studies reveal many types of cuticular structures, detailed analysis of which is beyond the scope of this paper. However, we have included the photographs for documentary purposes.

The cuticular structures range from microtrichiae and cuticular granules, to small glandular (?) openings, and even intersegmental sensory (?) structures. Microtrichiae are the most frequently observed of these and can be seen in all genera on various body parts, especially the wings (figs. 120D, E). Cuticular granules also appear in many genera and can best be seen in the SEM of the gular region of *Enicocephalus ningulus* (fig. 72E). Their absence or presence and distribution on the forefemur is sometimes diagnostic of species in that genus. These granules often grade into,

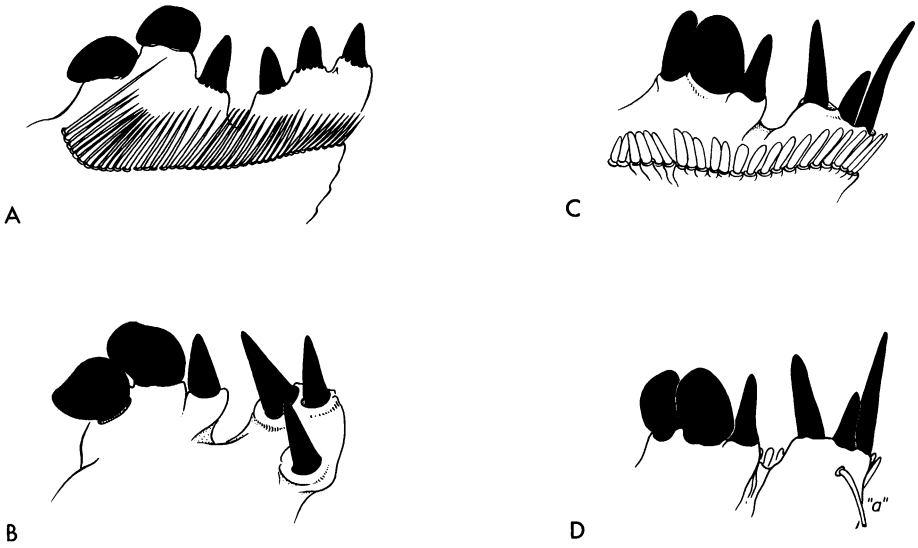


Fig. 11. Foretibial spines of Aenictopecheinae. **A**. *Gamostolus subantarcticus*, inner view. **B**. *Boreostolus americanus*, outer view. **C**. *Tornocrusus penai,* inner view. **D**. Same, outer view of opposite leg, showing spine "a".

or appear exclusively as, one- to several-toothed spicules (fig. 79D).

Small glandular (?) openings appear in many forms, including pits with raised central holes (*Systelloderes culicis*, fig. 59F), dishes with holes (*Tornocrusus penai*, fig. 41F), and bare areas with holes (*Chiricocoris dybasi*, figs. 68B, C). In *Chiricocoris* the latter appear in aggregations on the abdominal sterna, suggesting a similarity to the androconia illustrated by Carayon (1984). However, these are found in the female (males are unknown).

Papillar projections are found between the sterna and ventral connexival plates of *Systelloderes culicis* (figs. 59D, E), perhaps functioning as sensors to indicate the expanded or contracted condition of the abdomen.

A perusal of the SEMs will reveal the variety and range of the above structures. We hope that knowledge of their presence may prove useful for orienting future investigations.

Legs. We have explored four characters of the legs for taxonomic purposes: proportions, chaetotaxy of the apex of the foreleg, chaetotaxy of the mid and hind tibiae, and surface ornamentation.

Proportions tend to be sexually dimorphic, and as a rule, legs of females are stouter than those of males. Proportions are usually consistent within a given species, although in several species we encountered situations which tended to cast doubt on their stability. For example, we have two groups of *Neoncylocotis montanus* from Rancho Grande, Venezuela, collected eight years apart. In all observable characters they seem identical, with the exception of their leg proportions (table 14). We do not know whether they reperesent two species, or if they represent one species whose morphometrics reflect different environmental conditions during ontogenesis.

The forelegs of enicocephalids terminate in distinctive arrays of tibial and tarsal spines, which, together with the tarsal claws, form opposable, crablike pincers. These spines are taxonomically useful on a subfamilial, generic, and occasionally specific level. Given the loss and/or fusion of genitalic structures in the Enicocephalinae and Alienatinae, they are among the most useful and reliable diagnostic characters in these two subfamilies.

The New World aenictopecheine genera have 6 or 7 foretibial spines arranged linearly in two groups separated by a deep notch (figs. 10A, 11). The presence of spine *a* and its degree of differentiation from a normal fore-

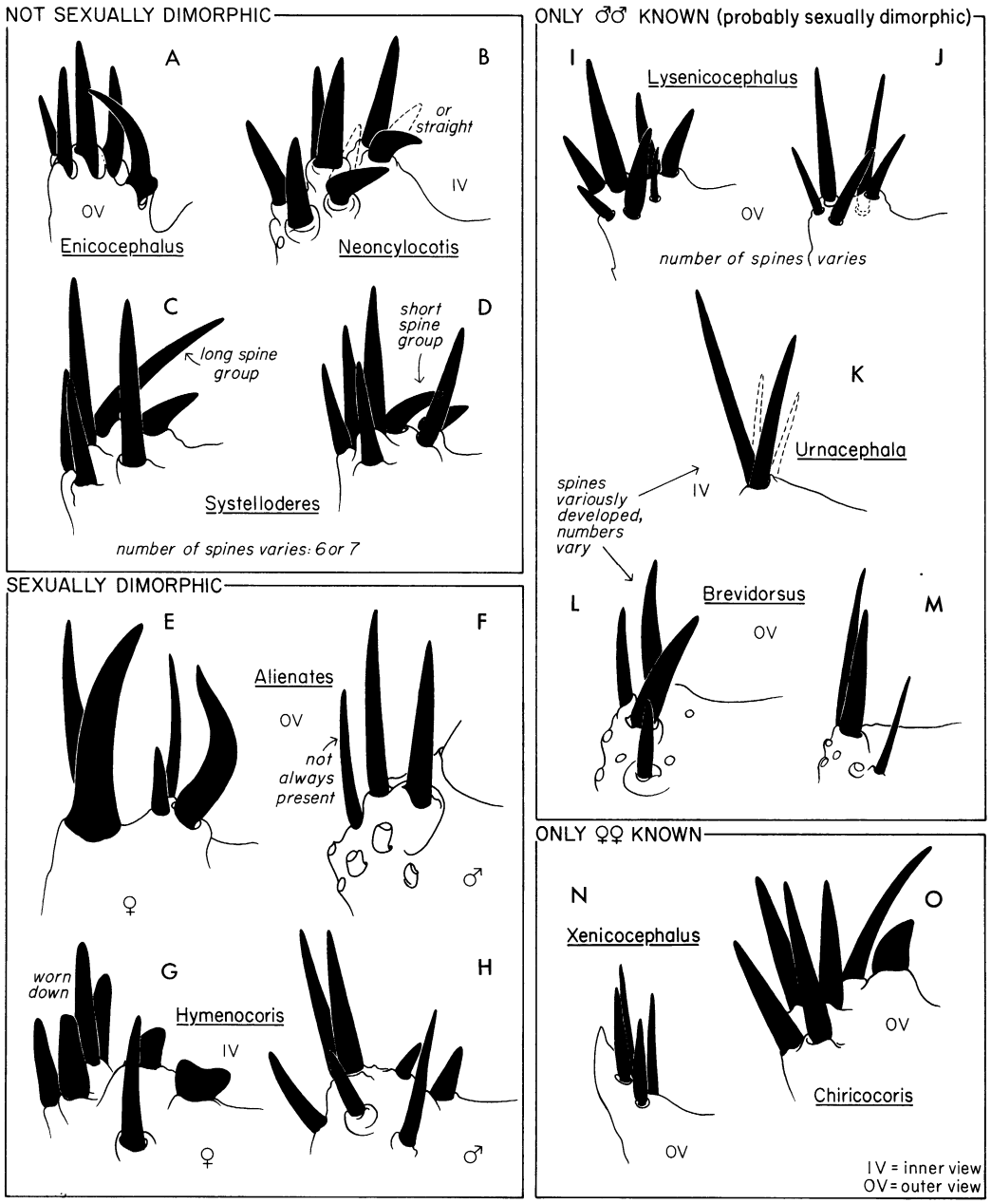


Fig. 12. Foretibial spines of Enicocephalinae and Alientinae.

leg seta is variable. It was first described by Štys (1980) in *Australostolus monteithi* and is also present in the genus *Tornocrusus* (fig. 39C, lying down). It is absent in *Boreostolus* and *Gamostolus*.

Enicocephaline foretibial spines are variations of a generalized pattern (figs. 10B, 12). When sexual dimorphism is apparent, as in *Hymenocoris formicinus*, the spines of adult females and nymphs of both sexes are identical, while those of males are generally thinner, more reduced, and less modified. In the three genera known only from males, *Urnacephala*, *Brevidorsus*, and *Lysenicocephalus*,

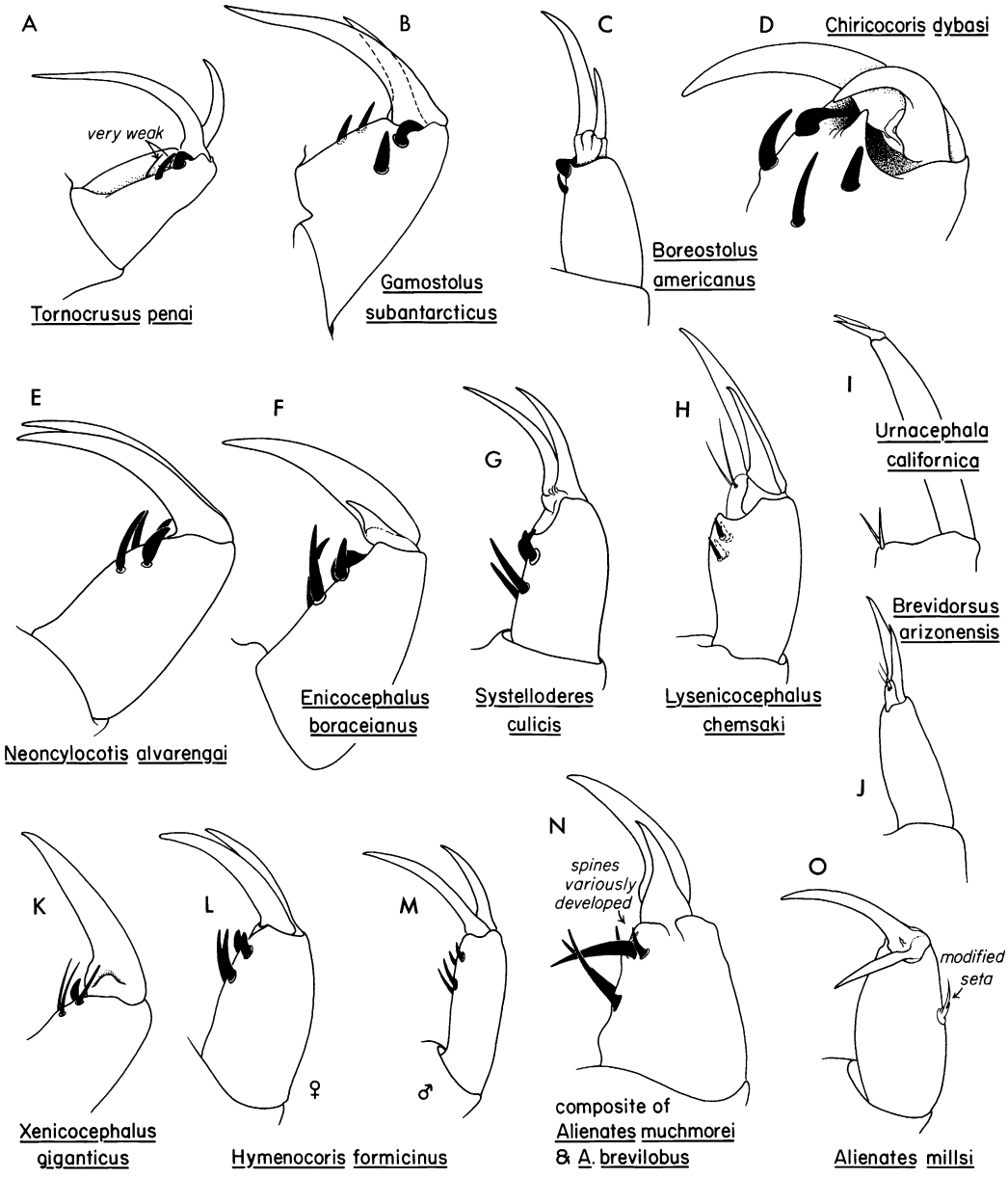


Fig. 13. Foretarsi, tarsal spines, and claws of Enicocephalids. **A**. *Tornocrusus penai*, ♂. **B**. *Gamostolus subantarcticus*, ♂. **C**. *Boreostolus americanus*, ♀. **D**. *Chiricocoris dybasi*, ♀. **E**. *Neoncylocotis alvarengai*, ♂. **F**. *Enicocephalus boraceianus*, ♀. **G**. *Systelloderes culicis*. **H**. *Lysenicocephalus chemsaki*, ♂. **I**. *Urnacephala californica*, ♂. **J**. *Brevidorsus arizonensis*, ♂. **K**. *Xenicocephalus giganticus*, ♀. **L**, **M**. *Hymenocoris formicinus*, ♀ and ♂. **N**. *Alienates brevilobus*, ♀, showing possible recurved 6th spine. **O**. *A. millsi*, ♂. A, B, inner views. C–O, outer views.

foretibial spines are highly reduced and somewhat variable in number even within a species. These factors cast doubt on their taxonomic value. There is at least a possibility that in the above four genera, adult males do not eat, and thus do not need the spines for handling prey (see Biology).

The foretibial spines of Alienatinae are

somewhat modified from the generalized enicocephaline type (fig. 10C). However, they are possibly homologous with spines III, IV, V, VI, and VII. They appear closest to those of *Enicocephalus*, having five developed spines, and sharing with that genus the distinctive strongly arched spine VI directed away from the tarsal claws.

The mid- and hind tibiae of enicocephalids bear various combinations of apical and subapical bristle combs and enlarged spines (fig. 14). A summary of their occurrence in New World genera is presented in table 6. The most frequently encountered condition consists of two linear bristle combs separated by a small space containing two enlarged spines. The aenictopecheine genera *Gamostolus* and *Boreostolus* lack the bristle combs entirely, and have 5–7, and 2 subterminal spines, respectively. *Tornocrusus* has only 1 spine and 1 continuous bristle comb. *Enicocephalus* and *Neoncylocotis* have 2 main spines with 1–3 weaker central or lateral spines. When there are more than 2 spines, the more lateral ones tend to grade into the normal leg setae and it becomes problematical whether or not to call them "spines."

The foretarsus of all known New World Enicocephalidae is 1-segmented. Each normally bears 4 spines on its inner surfaces (fig. 13). Exceptions to this are males of *Alienates*, *Urnacephala*, and *Brevidorsus*, which lack spines, and *Boreostolus*, which has only 2. Females of *Alienates* have 1 distinctive spine that is nearly as large as the claws, plus 4 or 5 others that are variously developed and sometimes difficult to distinguish from normal foreleg setae. The relative length of the foretarsus also furnishes a useful character. In most enicocephalids the foretarsus is not much, if any, longer than wide at its base. In the males of *Hymenocoris*, *Urnacephala*, and *Brevidorsus* the foretarsus is long and very slender.

There is a tendency among the Enicocephalidae for the outer (posterior) foretarsal claw to become shorter or to nearly disappear. Only in *Neoncylocotis* and *Urnacephala* are the two claws of equal length. The outer claw is extremely short in *Enicocephalus*, from ¼ to ⅔ the length of the inner claw. It disappears altogether in *Xenicocephalus*, being represented by a minute basal hump next to the remaining inner claw. We have also noticed the asymmetry described by Štys (1986) in which the inner (anterior) parempodial seta is reduced while the inner tarsal claw remains long, and the outer (posterior) parempodial seta remains long while the outer tarsal claw is reduced. This can be observed, for example, in *Enicocephalus* (figs. 72G), *Boreostolus*, *Alienates*, and *Systelloderes* (fig. 57D).

The hind tarsi of all New World Enicocephalidae are 2-segmented, with the exception of those of *Alienates*, which are 1-segmented.

Surface ornamentation of the legs is taxonomically useful in *Enicocephalus* and *Neoncylocotis*, and to a lesser degree in other genera. The inner surface of the forefemur is often covered with a single patch of microstructures varying from hemispherical globules ("cuticular granules") to one or several-toothed spicules (figs. 75D). The location, size, and shape of the patches and the mixtures of types of microstructures are often species-specific.

An area of closely spaced wide and short setae is found on the inner surface of the distal portion of the foretibia in *Neoncylocotis* and *Xenicocephalus* (fig. 150D), as well

TABLE 6
Summary of Occurrence of Spines and Bristle Combs on Apices of Mid and Hind Tibiae of New World Genera

Genus	Spines	Bristle combs
Alienates	2[a]	2
Boreostolus	2	0
Brevidorsus	2	2 (narrowly spaced)
Chiricocoris	2	2
Enicocephalus	2[b]	2
Gamostolus	2[c]	0
Hymenocoris	2	2 (narrowly spaced)
Lysenicocephalus	2	2
Neoncylocotis	2[d]	2
Systelloderes	2	2
Tornocrusus	1	1
Urnacephala	2	2
Xenicocephalus	1 or 2	2

[a] Also 1 modified central.
[b] Also 1 smaller central.
[c] Also several small lateral.
[d] Also 1 smaller central.

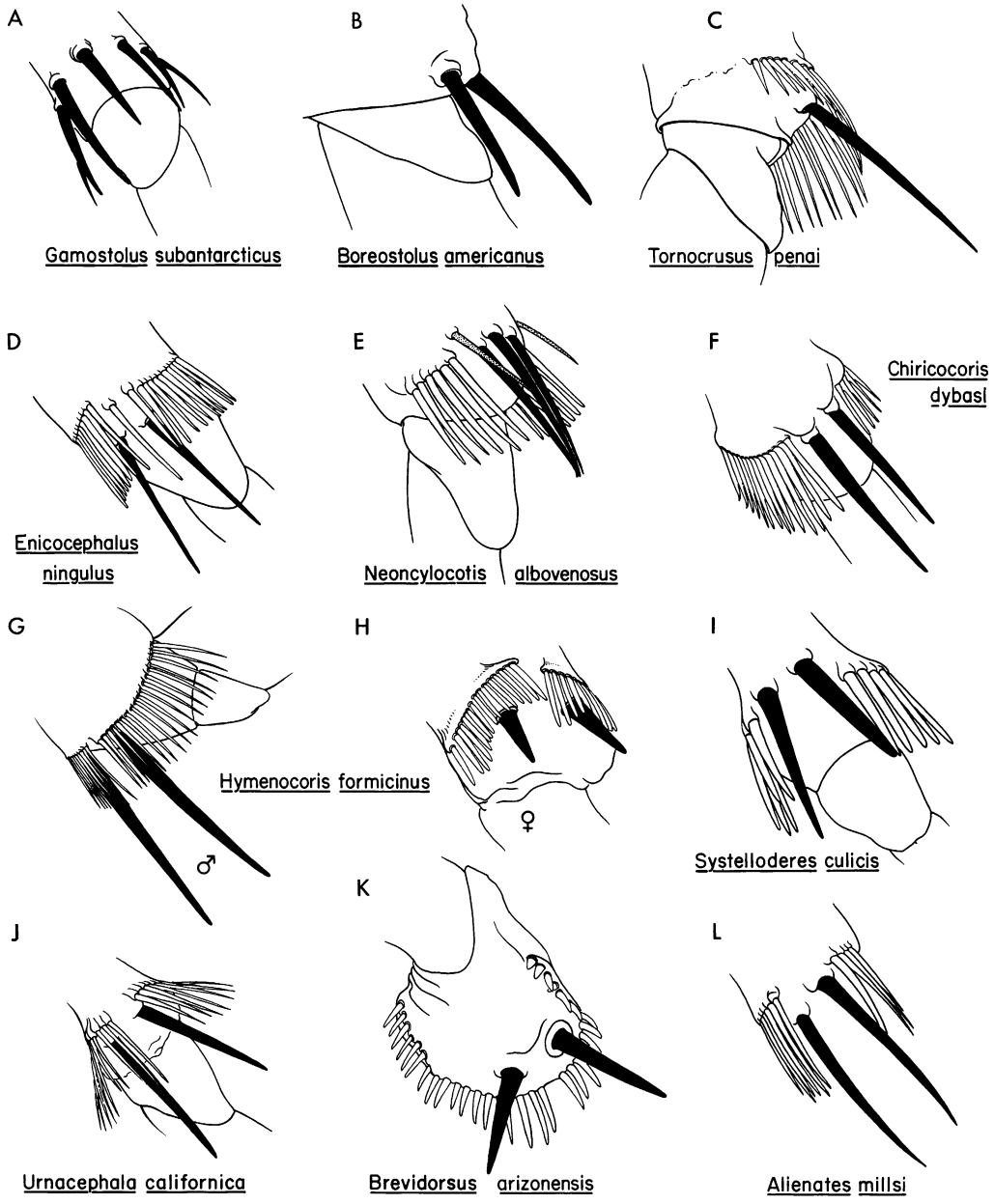


Fig. 14. Hind legs of Enicocephalidae, showing apical bristle combs and spines. **A.** *Gamostolus subantarcticus*, ♂. **B.** *Boreostolus americanus*, ♀. **C.** *Tornocrusus penai*, ♂. **D.** *Enicocephalus ningulus*, ♂. **E.** *Neoncylocotis albovenosus*, ♀. **F.** *Chiricocoris dybasi*, ♀. **G, H.** *Hymenocoris formicinus*, ♂ and ♀. **I.** *Systelloderes culicis*, ♂. **J.** *Urnacephala californica*, ♂. **K.** *Brevidorsus arizonensis*, ♂. **L.** *Alienates millsi*, ♂.

as in such Old World genera as *Euchelichir*, *Oncylocotis*, and *Usingeriella*. We consider the absence or presence of this field as useful in the definition of genera.

In several instances leg setae of males are modified. *Alienates* has setae that are barbed basally (fig. 152F), and those of *Neoncylocotis clavisetosus* males are clavate (fig. 127E).

GENITALIA, HOMOLOGIES, AND PHYLOGENY OF NEW WORLD TAXA

Three subfamilies of enicocephalids exist in the New World: the Aenictopecheinae, the Enicocephalinae, and the Alienatinae. The male genitalia of the former consist of a phallus and moveable parameres, whereas the genitalia of the latter two subfamilies are characterized by lack of a phallus, immobile parameres, and extreme reduction and fusion of associated terminal sclerites.

The genera *Gamostolus*, *Boreostolus*, and *Tornocrusus*, from the New World, together with *Australostolus* Štys from Australia, form the Aenictopecheinae, a monophyletic group characterized by the unique structure of the male and female genitalia, foreleg armature, wing venation, and overall shape. Štys is currently revising the suprageneric classification of the group, and is involved in an ongoing study of new Indo-Pacific material, including *Aenictopechys* and other Old World genera often included in the Aenictopecheinae, namely *Lomagostus*, *Nymphocoris*, and *Maoristolus*. The taxonomic rank of many of these groups may ultimately be raised to reflect the true diversity of the Aenictopecheinae.

Since the three New World genera so clearly fall within the strict definition of the subfamily, their extensive analysis has done little to elucidate the larger taxonomic problems associated with this evolutionary line. It is clear that the key to a comprehensive understanding of this subfamily lies in taxa outside the New World. The three genera will therefore not be discussed at great length here, but a brief summary of their salient features will be presented and illustrated.

The ground plan of the genitalia of the Aenictopecheinae has been meticulously elucidated for *Australostolus monteithi* by Štys (1980). The three New World genera differ from this in details only. The male terminalia consist of three parts (figs. 8A, C, H; 48A, B, E, F): (1) the pygophore, a cylindrical assemblage of sclerites, open behind, formed from the sclerites of segment 9 and varying dorsally from heavily sclerotized to completely membranous; (2) the proctiger (segments 10 and 11), projecting caudad from the dorsal portion of the pygophoral ring; and (3) the genitalia themselves, consisting of a T-shaped phallus and 1 + 1 parameres, also projecting caudad but from the ventrolateral edges of the pygophore. Each arm of the T-shaped phallus is firmly attached to the base of its corresponding paramere and this assemblage is fixed to the lateral apodemes of the pygophore by a membranous point of attachment to the outer bases of the parameres.

Females are known from all three genera and are also nearly identical in their basic structure to that of *Australostolus monteithi*. The ventrites of segments 8 and 9 each bear a pair of valvifers and valvulae, arranged as in figure 8B, D–G. (See also SEMs of males and females of the three genera).

Although *Gamostolus*, *Boreostolus*, and *Tornocrusus* clearly form a monophyletic group in the New World, their interrelationships with one another are more problematic. Their characters are distributed in a mosaiclike pattern that is not resolvable without a better knowledge of the remainder of the world fauna, now under consideration by Štys. Until character polarities are better understood, it is meaningless to establish a hierarchy of New World genera alone. Instead we prefer here to update the table of characters presented by Stys (1980; our table 7), to the larger end of eventually seeing the subfamily elucidated on a worldwide basis.

The Enicocephalinae and Alienatinae belong to the evolutionary line that includes the Phallopiratinae-Phthirocorinae-Enicocephalinae-Alienatinae (Štys, 1985). The male genitalia of this line are characterized by the presence of highly transformed derivative of auchenorrhynchan-type genital plates, immobile parameres, and lack of a phallus. The tribe Monteithostolini, from New Caledonia, shows the greatest structural richness in its genitalia. Compared to *Monteithostolus genitalis*, the New World taxa are highly apomorphic.

The subfamilies Enicocephalinae and Alienatinae show extreme reduction and fusion of the genitalia and associated structures, so much so that establishing homologies has long

TABLE 7

Update of Štys's (1980) Table Comparing Characters of Aenictopecheine Genera (New Zealand material not included)

Character	*Gamostolus*	*Boreostolus*	*Tornocrusus*	*Australostolus*	*Lomagostus*	*Aenictopechys*
Hook on paramere	none	well-developed	small protuberance	small protuberance	none	none
Postocular constriction	+	+	+	+	+	−
Interocellar distance as compared with distance from ocellus to lateral margin of head	larger	larger	equal	larger	larger	larger
Proepimera	large	large	minute	minute	minute	minute
Apomorphies of forewing, wing morphs	none, macropterous	none, macropterous and brachypterous	none, macropterous and brachypterous	none, macropterous	Cu tends to fuse with Pcu + 1An[a]	M + Cu and Cu tend to coalesce with Pcu and 1An; Pcu and 1An not separated proximally
Protibial projection	cleft	cleft	cleft	cleft	cleft	entire
Spine α of foretibia	−[b]	−	+[c]	+	−(?)	−
Number of spines on foretarsus	4	2	4[d]	4	4	2
Combs on apices of mid and hind tibiae	−	−	+	−	−	+
Secondary sclerites between ventrites 1–2 and 2–3	+	−	?	−	?	?
Dorsal bridge of pygophore	very broad	narrow	incomplete (membranous)	narrow	rather broad	incomplete
Valvulae and valvifers	+	+	+	+	+	−
Apex of first valvula	bifid	simple	bifid	bifid	bifid	−
Spermatheca	bulbose	?	?	helicoid	?	bulbous
Distribution	southernmost Neotropics	east Palearctic and west Nearctic	Neotropics	Australia	Madagascar	Indonesia

[a] See Štys (1980).

[b] SEMs show thickened setae of the lateral tibial row, but these are clearly not homologous with spine α.

[c] In error in Štys (1980). Spine α shows up well in SEMs of *Tornocrusus*.

[d] In error in Štys (1980). The additional two tarsal spines are indeed present, but small.

been problematic. Their genitalia are roughly characterized by (fig. 9): the pygophore, a sclerotized ring composed mainly of the fused sclerites of segment IX and having a large posterior foramen; the proctiger, projecting posterodorsad from within the pygophore and composed dorsally of terga 10 and 11; the parameres and supradistal plate (of Štys, 1981b; equals lateral and median lobes of the pseudosternite of Jeannel, 1942); and the immobile guide, attached to the posteroventral edge of the pygophore and projecting upward. Close examination of the particularly unusual species, *Enicocephalus wygodzinskyi*, and the SEMs of *Systelloderes* and many other genera, has allowed us to relate structures to those of the basic monteithostoline ground plan, and thus elucidate the homologies to some degree.

Enicocephalus wygodzinskyi has a very large genital capsule with slightly less reduction and fusion than its congeners.MDSU/, making it possible to see several structures lacking in other enicocephalines. In some cases the structures can be related to those of the more pleisiomorphic *Monteithostolus genitalis* and *Phallopirates* spp. The ground plan of the monteithostoline line consists of two main parts (Štys, 1981b; fig. 9A): (1) the dorsal components—the parameres, the supradistal plate, terga 9, 10, and 11, and (probably) the medial plate; (2)the ventral components—the proximal plate with associated extensions, the infradistal plate, and sternum IX.

The "lateral lobes of the pseudosternite" of the Enicocephalinae have long been thought to be remnants of parameres, although authors have been reluctant to homologize them because they lack the setae found in most other Heteroptera. The parameres of *E. wygodzinskyi* have two areas with either trichoid sensillae or setae. The first is on the medial surface of the paramere, where there are minute sensillae (fig. 100B). These are also visible in the SEMs of *Hymenocoris formicinus* (fig. 105E). They are probably homologous with the trichoid sensillae found on the parameres of *M. genitalis* and *Phthirocorisella petrophila* (Štys, 1986), since they are closest to the attachment with the membranous vestige of the supradistal plate. The second area of setation is on the lateral parts of the parameres, where there are 8–10 true setae (fig. 100B). These correspond in their placement to the single seta on the midplate of the paramere of *Phallopirates palawanicus* (Štys, 1985). They also probably correspond to the lateral parts of the parameres of *M. genitalis*, but it is difficult to relate them because of the autapomorphic anterodorsal rotation of the latter and the fusion and reduction in *E. wygodzinskyi*. The retention of well-developed setae in this unique species, however, establishes more certainly the homology with true parameres. The corresponding parameral vestiges are present and devoid of setae in all enicocephaline (and alienatine) genera we have seen, and indeed in all *Enicocephalus* with the exception of *E. wygodzinskyi*. Other structures present in this species are an extremely minute and membranous remnant of the supradistal plate (median lobe of the pseudosternite, figs. 100B, G) and a lightly sclerotized floor beneath the proctiger. These structures are much more easily seen in the SEMs of *Systelloderes* and will be dealt with below. *E. wygodzinskyi* seems to lack tergum 10, unlike *E. ningulus*, which structure we have seen with the SEM (fig. 74E).

Two (1 + 1) vertically oriented, well-sclerotized somewhat internally located plates show up in slides of *H. formicinus* (fig. 9B, "basal part of paramere"), *Enicocephalus* spp., *Neoncylocotis* spp., and *Brevidorsus arizonensis*. They are devoid of setae. The plates are seemingly of dorsal origin and are always associated with the anterior and basal parts of the parameres. In their position and attachment they are most similar to the basal parts of the parameres of *Phallopirates* spp. (Štys, 1985), and may indeed be homologous with them.

Enicocephalus wygodzinskyi is less informative with respect to the ventral components. There is no reason to doubt Štys's contention that the guide is formed by the fusion of these components with the pygophore, but overwhelming evidence in support of this theory is not to be found here. Its guide is extremely expanded laterally, forming a huge leaflike plate covering the rear of the genitalia (figs. 100C, E–G). Although there are poorly and well-sclerotized areas, there are no obvious lines of fusion between plates. The ven-

tral surface may be formed basally by the proximal plates with their median membrane, and distally by the infradistal plate (fig. 100F). It tends to break where the heavy sclerotization of the proximal plates might end and the infradistal plate would fuse. The dorsal surface of the guide forms a tunnel leading to the functional gonopore at its tip. The homologies of the tunnel's structural components are unclear. Examination of the glycerine-cleared genital capsule of one of our specimens indicates that it might be formed laterally by the dorsal struts of the proximal plate (fig. 100F). Just how the roof is formed, or whether it joins to the dorsal components (through vestiges of a medial plate?) cannot be seen in our slide.

The genus *Systelloderes* in the New World differs markedly from all other Enicocephalinae and Alienatinae by the pleisiomorphic retention of a very well-developed supradistal plate (figs. 9E, 60A, B, D, E). This lies anterodorsal and parallel to the guide, the two structures from behind looking like a set of lips. It is attached to the medioventral parts of the parameres, as in *Monteithostolus* and the enigmatic *Enicocephalus wygodzinskyi* (where it exists as a minute, nearly membranous structure stretched between the parameres). All other enicocephaline and alienatine genera of which we have seen males (*Enicocephalus*, *Neoncylocotis*, *Hymenocoris*, *Brevidorsus*, *Lysenicocephalus*, *Urnacephala*, and *Alienates*) can be separated from *Systelloderes* by the apomorphic loss or extreme reduction of the supradistal plate. *Systelloderes* also has an autapomorphy that separates it from these other genera, i.e., the complete fusion of tergum 10 with the pygophore (figs. 60D, E).

The New World Enicocephalinae that show apomorphic loss of the supradistal plate should form a separate taxon, and we here resurrect the tribe Enicocephalini for this purpose. The Systelloderini, also resurrected here, is formally defined by the fusion of the tenth tergum to the pygophore (although, practically speaking, the pleisiomorphic supradistal plate is a much more obvious character). [The tribe Systelloderini was created by Jeannel 1942 (1941) and later regarded as a synonym of Enicocephalini by Štys 1969a (1968)].

The scanning micrographs of *Systelloderes* show a support ring surrounding the proctiger suspended from the posterodorsal edge of the pygophore (figs. 60D, E). This also appears in SEMs of *Urnacephala californica* (figs. 142E, F) and *Alienates millsi* (fig. 154E), and slides of *E. wygodzinskyi* (fig. 100F) and *Hymenocoris formicinus* (fig. 9B). The degree of development and amount of sclerotization of the support system varies, and the homologies of its parts can only be determined by piecing together information from an incomplete series of SEMs and slides. Its roof lies below the posterior edge of tergum 10 (except in *Systelloderes*, explained below), and its walls are attached to the lateral edges of tergum 10 and join ventromedially to form a (usually) membranous floor beneath the proctiger. Its walls seem to be formed by the tenth laterotergites (or posterolateral apodemes of tergum 10; of Štys, 1985), which are sclerotized and easy to see in *H. formicinus*, and somewhat less sclerotized and harder to see in other genera. The laterotergites are joined medially above and below the proctiger by a membrane, lending credence to their theoretical lateral derivation. The apparent difference in attachment in *Systelloderes* comes from the fusion of its tenth tergum to the back of the pygophore. Close examination of the SEMs reveals a furrow where the tergum has fused, and indeed the walls of the support are attached to its edges.

Štys (1981b) has discovered a floor beneath the proctiger in *Monteithostolus genitalis*, apparently formed by the ninth mediotergite and considered to be an autapomorphy of the Monteithostolinae. It would make sense for the floors to be formed by homologous structures, and the above discrepancy is disturbing. If the pygophore of the Enicocephalinae is formed by fusion of the ninth tergite, laterotergites, and sternum, then presumably more posterior sclerites must form the floor beneath the proctiger. The condition in the New World Enicocephalinae and Alienatinae seems to be closer to that illustrated by Štys (1985) for *Phallopirates borneensis*. Here the posterolateral apodemes of segment 10 have a similar relationship to the tenth tergum and proctiger. Presumably the lateral apodemes would then have fused ventromedially below the proctiger. Further studies are needed here,

since definitive establishment of homologies of the floor would mean that this is not an apomorphy for the Monteithostolinae (see also Štys, 1988).

A natural group within the Enicocephalini is formed by three genera of extremely small and delicate insects known from males only. *Brevidorsus* and *Urnacephala* have retained tergum 11 as a posteromedial tab on tergum 10 (figs. 63C, 142F). *Lysenicocephalus* shows a convexity on tergum 10 (fig. 117H), although our limited amount of material, lack of SEM examination, and its extremely small size make us less certain that this is tergum 11. These three genera also share short third pronotal lobes and lack basal cells in their wings. It is our hypothesis that females of these genera have reduced or absent wings and/or eyes, as in *Hymenocoris* and *Alienates*. We do not necessarily consider loss or reduction of wings or eyes as a synapomorphy, however, since it occurs in a mosaiclike distribution in otherwise unrelated genera. In the New World, reduction of wings and eyes is found in *Boreostolus*, *Tornocrusus*, and *Systelloderes*, and complete loss in females of *Hymenocoris* and the Alienatinae. These similarities in losses may be a result of convergence in some cases, and be true shared derived characters in other cases.

The question arises as to where the Alienatinae fit into the phylogenetic scheme of New World Enicocephalidae. If loss and reduction of wings and eyes are not necessarily reliable synapomorphies, there are only a few rather unconvincing characters left to relate them to any other taxon. The most probable affinity is to the above group of three genera. In the males, they all share the short third pronotal lobe and the extremely small size. All but *Lysenicocephalus* lack tarsal spines in the males. And, finally, *Alienates insularis* has a convexity behind tergum 10, possibly corresponding to tergum 11. On the other hand, *Enicocephalus* shares the derived extended arm of the forewing coupling mechanism with *Alienates*, and the two genera have similar sixth tibial spines. However, this seems to be outweighed by the similarities to the three small genera and until more evidence turns up, we consider the Alienatinae the sister group of *Brevidorsus-Urnacephala-Lysenicocephalus*.

It is quite possible that the Alienatinae is merely an ingroup of the Enicocephalini, but we are not prepared to eliminate the subfamily yet for several reasons. *Alienates* has several striking morphological differences, namely, the one-segmented tarsi of its mid and hind legs and the unique arrangement of the foretibial and foretarsal spines in the females. In addition, we have very few males and no females of the probable sister group for comparison.

The female genitalia of the Enicocephalinae and Alienatinae are highly reduced and not very informative. In general, the sclerites of segment 9 (at least) have fused to form a ring around the anus, and valvifers and valvulae are absent. In the SEMS of *Systelloderes*, however, two median membranous or semisclerotized folds are visible on the ventral surfaces of segments 8 and 9 (fig. 60F). These are undoubtedly vestiges of the reproductive structures, possibly first and second valvulae. They also appear very minutely in *Hymenocoris formicinus*.

There is a distinct median tab on the posteroventral edge of segment 8 in *Systellodereres* females (figs. 60C, F), the homology of which is unclear. A smaller version of the tab appears in *H. formicinus*, and a minute, hardly visible, one in *Enicocephalus* and *Neoncylocotis*. Similar structures are illustrated in the literature in Woodward's *Phthirocoris magnus* (1956), and in Štys's *Aenictopechys necopinatus* (1977). The function of this structure may become apparent when someone is able to watch *Systelloderes* adults mate. We suspect that it corresponds to the development of the supradistal plate in the male, perhaps serving as a "docking area" and that it enables the supradistal plate, the rudimentary valvifers, and the guide to interdigitate correctly. It is likely that the female genital opening is in the gap in the intersegmental membrane between segments 8 and 9, as proposed for *Monteithostolus* by Štys (1982b). A similar pocket can be seen in *Systelloderes* females (fig. 60F).

The following phylogenetic tree illustrating the higher relationships of the New World Enicocephalidae is based primarily on genitalic characters and serves to summarize the information presented above (fig. 15). It also utilizes somatic synapomorphies where they

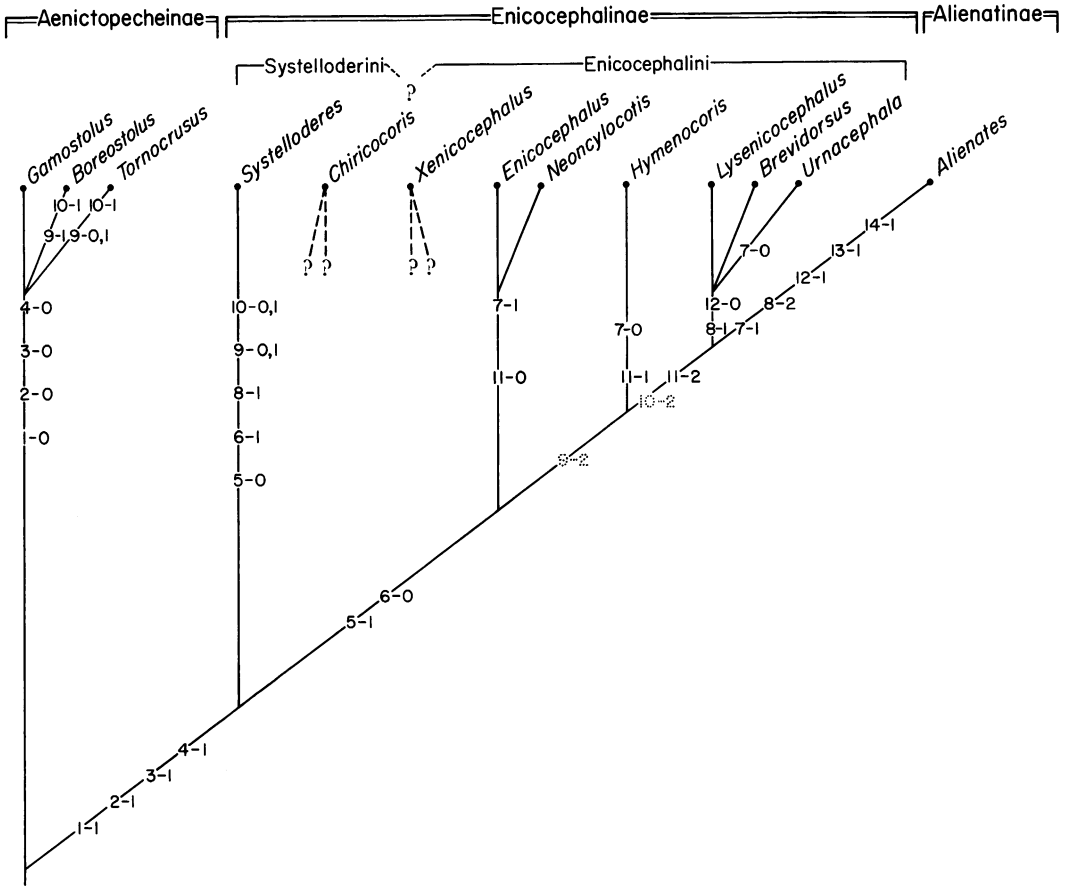


Fig. 15. Provisional scheme of relationships of New World Enicocephalidae. Due to large gaps in material and information, a more formal analysis has not been undertaken. Autapomorphies defining genera are not included, with the exception of *Systelloderes* and *Alienates*, each of which is a single genus in a higher taxon. The lowest character state number represents the most pleisiomorphic state, with some doubts about characters 7 and 11. The dotted numbers (9-2 and 10-2) represent uncertain information (1) because the females of *Lysenicocephalus*, *Brevidorsus*, and *Urnacephala* are not formally known, and (2) because loss or reduction of wings and eyes may or may not be synapomorphies. *Chiricocoris* and *Xenicocephalus* are known from females only and cannot be placed at this time.

1. Parameres: 0—mobile, 1—immobile; **2**. Phallus: 0—present, 1—absent; **3**. Costal fracture in forewing: 0—present,1—absent; **4**. Foretibial spines: 0—in 2 groups of 3, separated by a cleft, 1—in 1 group of 5–7 (or more); **5**. Supradistal plate: 0—present, 1—absent; **6**. Tenth tergum: 0—present, freely moving, 1—indistinct, fused to pygophore; **7**. Mesosternum: 0—mesosternal complex long, forewing coupling groove long and horizontally oriented, 1—mesosternal complex short, forewing coupling groove short, sloping down posteriorly; **8**. Basal and discal cells of forewing: 0—2 cells, 1—1 cell, open or closed, 2—no cells; **9**. Forewings of females: 0—present, 1—micropterous or brachypterous, 2—absent; **10**. Eyes of females: 0—present, 1—small, 2—absent; **11**. Pronotal shape of males: 0—3rd lobe very wide and long, rounded laterally, 1—3rd lobe wide, medium length, pointed laterally, 2—3rd lobe short, ribbonlike, pointed laterally; **12**. Tergum XI: 0—present as tab on tergum 10, 1—present as convexity on tergum 10, 2—absent; **13**. Mid and hind tarsi: 0—2-segmented, 1—1-segmented; **14**. Foretarsal spines: 0—4 (occasionally 2), bases arranged in square configuration, 1—1 large curved spine surrounded by several thinner ones.

resolve groups above the level achieved by the genitalia. Wing and eye size characters are used reluctantly, since we cannot determine whether these are homologous or the result of convergence. The two enicocephaline genera known from females only (*Chiricocoris* and *Xenicocephalus*) cannot be reliably placed at this time. The illustration also excludes the autapomorphies defining genera, except for *Alienates*. This is in no way a definitive statement of the relationships of New World enicocephalids. Since there are still such large gaps in our material and information, it would be premature to attempt a more formal analysis at this time.

TYPE FIXATIONS

The method of type fixation and detailed notes on the history of six of the eight previously described genera can be found in Stys (1978). For convenience we have restated the method of type fixation under each genus and included fixations of the two more recently described genera.

KEY TO GENERA OF THE NEW WORLD

1. Foretibial spines stout, arranged linearly in two groups of three, separated by deep central notch (figs. 10A, 11); forewings of macropterous specimens with costal fracture (fig. 6A; may be lacking in brachypterous specimens); external male genitalia large (figs. 8A, C), parameres movable and well developed; phallosoma tubular and permanently extruded. Female gonapophyses well developed, rodlike (fig. 8B) ..... Aenictopecheinae, 2

   Foretibial spines in one group, varying from 2 slender spines to 7 or more stout ones (figs. 10B, C); forewings without costal fracture or absent altogether (figs. 6B, C); external male genitalia reduced to a single immobile flap, or "guide," attached ventromedially and truncate or rounded apically (fig. 9). Female gonapophyses extremely reduced or absent (fig. 8I) ..... Enicocephalinae and Alienatinae, 4

2. Foretarsus with 2 spines (fig. 18B); foretibial spine "b" arising below (more proximal) level of other spines (figs. 10A, 18E); male parameres with well-developed subapical hook (figs. 23I, J) ..... *Boreostolus* Wygodzinsky and Stys

   Foretarsus with 4 spines (fig. 29B); foretibial spine "b" arising even with, or above (more distad), level of other spines (fig. 29F); male parameres lacking hook (fig. 35D) 3

3. Mid and hind tibiae each with 1 continuous bristle comb and 1 enlarged spine (fig. 14C); foretibial spine "b" much longer (2X) than "c" (figs. 39C, 49L); spine "a" present and somewhat larger than normal leg seta (figs. 11D; 39C lying down); sclerotized dorsal bridge of pygophore of male absent (fig. 48A); parameres subrhomboid to subtriangular (figs. 48C, D); phallosoma apically bifid (figs. 46H, I); interocellar area raised and with a matte surface different in texture from surrounding head surface (fig. 39A) ..... *Tornocrusus* Kritsky

   Mid and hind tibiae with no bristle combs and 2–5 spines (figs. 14A, B); foretibial spine "b" subequal in length to spine "c" (fig. 29D); spine "a" absent (fig. 29A); sclerotized dorsal bridge of male pygophore broad and entire (fig. 36G); parameres ovoid (fig. 35D); phallosoma apically truncate (fig. 35E); interocellar area shining and not raised ..... *Gamostolus* Bergroth

4. Wings present, varying from micropterous to macropterous 8

   Wings absent 5

5. Mid and hind tarsi 1-segmented; eyeless, or at most with 4–5 ommatidia and a minute pigmented spot (figs. 172A, 168A); pronotum 2-lobed, the front lobe collarlike and the hind lobe greatly expanded (fig. 155C); foretarsus with a large curved spine below the tarsal claws, with 3 or 4 other spines variously developed (fig. 10C); abdomen well sclerotized ..... *Alienates* Barber, females

   Mid and hind tarsi 2-segmented (first segment sometimes small); eyes present; pronotum distinctly 3-lobed (figs. 72A, C); foretarsus with 4 spines (figs. 13E, F, L, M); abdomen membranous or with regularly arranged sclerotized patches (figs. 75E, K) 6

6. Abdomen with regularly arranged sclerotized patches (fig. 75E, K); hind lobe of pronotum as wide or wider than mid lobe (figs. 119A,

B); foreacetabula open behind (fig. 59B); spine VI of foretibia pointed; forefemur without a basal projection 7

Abdomen membranous (fig. 109); hind lobe of pronotum narrower than mid lobe (fig. 109); foreacetabula narrowly closed in most specimens (fig. 102F); spine VI of foretibia molar shaped (fig. 112E); forefemur with basal projection (fig. 109) ..... *Hymenocoris* Uhler, females

7. Outer foretarsal claw very short, from ¼ to ⅔ length of inner claw (figs. 72G, 75I); spine III of foretarsus sickle or half-moon shaped (fig. 10B); foretibial spine VI with a subbasal hump (figs. 12A, 76I) ..... *Enicocephalus* Westwood, caducous females

Outer and inner foretarsal claws subequal in length (fig. 120A); spine III of foretarsus conical (fig. 13E); foretibial spine VI without sub basal hump (fig. 12B) ..... *Neoncylocotis* n. gen., caducous females

8. Micropterous, or nearly so; head very elongate; eyes in some cases very small, composed of only a few ommatidia; ocelli in some cases obsolescent; pronotum flattened; outer claw of forelegs well developed but smaller than inner one; tarsal spine III half-moon shaped (fig. 10B); tibial spines V and VI curved, different from remaining spines (figs. 12C, D) ..... *Systelloderes* Blanchard (part)

Macropterous or brachypterous 9

9. Length less than 2.0 mm; mid and hind tarsi 1-segmented; forewings with venation reduced to 2 or 3 veins and 0 or 1 crossveins (fig. 6C); foretarsus without spines but with modified setae with basal barbs (fig. 13-O); forewing coupling hook extending well beyond costal edge (fig. 7K) ..... *Alienates* Barber, males

Length greater than 2.5 mm; mid and hind tarsi 2-segmented (first segment may be small); forewings with full complement of veins, or at most lacking m-cu and cu-1a crossveins; foretarsus with or without spines but with setae unbarbed basally; forewing coupling hook not so extended 10

10. Forewings lacking both basal and (closed) discal cells (fig. 64K) (= no crossvein between M and Cu) 11

Forewings having either a basal cell or a (closed) discal cell or both (figs. 143H, 116D) (= one or two crossveins between M and Cu; figs. 143H, 116D) 13

11. Foretarsal spines present; tarsal spine III half-moon shaped; tarsus stout, about as long as wide at base 12

Foretarsal spines absent; foretarsus slender, about twice as long as wide at base (known from males only) ... *Brevidorsus* Kritsky

12. Anterior acetabula closed (fig. 69E); foretarsus with a distinctive pointed process at base of tarsal claws (fig. 69C) (known from females only) ..... *Chiricocoris*, n. gen.

Anterior acetabula open (fig. 59B); foretarsus lacking process ..... *Systelloderes* Blanchard (part)

13. Basal cell lacking and discal cell closed (fig. 143H) (= one distal crossvein, cu-1a, between M and Cu) 14

Basal cell present and discal cell closed (fig. 148A) (= two crossveins, m-cu and cu-1a, between M and Cu) 15

14. Foretarsus lacking spines, and 5–6 times longer than wide (figs. 140D, E); guide apically truncate (fig. 143I) (known from males only) ..... *Urnacephala* n. gen.

Foretarsus with 4 spines (fig. 117F), and 2–3 times longer than wide; guide spoon-shaped (fig. 116I) (known from males only) ..... *Lysenicocephalus* n. gen.

15. Foretibia with 4 spines subbasal in position, with a pointed projection extending beyond them (figs. 149C, D); very large, greater than 9 mm in length; entire head, body, wings, and legs densely covered with cuticular tubercles; foretrochanter ventrally with a heavily sclerotized ridgelike projection; a single stout foretarsal claw on each tarsus ..... *Xenicocephalus*, n. gen.

Foretibiae with 5 or more spines, terminal in position (figs. 75H, I); less than 8.6 mm in length 16

16. Foretarsal claws nearly equal in length; tarsal spine III conical (fig. 124C); tibial spine VI conical without subbasal hump (fig. 124C); at least a few setae present in lumens of forewing cells 17

Outer foretarsal claw reduced, ¼ to ⅔ length of inner (fig. 75I); tarsal spine III half-moon shaped (fig. 75H); tibial spine VI with distinct subbasal hump (fig. 76I); no setae in lumens of forewing cells ..... *Enicocephalus* Westwood

17. Scalelike setae on dorsal surface of abdomen (figs. 121A, C); apex of mid and hind tibiae with 2 or 3 spines outside, or as part of, semicircle formed by bristle combs (fig. 14E) ..... *Neoncylocotis*, n. gen.

Setae on dorsal surface of abdomen simple; apex of mid and hind tibiae with 2 spines within the semicircle formed by bristle combs (figs. 14G, H); slender, delicate insects; stigma of forewing frequently red ..... *Hymenocoris* Uhler, males

SYSTEMATICS

AENICTOPECHEINAE

GAMOSTOLINI

Boreostolus Wygodzinsky and Štys

Boreostolus Wygodzinsky and Štys, 1970: 1–7. — Štys, 1970b: 225, 239. — Kritsky, 1977b: 166, 168. — Štys, 1977: 200, 208–209. — Štys, 1978 (1977): 242. — Štys, 1980: 303, 305–306, 320. — Štys, 1982a (1980): 485.

TYPE SPECIES: *Boreostolus americanus* Wygodzinsky and Štys. Fixation by original designation.

DISTRIBUTION: Holarctic. There are two described species, one from the northwestern United States and the other from the Ussuri region of the U.S.S.R. (fig. 16). Kerzhner (1988a) indicated that specimens from the Magadan region of the USSR show characters similar to *B. americanus* and that clinal variation may be involved.

DIAGNOSIS: The genus *Boreostolus* can be distinguished from other Aenictopecheine genera by the following characters:

Outermost spine of outer group of spines on apical projection of foretibia inserted basad of level of two adjacent spines (fig. 18E); foretarsus with only two spines (fig. 18B); dorsal bridge of pygophore very short, in shape of narrow transversal band (fig. 23H); parameres of male subrectangular in outine, with a subapical hook-shaped process (figs. 21C, 23I, J); phallus simple at base, apically capitate, capitulum with projections and minute spinelike cuticular processes (figs. 23K–N); first valvulae of female completely fused to sternum VIII, simply rounded apically, forming a trough for reception of second valvulae (figs. 21E, F, 25-O).

DESCRIPTION: (The following is a summary of the extensive original description by Wygodzinsky and Štys, 1970, combined with new information derived from the SEM photographs.)

Medium to large size species, 3.3–6.3 mm. Head, abdomen, and appendages polished, thorax dull. All setae simple, slender, lacking setiferous tubercles. Macropterous, brachypterous, or micropterous.

Macropterous form: Head with deep postocular impression (fig. 17A). Eyes of male medium-size, not closely approximating beneath; eyes of female smaller. Antennal segments narrowly cylindrical, II and III subequal in length, IV slightly shorter (fig. 22A). Pronotum unarmed, strongly flattened above, with faint to obsolescent transverse impressions separating the lobes (fig. 17A). Lateral outline of pronotum notched at level of pleural sulcus. Proepisternum and proepimeron each triangular and quite reduced (fig. 23B). Anterior coxal cavities open behind in both sexes. Scutellum subsemicircular. Meso- and metathorax as in figure 23B. Mesosternum well developed and long. Dorsolateral groove present above mesosternum receiving costal edge of forewing at rest (fig. 19B). Cuticular evaporatory structures present on metasternum of female (fig. 20E).

Forelegs stout. Coxae and ventral surfaces of femur with minute scalelike structures. Projection of inner apical angle of tibia prominent (fig. 18A), in the form of two distinct tubercles each bearing three spines (figs. 18D, E; see Diagnosis). Tarsus with only two spines (fig. 18B), the distal one half-moon shaped, the proximal one erect, conical. Foretarsus with two claws, inner about twice as long as outer (fig. 18A). Mid and hind tibiae lacking bristle combs but with two strong spines (fig. 18F); tarsus two-segmented.

Forewings with fracture at center of costal margin. Basal cell present, discal cell closed (fig. 22A). Setae on basal half of forewing of medium length, more numerous on costal margin. Setae on veins of distal half of forewing slightly shorter than others, very sparse. Lumens of cells lacking setae (fig. 20A). Hind wing without setae. Wing coupling device present beneath hind edge of forewing at apex of claval suture, roughly C-shaped, beset with elongate, toothlike processes at end of each arm of "C" (fig. 20B). Hind wing edge with many foliaceous structures at level of wing coupling device (fig. 20C).

Abdomen with dorsum weakly but uniformly sclerotized. Connexival plates in males and females in one row on each side, most closely associated with tergites. Abdominal sterna separated from connexival plates by wide membranous zone. Spiracles situated

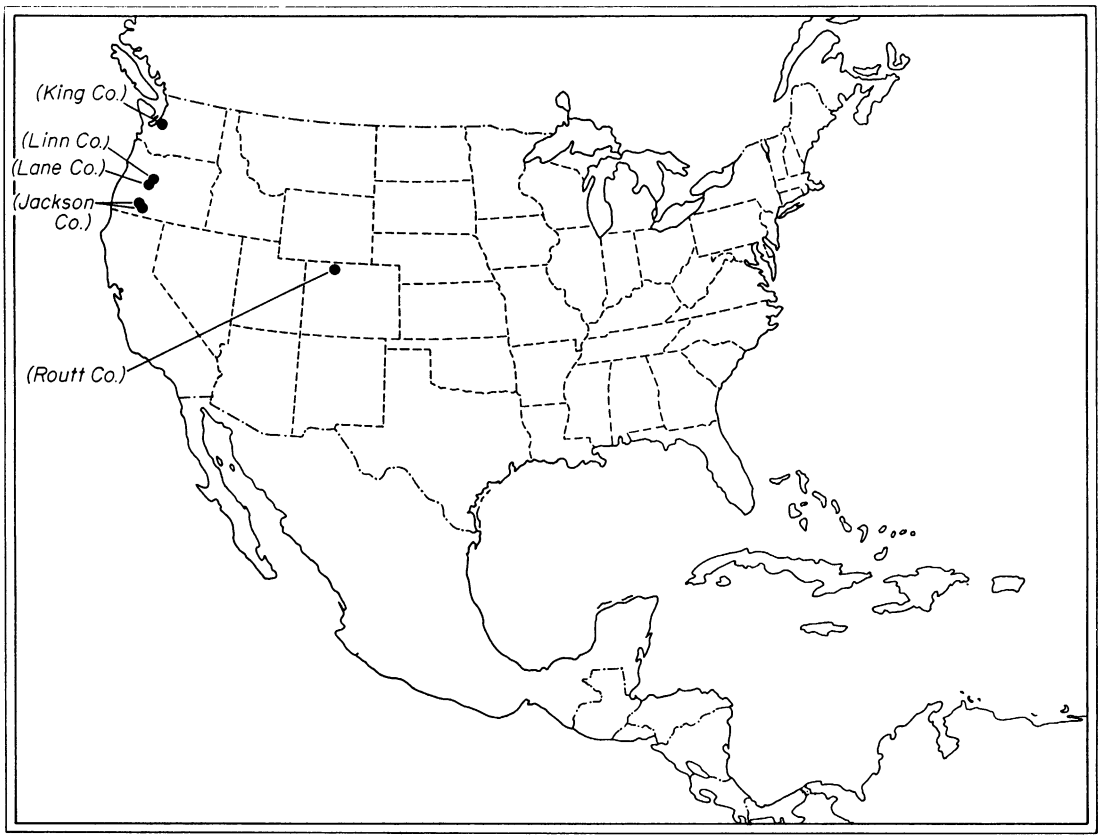


Fig. 16. Distribution of *Boreostolus* in the New World. *B. americanus* (●).

on anterior fifth of connexival plates of segments I–VIII. Abdominal terga covered by short and medium-size setae and by serially arranged macrochaetae, 3 + 3 on each segment.

Eighth abdominal segment of male with completely separated tergum and sternum. Pygophore large, almost completely free, only its extreme base invaginated into eighth segment. Anterior dorsal bridge of pygophore present, short, in shape of a narrow transverse band (fig. 23H). Tenth tergum present, forming a tonguelike flap above the distal portion of the phallus, and approximately as long as wide (figs. 21B, C). Parameres and phallus inserted close to posterior portion of pygophore, forming independent, permanently extruded unit.

Parameres horizontal in position, subrectangular, trough-shaped, laterally convex, medially deeply concave (figs. 21B, C; 23E, F, H, I, J). Dorsal free edge subapically with broad, rounded projection, the apical part of paramere formed by rounded tubercle closing trough. Ventral free edge below tubercle with curved, hooklike projection with serrated anterior margin (figs. 23I, J). Almost entire ventral and lateral walls and laterodistal part of dorsal wall of paramere with long slender setae. Medial concave surface glabrous, except for group of short setae distally.

Phallus simple, anchor-shaped, sclerotized, permanently erected, lacking evaginable portion (figs. 23K–N). Proximal part, homologous to basal plates, in shape of simple transverse sclerite. Medial portion of phallus tubular, curved, simple; distal portion widened into a "capitulum" with projections and minute cuticular processes. Ejaculatory duct wide, without observable reservoir; secondary gonopore situated at apex of capitulum.

Eighth and ninth terga of female not mod-

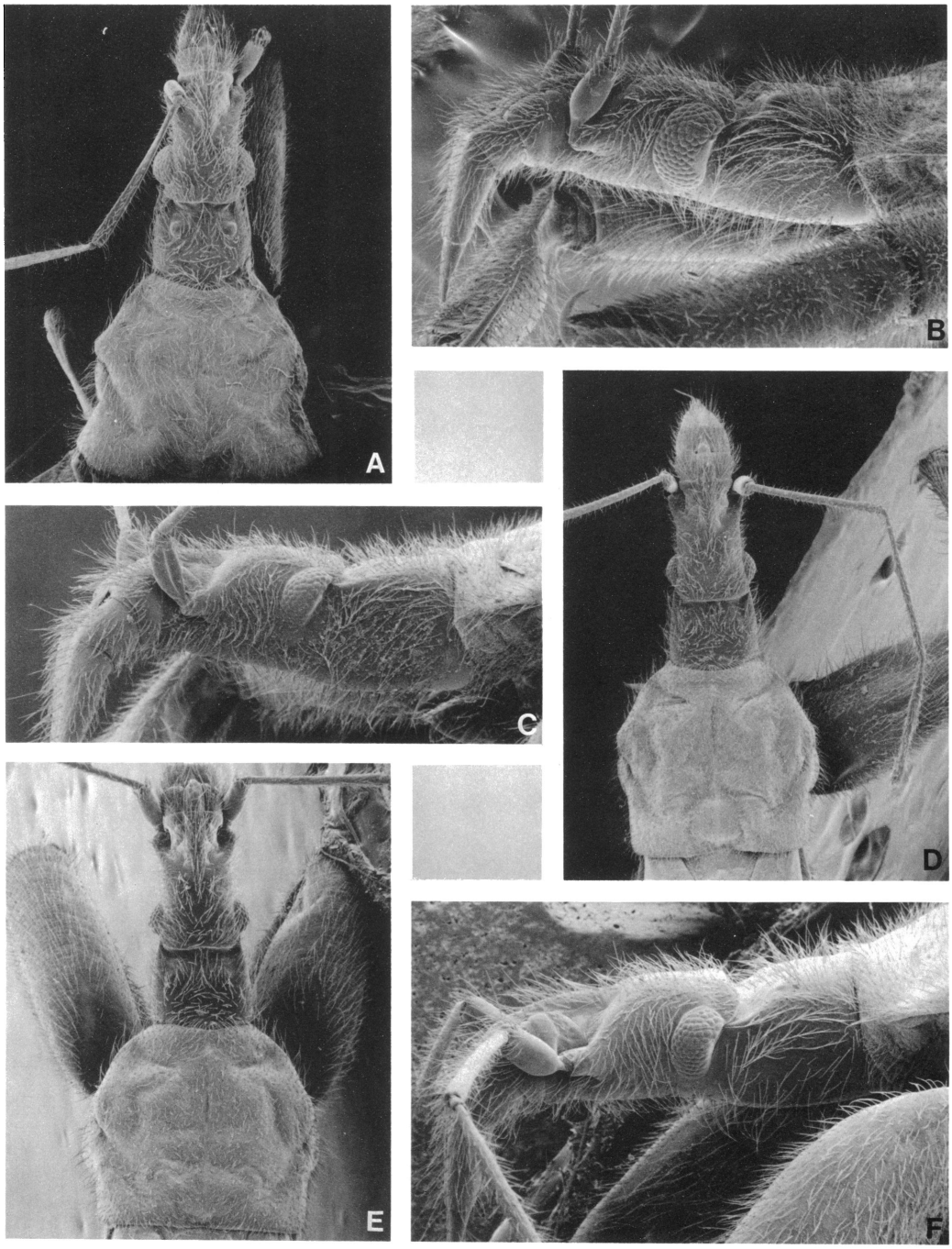


Fig. 17. *Boreostolus americanus*. **A**. Macropterous ♀, dorsal view of head and pronotum. **B**. Same, lateral view of head. **C**. Micropterous ♀, lateral view of head. **D**. Same, dorsal view of head and pronotum. **E**. Micropterous ♂, dorsal view of head and pronotum. **F**. Same, lateral view of head.

ified, the latter posteriorly excised, the ventral connexival plates of both continuous with dorsal tergum. Sternum VIII separated from laterotergal region by wide membrane; sternum not subdivided longitudinally, posteriorly with two pairs of projections completely

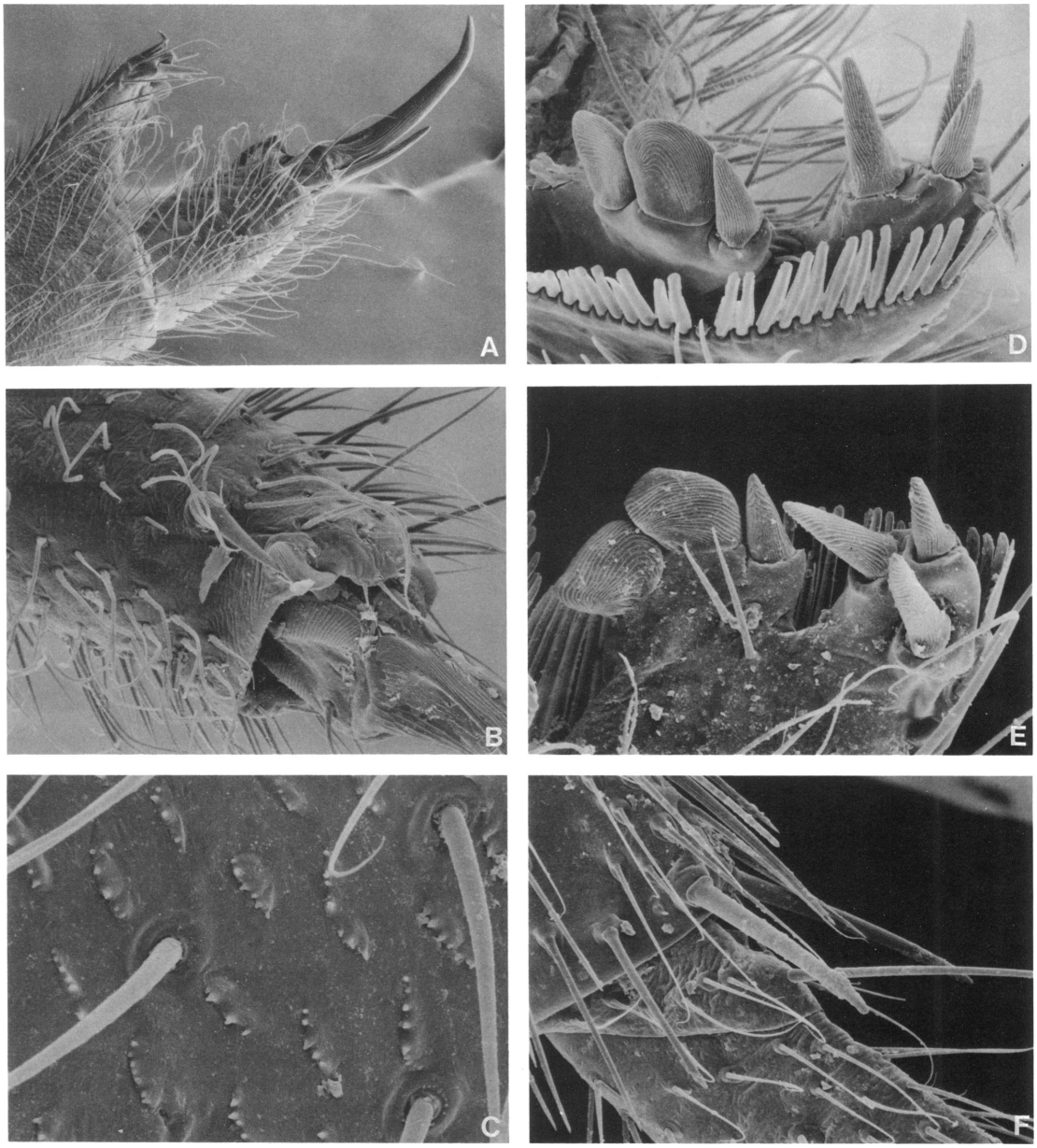


Fig. 18. *Boreostolus americanus*. **A**, **B**, **D**. Macropterous ♀. **A**. Apex of foreleg. **B**. Tarsus, showing two tarsal spines. **D**. Apex of foretibia, showing spines and bristle comb (outer view). **C**, **E**, **F**, Micropterous ♀. **C**. Detail of inner surface of forefemur. **E**. Apex of foretibia (inner view). **F**. Hind leg, showing large spines and no bristle comb.

fused to sternum at their bases. Outer pair representing first valvifers fused with sternum; inner pair representing first valvulae (fig. 25-O), longer than outer pair, scoop-shaped, forming a trough enclosing second valvulae. First valvulae beset ventrally with minute sensory setae; each valvula articulating mediolaterally with condyle of first valvifer. Second valvifers well individualized, strongly sclerotized, closely associated with medial margins of tergum IX. Second valvulae weakly sclerotized, narrowly rod-

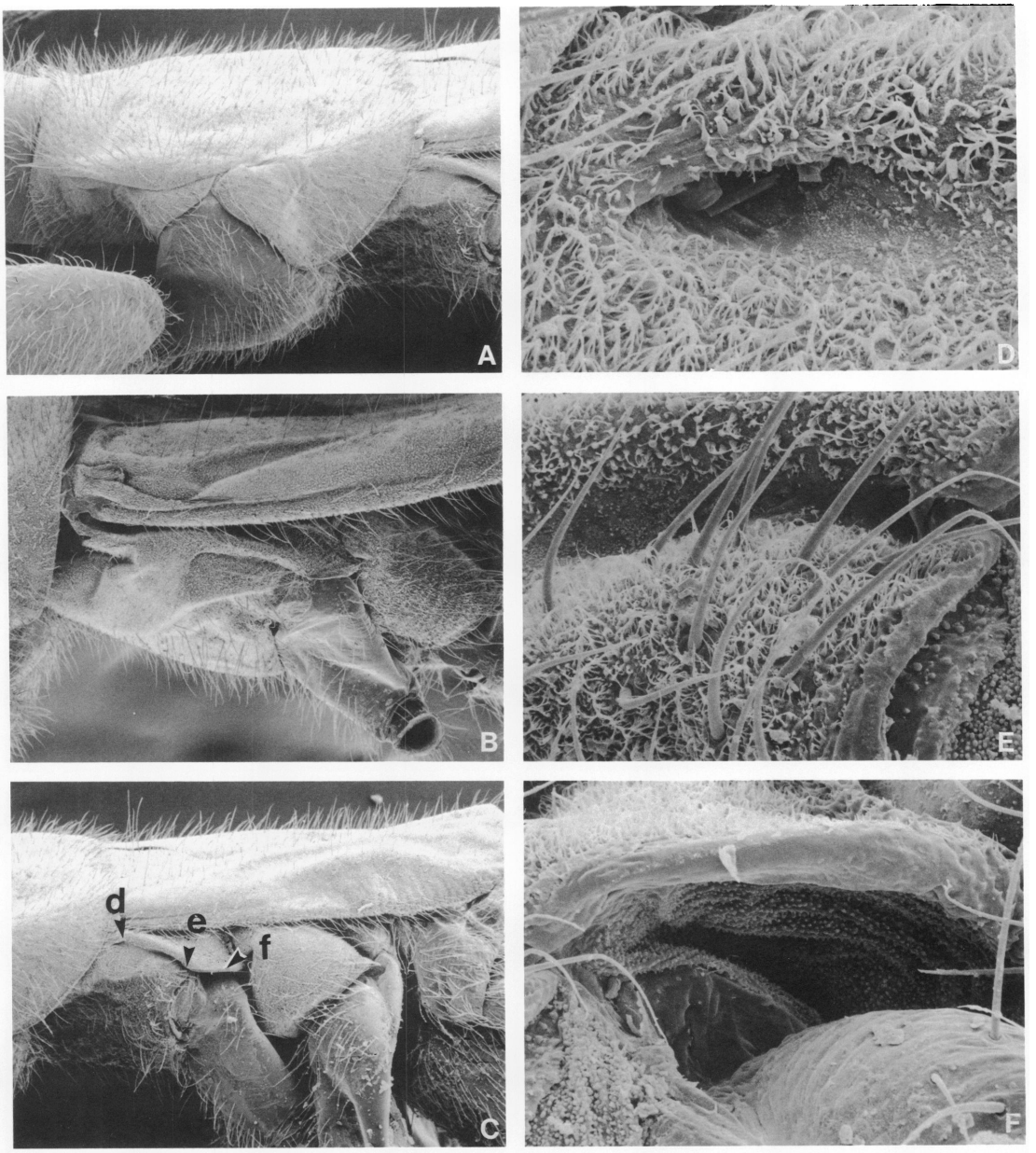


Fig. 19. *Boreostolus americanus*, lateral views. **A**, **C–F**. Micropterous, ♂. **B**. Macropterous, ♀. **A**. Prothorax. **B**. Meso-metathorax, showing wing-to-body coupling groove. **C**. Meso-metathorax. **D–F**. Details of figure 19C. **D**. Forepart of apodemal sulcus. **E**. Mesopleural suture above mesoleg. **F**. under surface of mesepimeron.

shaped, tapering toward apex (fig. 25M). Gonangulum inverse T-shaped, posterior transverse part fused with tergum IX and articulating with second valvifer, anterior rod-like part free.

Brachypterous form: Very similar to macropterous form. Head proportions similar, ocelli present. Wings covering approximately two-thirds of abdomen, veins as in macropterous form. Meso- and metathorax developed, as in macropterous form.

Micropterous form: General characters

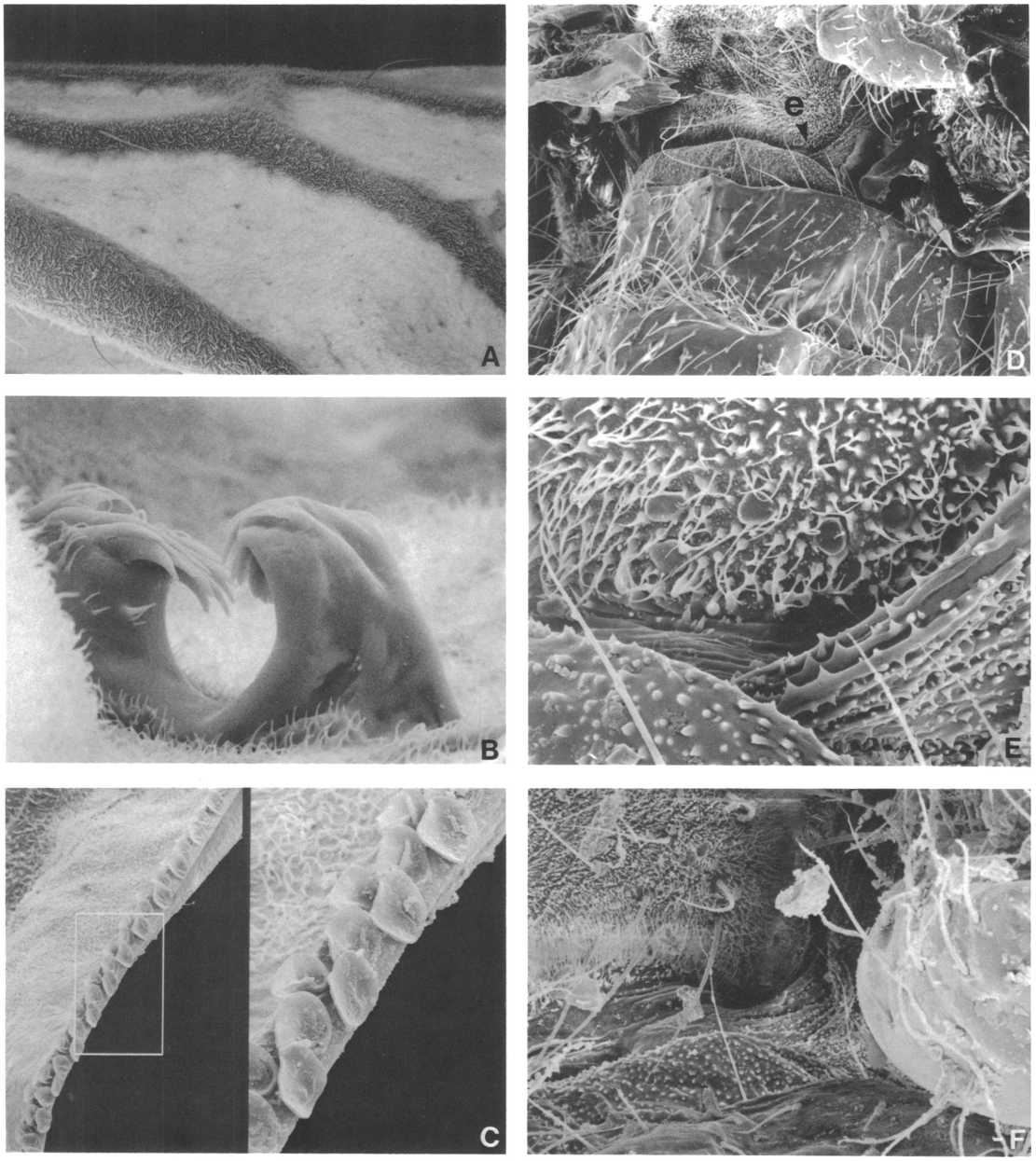


Fig. 20. *Boreostolus americanus*. **A–E**. Macropterous ♀. **A**. Forewing veins, showing no setae in lumens. **B**. Wing coupling mechanism on posterior edge of forewing. **C**. Hind wing edge at level of wing coupling mechanism, showing foliaceous structures. **D**. Thoracicoabdominal junction, ventral. **E**. Detail of egress of ventral scent gland at thoracicoabdominal junction. **F**. Micropterous ♂, same scent gland egress as above.

much as in macropterous form (fig. 22B). Eyes much smaller, ocelli very small or obsolescent. Hind lobe of pronotum not wider than midlobe. Scutellum subtriangular. Forewings reduced to short pads with indistinct venation, covered with numerous short setae and one conspicuous macrochaeta on basal fourth of wing; costal fracture faintly indicated. Hind wings present as very short lobes completely hidden by forewings (in error in original de-

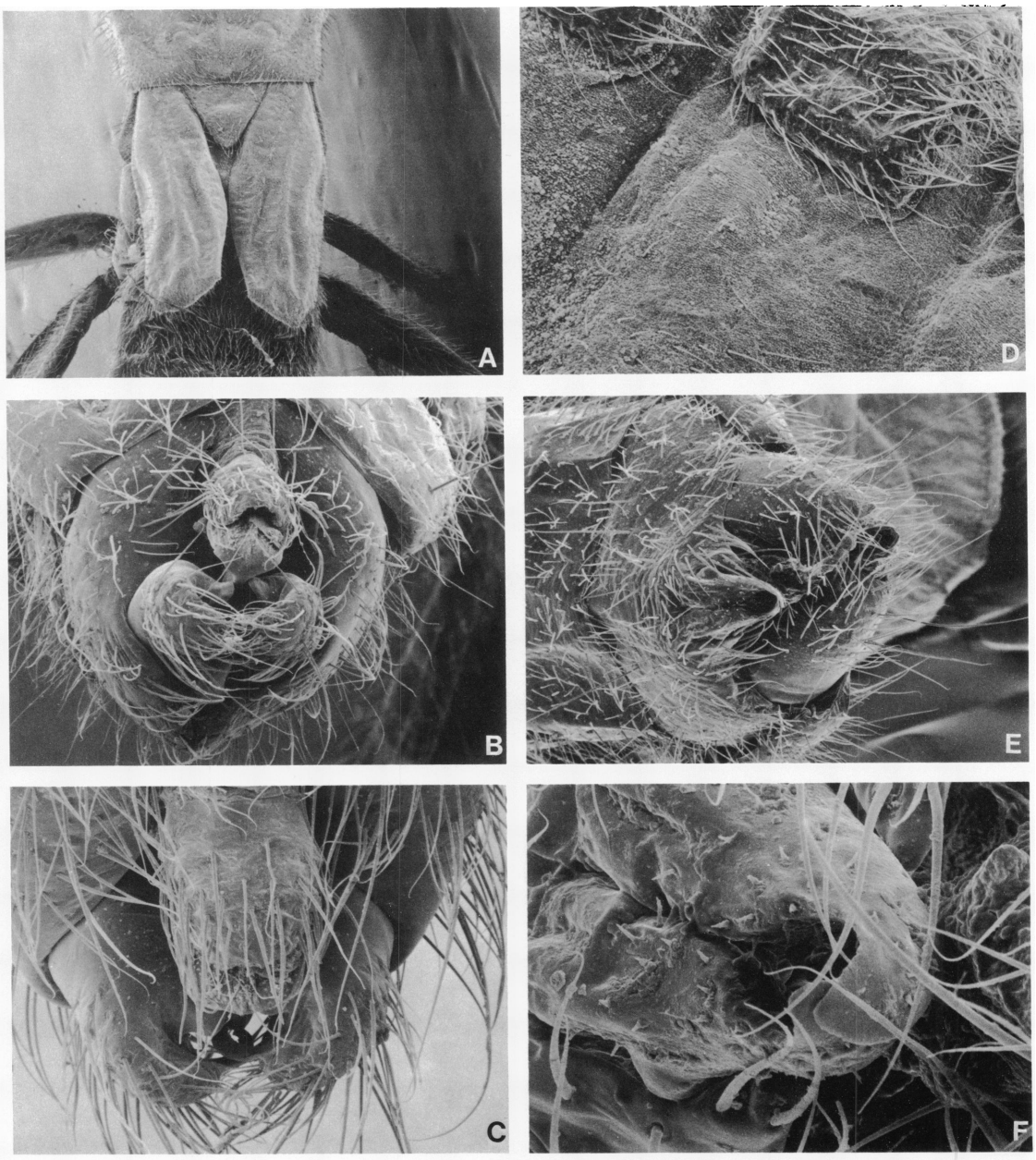


Fig. 21. *Boreostolus americanus*. **A–C**. Micropterous ♂. **A**. Dorsal view of wings. **B**. Genital capsule, posterior view. **C**. Genitalia, dorsal view. **D**. Micropterous ♀, venter of sternum IV and connexival plate with spiracle. **E, F**. Macropterous ♀. **E**. Ventral view of female gentalia, showing first and second (shriveled) valvulae. **F**. Closeup of first valvulae.

scription). Meso- and metathorax reduced. Metathoracic synpleuron and wing-body coupling trough short, about half as long as in macropterous forms.

Fifth (?) Instar Nymph (fig. 26): General body shape, proportions, and foreleg armature as in adults. Eyes well developed, containing small, pigmented ommatidia. Wingpads not meeting medially, longer than wide, and rounded posteriorly. Abdomen not well

sclerotized. Rudimentary sexual structures discernible.

Boreostolus americanus
Wygodzinsky and Štys
Figures 16–26

Boreostolus americanus Wygodzinsky and Štys, 1970: 3–12. — Štys, 1970b: 225. — Štys, 1978 (1977): 242.

DISTRIBUTION: Northwestern United States; Colorado west to Oregon and Washington.

DIAGNOSIS: *Boreostolus americanus* can be distinguished from *B. sikhotalinensis* Wygodzinsky and Štys, by the following characters: Length larger, about 5 mm; vertex between eyes flattened in lateral view; sides of hind lobe of head slightly diverging but not convex; eyes comparatively larger, about one-fourth as wide as synthlipsis, with about 40 ommatidia; ocelli distinct, their diameter approximately one-seventh of their distance; antennae comparatively long and slender; claval suture of forewings conspicuous; second valvulae pointed apically.

ADDITION TO DESCRIPTION: We here add to Wygodzinsky and Štys' (1970) extensive description the following proportion table (table 8) to assist in comparison of the wing morphs and to elucidate any differences between specimens from the different geographical areas (see Discussion).

Fifth (?) Instar Nymph: General body shape, proportions, and foreleg armature as in adults. Sclerotization variable, but always lighter than adults. Eyes fairly well-developed with 35–45 small dark red ommatidia. Wingpads not meeting medially, longer than wide, and rounded posteriorly. Macrochaetae present on dorsum of abdomen as in figure 26.

MEASUREMENTS: See Appendix.

HOLOTYPE: Macropterous male, USA: COLORADO: *Routt Co.*: Clark, 2188 m, July 18, 1943 (O. Bryant; CAS); examined.

MATERIAL EXAMINED: USA – **Oregon**: *Jackson Co.*: 8 mi SE of Lakecreek South Fork, Little Butte Creek, 719 m, under rock at edge of creek, May 21, 1964 (R. Hansell; AMNH), 1 macrop. ♀, allotype; Dead Indian Soda Springs, 23 mi ESE of Eagle Point, 828 m, under rock along Dead Indian Creek, just below Springs, May 21 and June 17, 1960 (K. M. Fender, L. G. Gentner; AMNH, OSU), 2 microp. ♀, paratypes (1 pinned and on five slides); 22 mi ESE of Eagle Point, S Fork Little Butte Creek, 781 m, June 23, 1978 (J. Schuh, L. and N. Herman; AMNH), 10 nymphs (in alcohol). *Lane Co.*: H. J. Andrews Experimental Forest, cement bridge, under rocks in sand, April 19, 1983 (G. Stonedahl; AMNH), 1 microp. ♀. *Linn Co.*: House Rock Camp, under rocks near stream, May 25, 1981 (Gary L. Peters; AMNH), 2 microp. ♀, 1 brachypterous ♀, 1 microp. ♂, and 2 nymphs (in alcohol); same May 23, 1981 (Jerry Cassis; AMNH), 1 macrop. ♀ (used for SEM); House Rock Campground on Highway 20, April 21, 1983 (G. Stonedahl and G. Parsons; AMNH), 3 microp. ♂, 2 macrop. and 4 microp. ♀ (in glycerine; 1♂ and 1 of each ♀ used for SEM). **Washington**: *King Co.*: Carnation, Tolt River, T25 NR7E Sec 22 NW¼, April 22, 1984 (J. R. La Bonte; AMNH), 1 macrop. ♀ (in glycerine).

BIOLOGY: See discussion in Biology section.

DISCUSSION: There is some question as to whether our *B. americanus* specimens from Oregon are conspecific with the holotype from Colorado. The type is a macropterous male, and the only known specimen of that wing morph and sex. Thus comparsions have to be made between the type and either macropterous females, or micropterous males, neither of which provide optimal information. No character differences seemed to hold up well enough to justify establishing another species for the West Coast specimens. Coloration is very similar. Length varies considerably (4.5–6.3 mm), but it is unclear whether this is due to differences in populations, sexual dimorphism, differences between the wing morphs, or environmental factors. Many of the longer specimens were in alcohol and had distended abdomens. The greatest differences in proportions were evident not between specimens from the two geographical areas, but between macropterous and micropterous wing morphs (see table 8). This shows up in the ratio of eye length to anteocular distance, the latter being considerably larger in the micropterous forms. It also occurs in the ratio of eye width to synthlipsis, numerically confirming the distinctly smaller eye size of the micropterous forms.

In short, we cannot find a valid reason to erect a separate species for the West Coast specimens and conclude that all of our spec-

TABLE 8
Proportions of Groups of *Boreostolus* by Sex, Wing Morph and Locality
(L = length; W = width)

	Male holotype, macropterous, Colorado	Males, micropterous, Oregon	Females, allotype + 1 macropterous, Oregon	Female, macropterous, Washington	Female, brachypterous, Oregon	Females, micropterous, Oregon
Length	4.7 mm	4.5–5.4 mm	4.8–4.9 mm	4.9 mm	6.3 mm	5.5–6.0 mm
Head L/pronotum L	1:1.1	1:1.0	1:0.9	1:0.9	1:1	1:1
Head L/W across eyes	1:0.5	1:0.5	1:0.5	1:0.5	1:0.5	1:0.5
Eye L/anteocular distance	1:1.3	1:1.8	1:1.1	1:1.1	1:1.1	1:1.8
Eye W/synthlipsis	1:2.7	1:4.0	1:2.7	1:3.1	1:2.5	1:4.6
Hind lobe head L/hind lobe head W	1:1.6	1:1.4	1:1.4	1:1.5	1:1.5	1:1.5
Antennal segments I–IV	1:2.8:3:2.4	1:3:3:2.1	1:2.5:2.6:2.1	1:2.8:2.7:2.4	1:3:3:2.4	1:2.8:2.8:2.3
Antennal L/head plus pronotum L	1:0.8	1:0.8	1:0.8	1:0.8	1:0.8	1:0.9
Midlobe pronotum W/hind lobe W	1:1.1	1:1	1:1.1	1:1.1	1:1.2	1:1
L/W forefemur	1:0.40	1:0.42	1:0.40	1:0.36	1:0.38	1:0.43
L/W hind femur	1:0.28	1:0.28	1:0.28	1:0.25	1:0.23	1:0.31
L/W foretibia	1:0.34	1:0.37	1:0.36	1:0.33	1:0.24	1:0.36

imens are *B. americanus*. We feel that a different conclusion might be reached only after collection of more material, especially a macropterous male from Oregon or Washington.

Looking at the 12 available nymphs, we were not able to determine for certain their instars, sex, or wing condition. We hypothesize that the most common form in our material, illustrated here in figure 26A, is a fifth instar macropterous female. In non-Aenietopecheine genera, sex cannot be determined from fifth instar nymphs, but in this case two types of rudimentary sex organs could be observed. Figure 26D is probably a female, with the heavily sclerotized structures being the rudimentary first valvifers. Figure 26C is probably a male, showing rudimentary parameres. One other nymph, which was larger and more sclerotized than the commonest form, had smaller wing pads (fig. 26B) and barely discernible sexual structures; this was either a fourth instar or a micropterous fifth instar, sex unknown. It will be necessary to wait for more nymphal material before drawing any concrete conclusions relating to the above forms.

Gamostolus Bergroth

Gamostolus Bergroth, 1927: 683. — Usinger, 1932: 150. — Jeannel, 1942 (1941): 297, 361. — Usinger, 1945 (1944): 325, 329. — Wygodzinsky, 1949: 354. — Woodward, 1956: 395, 402, 405. — Villiers, 1958: 14–15, 25–26. — Štys, 1969b: 355. — Wygodzinsky and Štys, 1970: 7. — Štys, 1970b: 239. — Kritsky, 1977b: 161, 166. — Štys, 1977: 208–209. — Štys, 1978 (1977): 242. — Štys, 1980: 303, 305–306. — Wygodzinsky and Štys, 1982: 129.

TYPE SPECIES: *Henicocephalus subantarcticus* Berg. Fixation by original designation.

DISTRIBUTION: *Gamostolus* is most common in the Araucanian subregion of South America. It is most frequent on the mainland and on islands close to Tierra del Fuego. It also occurs northward to Chiloé, Chile, up the Cordillera to Cumbal, Colombia, and to Aragua, Venezuela (the last two localities known from nymphs only; see Discussion; fig. 27).

DIAGNOSIS: *Gamostolus* can be distinguished by the following characters: Outermost spine of outer group of spines of foretibia inserted at same level as, or more distally than, adjacent two spines (fig. 29D); foretar-

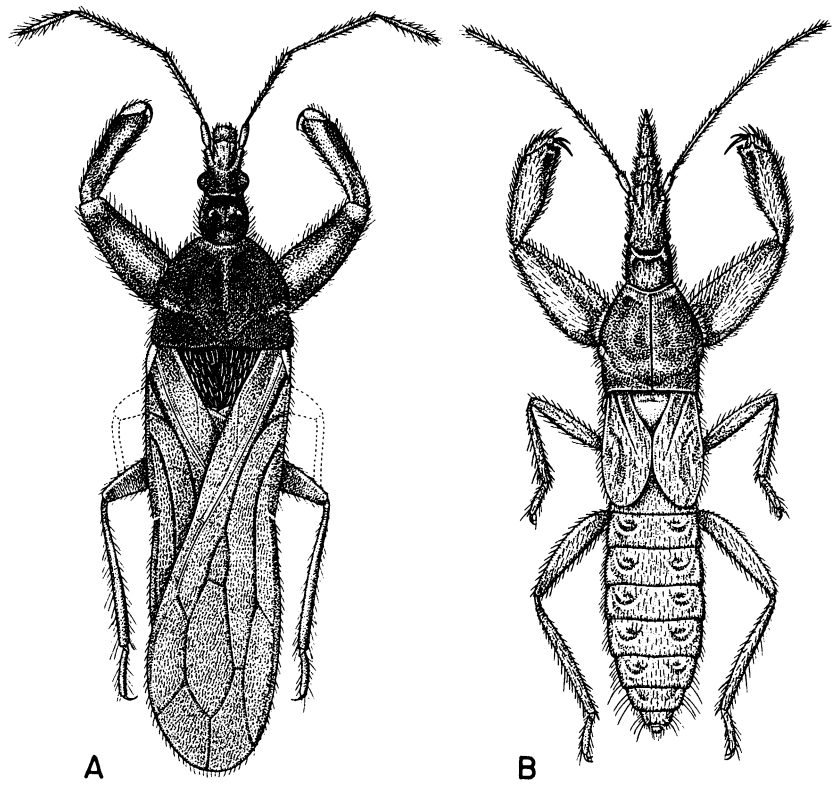


Fig. 22. *Boreostolus americanus*. **A**. Male holotype. **B**. Micropterous ♀. (From Wygodzinsky and Štys, 1970)

sus with four spines (fig. 29B); dorsal bridge of pygophore large, occupying most of dorsal surface of pygophore; parameres of male oval, without projection (fig. 35D); phallus at base with wide funnel-shaped structure, apically simply tubular and lacking projections or cuticular processes (fig. 35E); first valvulae of female not completely fused to sternum VIII, apically with a bifid projection, and not forming trough (figs. 36D, F).

ADDITIONS TO DESCRIPTION:: Large species (over 6 mm). Head, abdomen, and appendages polished, thorax dull. Setiferous tubercles lacking. All setae simple, slender. Macropterous in both sexes.

Adult: Head with postocular impression distinct (figs. 28A, B). Eyes of male larger than those of female, but not closely approaching on under surface of head. Ocelli closer to sides of head than to each other. Antennal segments narrowly cylindrical, segments II–IV subequal in length. Rostrum short and stout, extending forward in preserved specimens (figs. 28C, D).

Pronotum unarmed, faintly convex above (figs. 28A, B). Transverse impressions separating the three lobes faint, obsolescent in middle. Proepimera and proepisterna somewhat reduced above forecoxae, visible from above (figs. 28B, 30A).

Scutellum broadly triangular (figs. 30D, 34A), flanked posterolaterally on each side by auricle of metathoracic scent gland covered by folded forewings (figs. 30E, F).

Meso- and metathorax (fig. 30E) with a groove above metathoracic synpleuron receiving costal edge of forewing at rest.

Forewings (figs. 6A, 34E) with fracture at center of costal margin. Basal cell present, discal cell closed, the former slightly shorter than the latter. Stigmal cell extending beyond stigma, not subdivided. Pcu and 1An well separated on basal half of clavus. Setae on proximal half of forewing long, arranged in

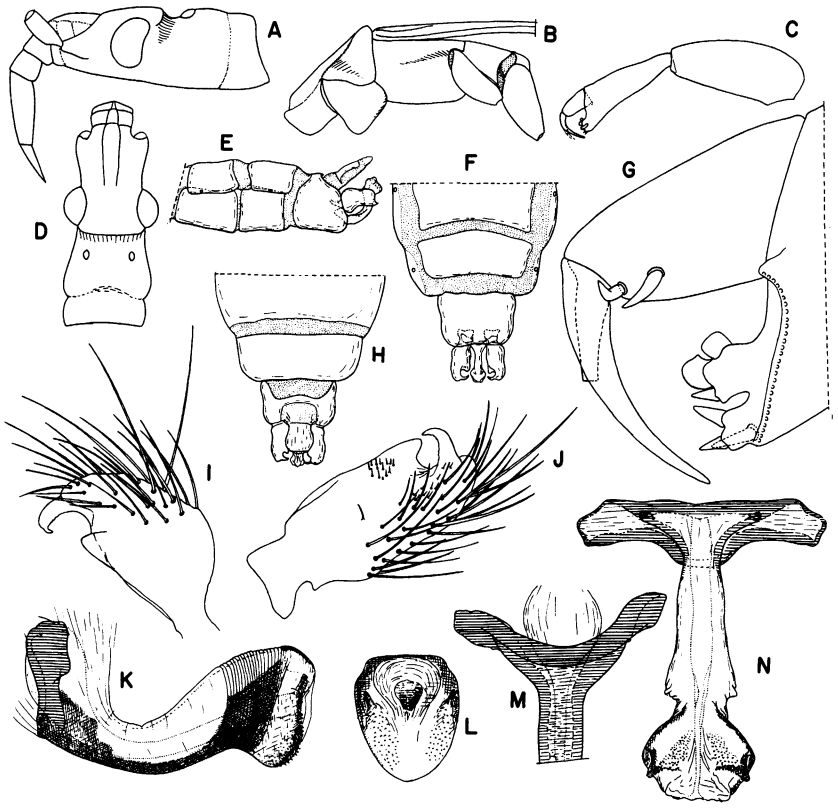


Fig. 23. *Boreostolus americanus*, ♂. **A**. Head, lateral view. **B**. Thorax, lateral view. **C**. Femur, tibia and tarsus of foreleg. **D**. Head, dorsal aspect. **E**. Apex of abdomen, expanded, side view. **F**. Apex of abdomen, ventral aspect. **G**. Apex of foretibia, with tarsus and claws. **H**. Apex of abdomen, expanded, dorsal view. **I**, **J**. Paramere. **K**. Phallus, lateral. **L**. Apex of phallus, posterior. **M**. Phallus, base, dorsal aspect. **N**. Phallus, ventral. (from Wygodzinsky and Stys, 1970)

two series on veins, though more numerous on costal margin. Setae on veins of distal half of wing very short, sparse. Cells lacking setae (fig. 32D), but space between costal margin and R + M setose. Hind wing with apical portion of "cell" beyond insertion of posterior free vein, over two times as long as wide. Setae completely absent.

Wing coupling device at distal end of clavus of forewing. Device C-shaped (fig. 32E), with two arms of "C" extending down from under surface of wing. Arm closest to wing edge with short, rounded projections apically; other arm with projections long, slender, and pointed. Edge of hind wing at level of wing coupling device rolled inward and beset with foliaceous structures (fig. 32F).

Front legs very stout, thicker in females than in males, but with spines similar in both sexes. Coxae and under surface of forefemur with minute cuticular scalelike structures. Projection of inner apical angle of foretibia very prominent, with an apical ridge bearing six spines, divided into two groups of three spines each, by a small incision (figs. 11A, 29D, E). Outer group composed of three conical spines subequal in length; outermost spine inserted distal to innermost. Inner group consisting of one outer conical and two inner, subsemicircular spines. Tarsus with four spines (figs. 13B, 29B); spine III halfmoon-shaped, closely adpressed to tarsus; I, II and IV erect, conical; all well developed. Tarsal organ dorsally situated. Foretarsus with two claws, the inner about twice as long as the outer (figs. 13B, 29A). Mid and hind tibiae

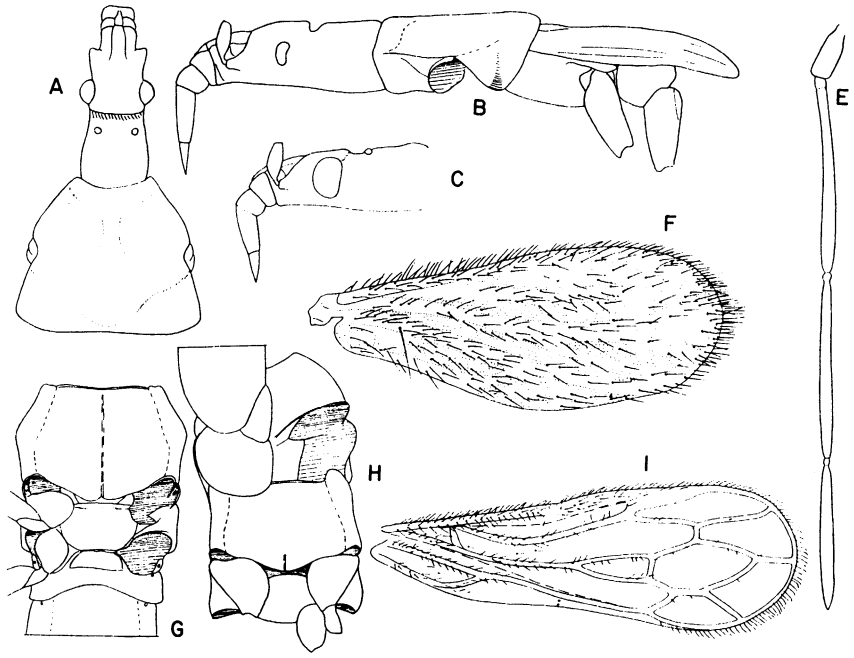


Fig. 24. *Boreostolus americanus*. **A**. Macropterous ♀, head and pronotum, dorsal. **B**. Micropterous ♀, head and thorax, lateral. **C**. Macropterous ♀, head, lateral. **D**. Omitted. **E**. Micropterous ♀, antenna. **F**. Brachypterous ♀, forewing with veins. **G**. Macropterous ♀, meso- and metasternum, and base of abdomen. **H**. Micropterous ♀, thorax, ventral. **I**. Macropterous ♀, forewing. (from Wygodzinsky and Štys, 1970)

with two large apical spines, but lacking bristle combs (fig. 14A, 32A, B). Mid and hind tarsi two-segmented.

Abdomen variously beset with single to many-toothed cuticular structures (fig. 33B). Connexival plates in one row separate from sternites, and most closely associated with tergites. Spiracles near ventral edges of connexival plates II–VIII (figs. 32C, 35A), and on lateral membrane on segment I.

Pygophore of male large, not invaginated into eighth segment (figs. 33A–C); anterior dorsal bridge very long, almost completely covering dorsal surface of pygophore (fig. 35G). Parameres and phallus inserted at posterior wall of pygophore, well developed, permanently extruded. Parameres inserting directly on lateral extremities of basal plate without intervening sclerites. Parameres suboval (fig. 35D), strongly sclerotized, inner basal edge membranous; with numerous setae. Phallus short, tubular, with basal funnellike structure (fig. 35E). Basal plate in shape of simple transverse sclerite (figs. 35H–K). Tenth tergum wider than long (fig. 35G).

Eighth abdominal sternum of female entire, incised medially. First valvifers fused to sternum VIII (fig. 36F). First valvulae in form of opposing narrow blades (figs. 36D, F), forming channel that encloses second valvulae. Second valvulae (fig. 36E, G) with many small teeth apically.

Fifth instar nymph (fig. 37): General shape stout. Eyes well developed. Antennae slender. Neck not distinct. Wing pads not meeting medially, longer than wide, rounded posteriorly. Abdomen membranous; terga III–VII with ordinary setae and with macrochaetae (1 + 1 submedian, 1 + 1 sublateral and 1 + 1 lateral).

DISCUSSION: Until now, the range of *Gamostolus* was thought to be limited to southern South America. We now have in our possession three nymphs of *Gamostolus* sp. (see Material Examined under *G. subantarcticus*) which seem to extend the range northward

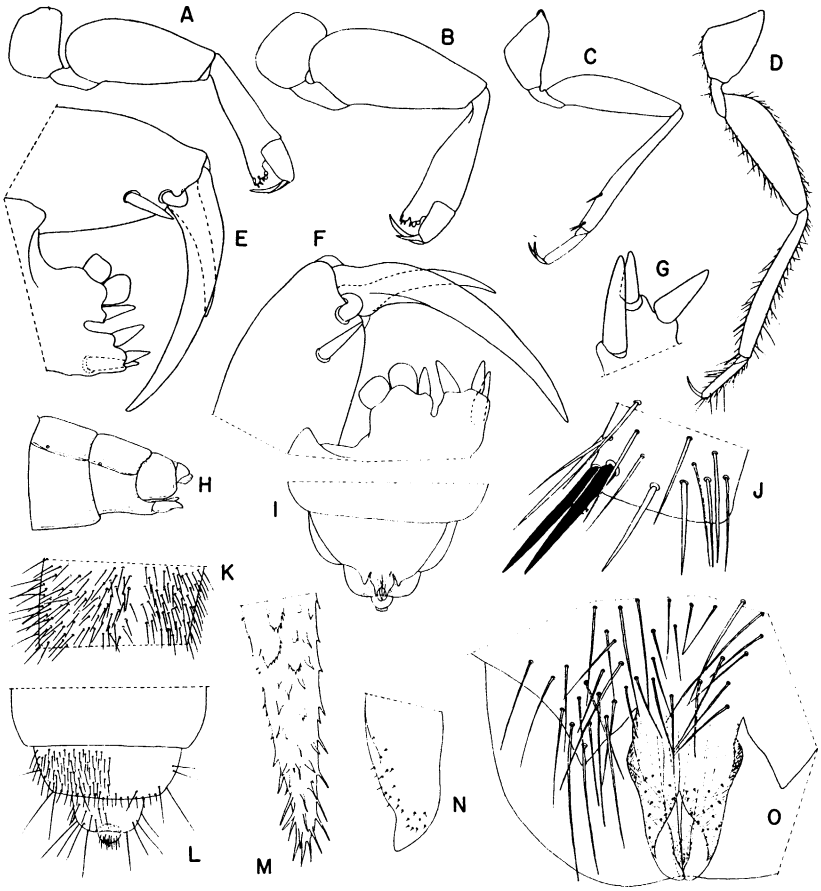


Fig. 25. *Boreostolus americanus*, ♀. **A**. Macropterous, foreleg. **B**. Micropterous, foreleg. **C**. Macropterous, hind leg. **D**. Micropterous, hind leg. **E**. Macropterous, apex of foretibia with tarsus. **F**. Micropterous, apex of foretibia with tarsus. **G**. Micropterous, outer group of tibial spines, different view. **H**. Micropterous, apex of abdomen, side view. **I**. Micropterous, apex of abdomen, ventral aspect. **J**. Macropterous, apex of hind tibia. **K**. Macropterous, detail of chaetotaxy of forefemur. **L**. Micropterous, apex of abdomen, dorsal view, with setae. **M**. Micropterous, apex of second valvula. **N**. Micropterous, apex of first valvula. **O**. Micropterous, genital appendages, as seen in cleared abdomen. (from Wygodzinsky and Štys, 1970)

to Aragua, Venezuela. This would suggest that collecting in the intervening areas might reveal a range encompassing the entire Andean cordillera.

Gamostolus subantarcticus (Berg)

Henicocephalus subantarcticus Berg, 1883: 116. — Bergroth, 1889: 319. — Breddin, 1897: 14.
Gamostolus subantarcticus: Bergroth, 1927: 693. — Jeannel, 1942 (1941): 298. — Usinger, 1945 (1944): 324, 326–328. — Wygodzinsky, 1949: 354. — Woodward, 1956: 392, 395. — China, 1963: 707. — Štys, 1970a (1968): 450. — Štys, 1969b: 361–362. — Štys, 1978 (1977): 242.

DISTRIBUTION: Southern South America, from Tierra del Fuego, Argentina, north to Osorno Province, Chile. May occur farther northward (see Material Examined and generic discussion).

DIAGNOSIS: This is the only described species in the genus *Gamostolus* and can be distinguished by the structure of the genitalia and the unique body proportions in both sexes.

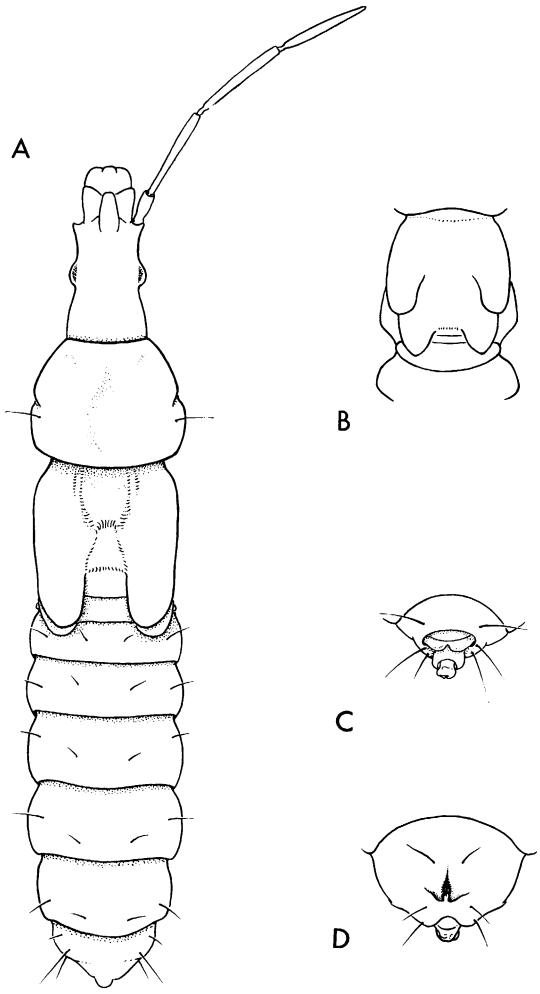


Fig. 26. *Boreostolus americanus*, nymphs. **A**. Macropterous ♀, 4th or 5th instar. **B**. Wingpads of macropterous 4th or micropterous 5th instar. **C**. ♂, 5th instar, ventral view of genital region. **D**. ♀, 5th instar, ventral view of genital region.

DESCRIPTION: We add to the previous descriptions of this species the proportions in table 9, in order to be consistent with other sections of this work.

DISCUSSION: The syntype we examined is a female with the following label data: Staten Island, Dr. Spegazzini, collection M. S. Pennington. According to Berg's (1883) original description, this is one of many specimens collected under rocks by Dr. Carlos Spegazzini on his expedition to "Tierras Australes" in May, 1882. We were fortunate to be able to see this syntype while it was on loan to the USNM. It is now in the Facultad de Ciencas Naturales y Museo at La Plata. Two other syntypes are at the Museo Argentino de Ciencas Naturales "Bernardino Rivadavia" in Buenos Aires. A lectotype needs to be designated following examination of the other syntypes.

SYNTYPE: Female, Argentina, Staten Island, Dr. Spegazzini, collection M. S. Pennington (La Plata); examined (see Discussion).

MATERIAL EXAMINED: Syntype, above, plus: CHILE. – **Magallanes Prov**.: Islas Wollaston; Isla Herschel, Expedicion Inst. Miguel Lillo, January 11, 1949 (Olrog, Budin, and Vervoorst; AMNH), 5♂ and 2♀ (one ♂ used for SEM); Isla Navarino, Canal Beagle, Puerto Williams, 400 m, February 1, 1957 (T. Cekalovic; AMNH), 1♀ and 2 nymphs; Punta Arenas, R. Las Minas, November 2–4, 1960 (L. E. Peña; AMNH), 1♀ (used for SEM); November 2–4, 1960 (L. E. Peña; AMNH), 1♀. **Osorno Prov**.: Parque Nacional Puyehue, Volcan Casa Blanca, 1270 m, trap site 667, treeline in *Nothofagus* forest, December 20–25, 1982 (A. Newton and M. Thayer; AMNH), 1♂ and 1♀.

Gamostolus spp.: COLOMBIA. – Cumbal, 3400 m (no collector; AMNH), 1 nymph. VENEZUELA. – Estado Aragua: Rancho Grande, 1100 m, rain forest, June 23–27, 1971 (W. L. and D. E. Brown; AMNH), 2 nymphs.

Tornocrusus Kritsky

Tornocrusus Kritsky, 1977b: 161. — Štys, 1978 (1977): 252; Štys, 1980: 304–306. — Wygodzinsky and Štys, 1982: 129.

TYPE SPECIES: *Tornocrusus Štysi* Kritsky. Fixation by original designation.

DISTRIBUTION: Central and South America. This genus occurs from Costa Rica through western South America to Peru. It also occurs in northern and eastern South America from Venezuela to southern Brazil (fig. 38).

DIAGNOSIS: *Tornocrusus* differs from other New World Aenictopecheinae by such essential characters as the structure of the pronotum, the extremely reduced proepimera (fig. 40A), the presence of only one large spine and one bristle comb on the apices of the mid

Fig. 27. Distribution of *Gamostolus*. *G. subantarcticus* (●). Undescribed (■).

and hind tibiae (figs. 14C, 40F, G), the complete absence of a sclerotized dorsal bridge of the pygophore (fig. 54A), the shape of the parameres, and the structure of the phallus. The extremely long and apically filiform inner claw of the foretarsus and the very delicate tarsal spine I also serve to distinguish this genus (see Discussion). In addition, the ocelli are separated by a dull patch of cuticular microtrichiae, which contrasts with the shine of the surrounding head (fig. 39A).

REDESCRIPTION: Small species (3.0–5.1 mm). Head, abdomen and appendages polished, thorax and wings dull. Setiferous tu-

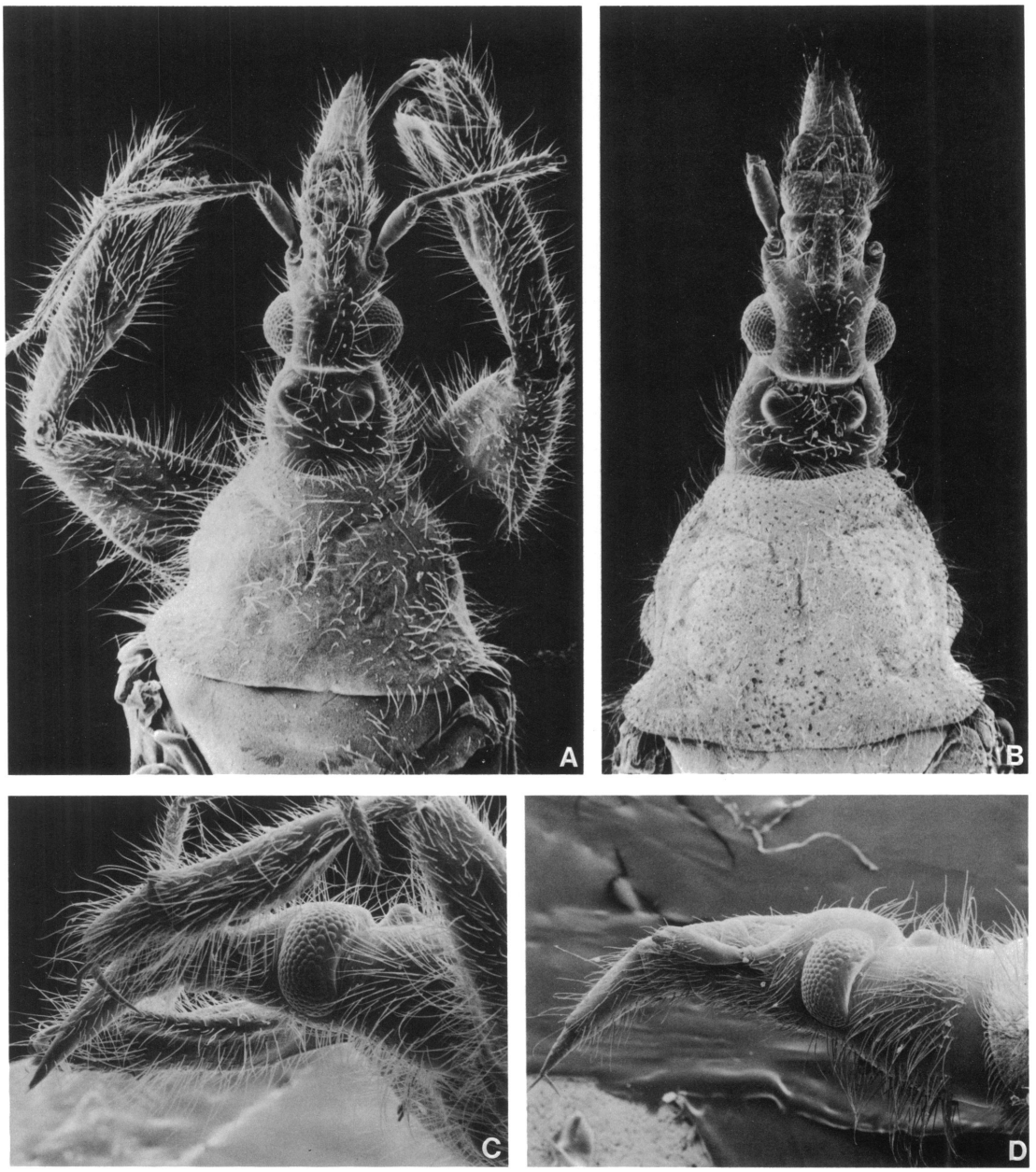


Fig. 28. *Gamostolus subantarcticus*. **A**. Head and pronotum of ♂, dorsal. **B**. Same, ♀. **C**. Side view of head, ♂. **D**. Same, ♀.

bercles absent. All setae simple, slender. Macropterous.

Head with distinct postocular impression (fig. 39A). Eyes of males larger than those of females, but not closely approaching on lower surface of head. Ocelli separated by two to four times their width. Antennal segments narrowly cylindrical; segments II–IV subequal in length. Rostrum short and stout, extended forward in preserved specimens.

Pronotum unarmed, faintly convex above, sides only slightly diverging posteriad (fig.

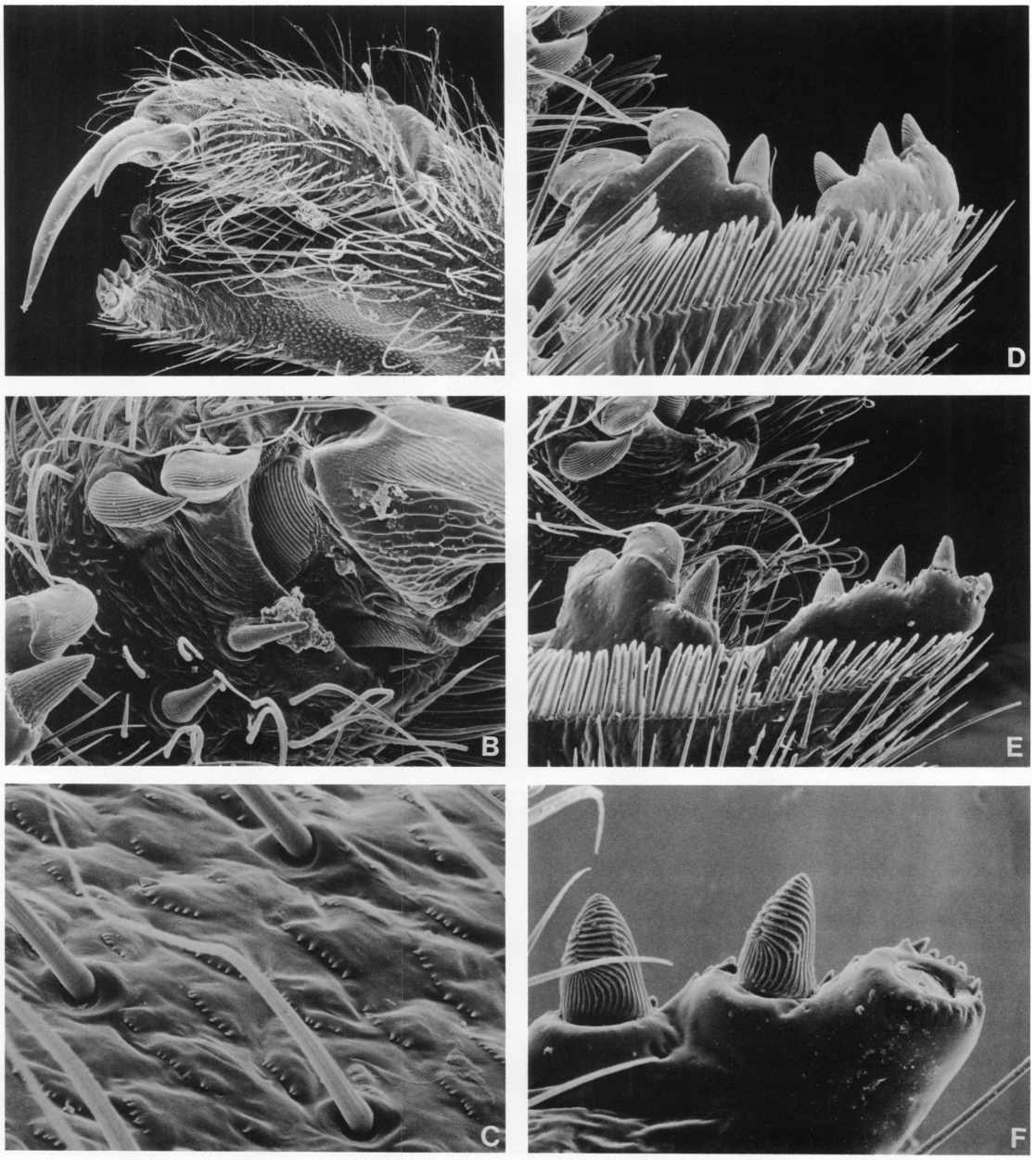


Fig. 29. *Gamostolus subantarcticus*, ♀. **A**. Apex of foreleg, outer view. **B**. Foretarsus, showing four spines. **C**. Detail of surface of forefemur. **D**. Apex of foretibia, inner view. **E**. Same, aberrant specimen with extra spine (on right). **F**. Outer three foretibial spines, normal configuration (one missing).

39A). Transverse impressions separating the three lobes faint, obsolescent at middle. Lateral portions of posterior impression parallel to hind margin of pronotum. Midlobe with shallow median longitudinal depression. Anterior acetabula open behind. Proepimera and proepisterna very small (fig. 40A). Wing-body coupling groove present, into which the costal margin of the forewing fits basally (fig. 40B).

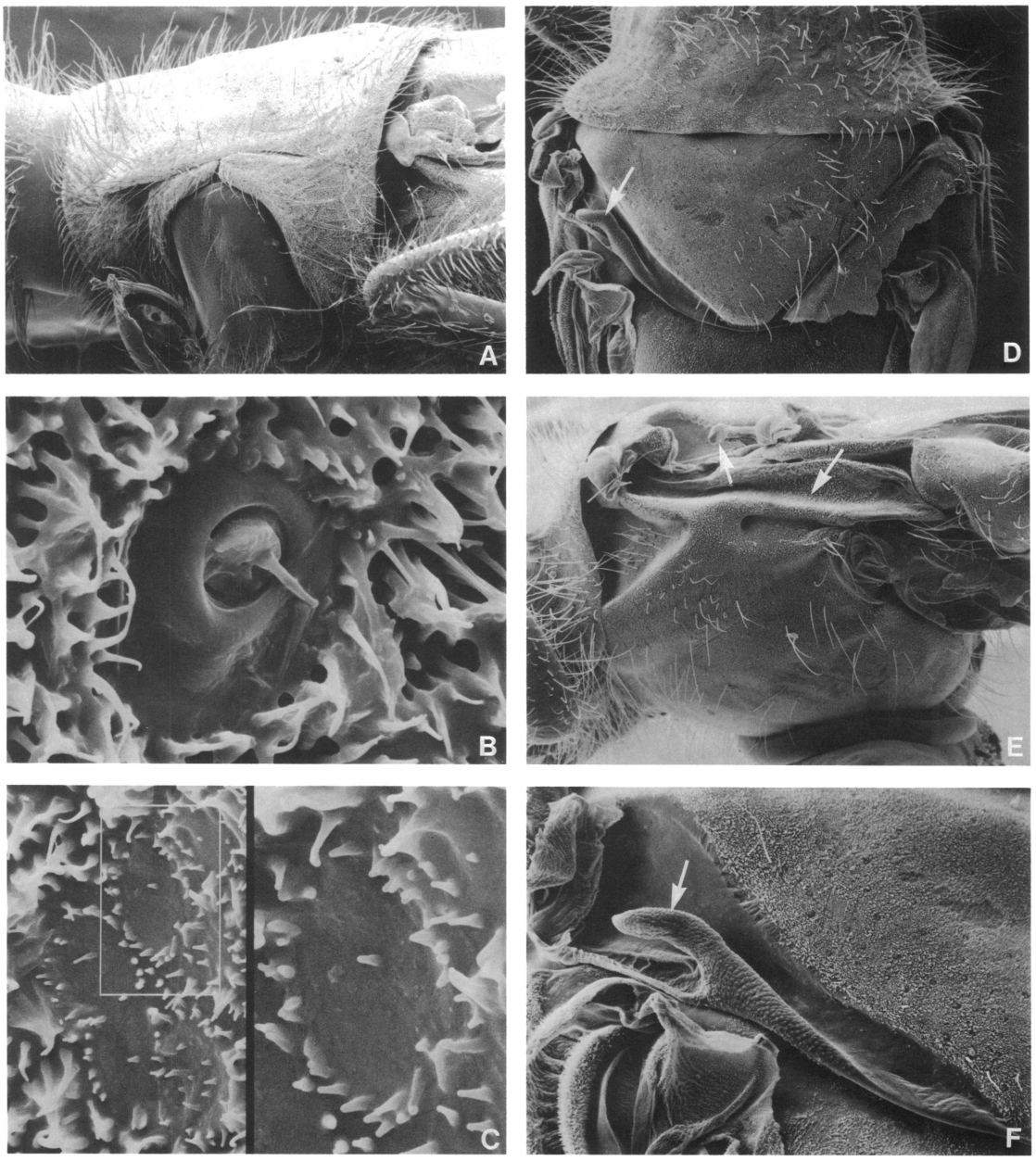


Fig. 30. *Gamostolus subantarcticus*. **A**. Pronotum, lateral, ♀. **B**. Detail of one minute "bare" spot on pronotum, ♀. **C**. Detail of "bare" spot on hind lobe of pronotum, ♂. **D**. Scutellum and left scent gland auricle, ♂ (arrow). **E**. Meso- and metathorax, lateral, ♂ (left arrow indicates scent gland auricle, right arrow, forewing-to-body coupling groove). **F**. Detail of scent gland auricle, ♂.

Forelegs stout, thicker in females than in males. Coxae and ventral surface of femur with minute scalelike structures in some species. Projection of inner apical angle of foretibia very prominent, with an apical ridge bearing six spines, divided into two groups of three by a small incision (figs. 11C, D, 39E). Outer group composed of three conical

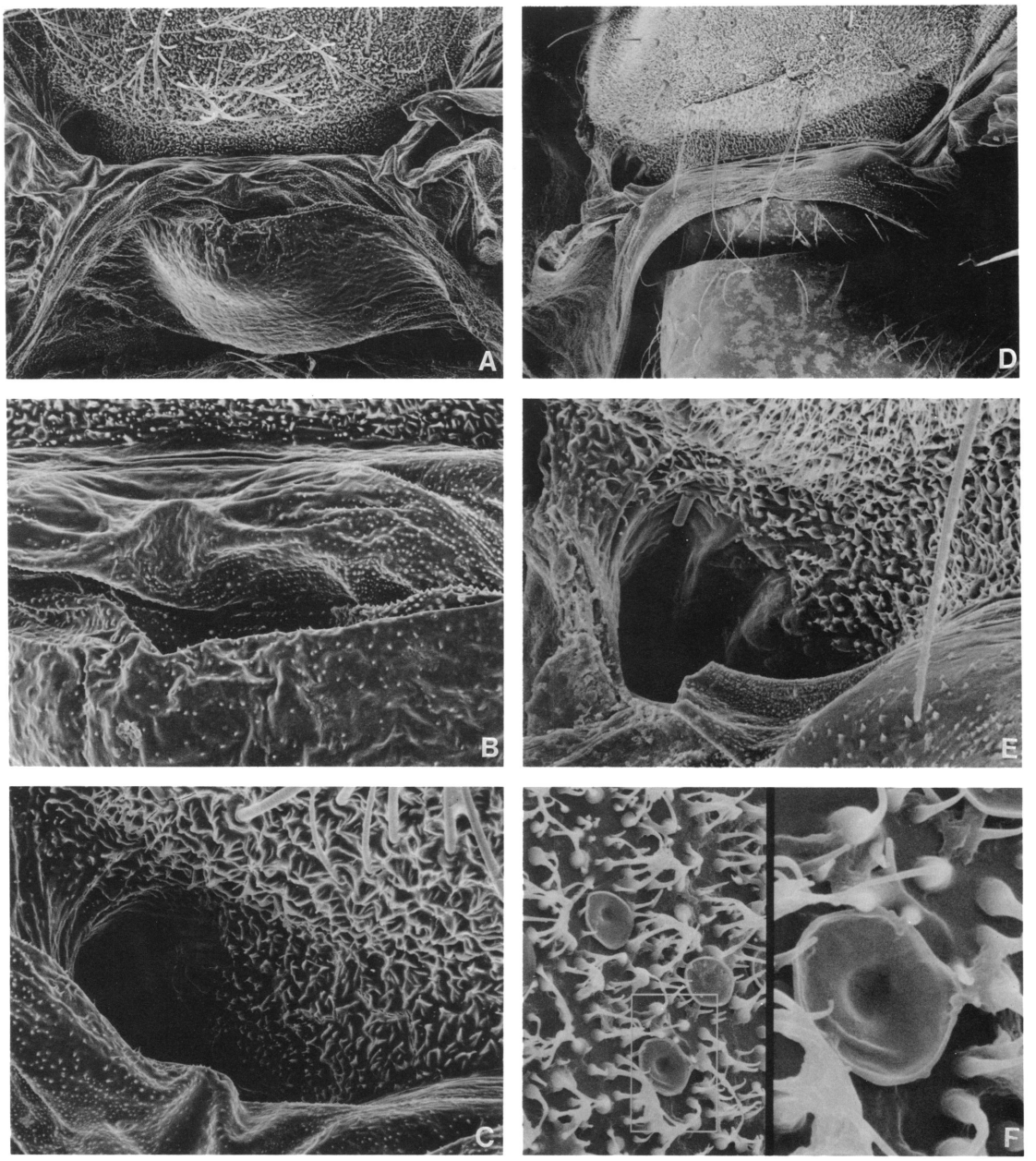


Fig. 31. *Gamostolus subantarcticus*. **A–C**. ♀. **A**. Thoracicoabdominal junction, ventral, showing left and right orifices of scent glands. **B**. Detail of center of abdomen (above) showing no median orifice. **C**. Detail of right (left side of photo A) thoracicoabdominal scent gland orifice. **D–F**. ♂. **D**. Thoracicoabdominal junction, ventral. **E**. Detail of right scent gland orifice. **F**. Close-up of cuticular structures on wall of above.

spines of unequal length, all inserted at identical level. Spine b at least twice as long as spine c (fig. 39C). Inner group consisting of one outer conical and two inner large subsemicircular spines. Tarsus with four spines (figs. 13A, 39F); spine III halfmoon shaped, closely adpressed to tarsus; I, II and IV erect, conical, more or less elongate, I extremely

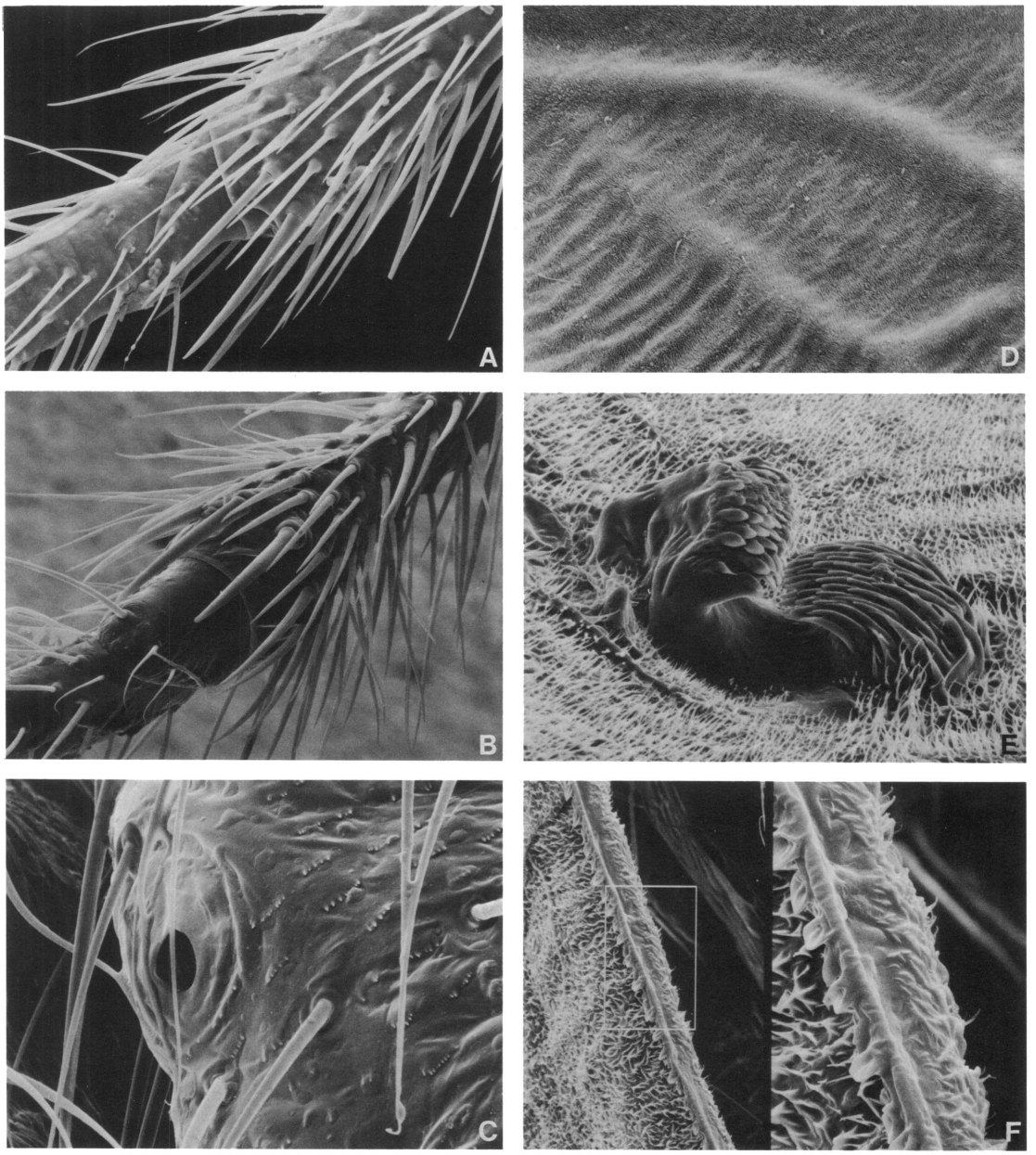


Fig. 32. *Gamostolus subantarcticus*. **A**, **B**. Apices of mid and hind tibiae of ♂, respectively. **C**. Spiracle on ventral connexival plate IV and detail of toothed cuticular structures, ♀. **D**. Forewing surface, ♂. **E**. Forewing coupling mechanism, ♀. **F**. Hind wing edge and detail, at level of wing coupling mechanism, showing foliaceous structures, ♀.

delicate, much thinner than II. Tarsal organ dorsally situated. Foretarsus with two claws, the inner one from 2 to 3 times as long as outer one, somewhat S-shaped and with its apical portion filiform. All legs with conspicuous long tactile setae. Apex of mid and hind tibiae with one arc-shaped bristle comb and only one large apical spine (figs. 14C, 40F, G).

Forewings with fracture at center of costal

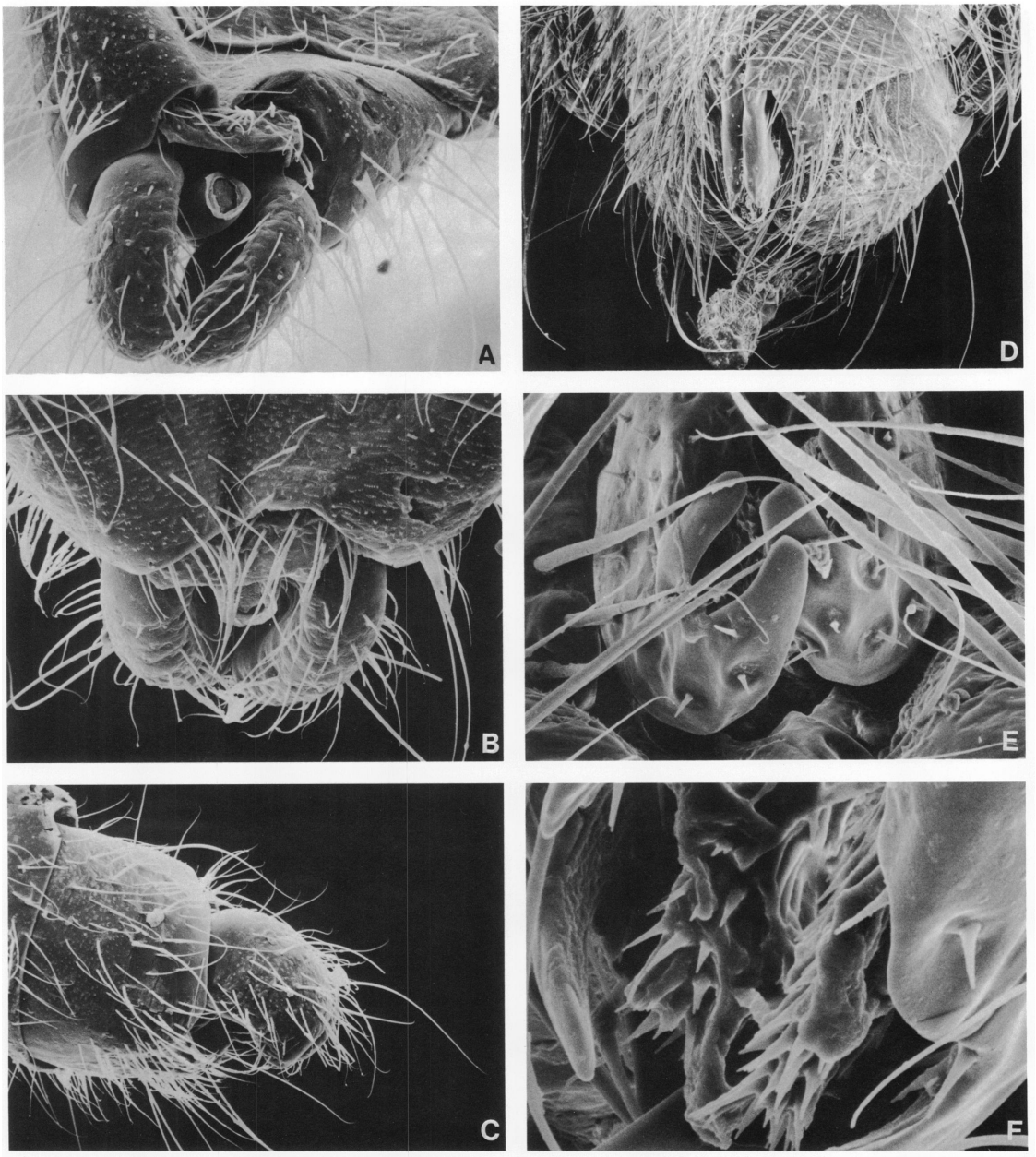


Fig. 33. *Gamostolus subantarcticus*. **A–C**. ♂ genitalia. **A**. Posterodorsal view. **B**. Dorsal. **C**. Lateral. **D–F**. ♀ genitalia. **D**. Ventral, showing first valvulae. **E**. Detail of apices of first valvulae. **F**. Detail of apices of second valvulae (enclosed by first valvulae).

margin (fig. 6A). Basal cell present, discal cell closed, the former from ⅓ to ½ as long as the latter. Stigmal cell not subdivided, extending beyond stigma. Pcu and 1An well separated on basal half of clavus. Setae on basal half of forewing long, arranged in two series on veins, though more numerous on costal margin. Setae of veins of distal half of forewing conspicuously shorter, sparse. Cells lacking setae (fig. 41A); space between costal margin and

TABLE 9
Proportions of *Gamostolus subantarcticus*

	Males	Females
Length	6.2–6.3mm	7.0–8.0 mm
Head L/pronotum L	1:0.9	1:1.1
Head L/W across eyes	1:0.6	1:0.7
Eye L/anteocular distance	1:0.5	1:0.7
Eye W/synthlipsis	1:2	1:2.8
Hind lobe head L/hind lobe head W	1:1.8	1:2.6
Antennal segments I–IV	1:2:2.2:1.8	1:2:2.2:1.7
Antennal L/head plus pronotum L	1:0.9	1:1
Mid pronotum W/hind lobe W	1:1.3	1:1.2
L/W forefemur	1:0.43	1:0.45
L/W hind femur	1:0.20	1:0.22
L/W foretibia	1:0.32	1:0.38

R bare. Apical portion of "cell" of hind wing, beyond insertion of posterior free vein, about 3 times as long as wide. Wing coupling mechanism on forewing C-shaped (fig. 41B); corresponding hind wing edge simple (fig. 41C).

Abdomen well sclerotized in both sexes, beset with setae and microtrichiae but otherwise lacking any patches of specialized structures. Connexival plates in both males and females not divided into dorsal and ventral rows, and not clearly separable from tergites except by their flexion in nondistended state. Spiracles on segments I–VIII in both sexes and located near ventral edge of connexival plates (or occasionally in intersegmental membrane separating connexival plates from sternites).

Pygophore of male large, not invaginated into eighth segment. Dorsal surface of pygophore completely membranous (fig. 50B). Parameres and phallus inserted on posterior portion of pygophore, well developed, permanently extruded. Parameres inserted directly on lateral extremities of basal plate without any intervening sclerites. Parameres subtriangular or rhomboid, strongly compressed laterally, beset with numerous setae and multitoothed microtrichiae (figs. 42D–F), their inferior border membranous. Phallus composed of subcylindrical, slightly swollen basal portion and membranous, tubular distal portion, which is apically bifid (figs. 50E–I).

Abdominal sternum VIII of female entire, apically incised at middle (fig. 50N). First valvulae partially fused to sternum VIII, scoop-shaped at end with two teeth apicoventrally (fig. 43F). Second valvulae rodlike, enfolded by first valvulae, and beset apically with mircrotrichiae (fig. 43F).

Fifth instar nymph (fig. 52G). General shape stout. Eyes well developed. Antennae slender. Neck not distinct. Wing pads not meeting medially, longer than wide, rounded posteriorly. Abdomen membranous; terga III–VII with ordinary setae and with macrochaetae (1 + 1 submedian, 1 + 1 sublateral, and 2 + 2 lateral).

DISCUSSION: We have examined the holotype of *Tornocrusus stysi* (type species) and have found that it differs in two main ways from the original generic description. First, the foretarsus bears four spines rather than two; spine I, especially, and sometimes spine II, are weak and often difficult to see.

Second, the scutellum is not notched apically, but its slightly sinuous sides form a somewhat rounded apex. The notched appearance at low magnification results from interferences from underlying tissue.

Tornocrusus species often differ subtlely and they are frequently difficult to separate from one another. For best results, all measurements and proportions should be figured out according to the measurement diagrams (fig. 4) and then compared to the proportion tables below (tables 10, 11), in addition to using the key and examining male genitalia.

Considerable incidence of teratology occurs in the wing venation of *Tornocrusus*. In

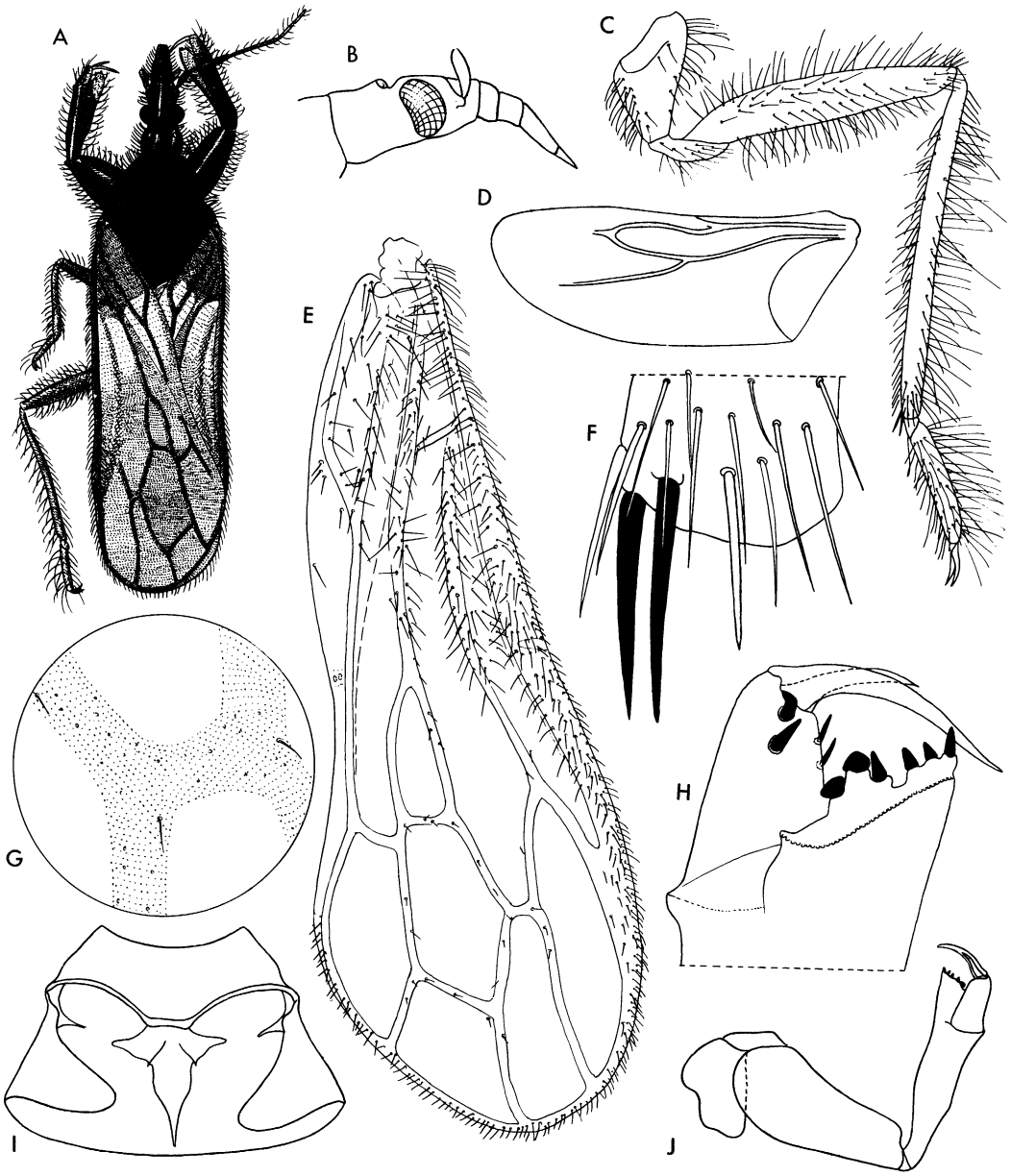


Fig. 34. *Gamostolus subantarcticus*, ♂. **A**. Dorsal view. **B**. Head, lateral. **C**. Hind leg. **D**. Hind wing. **E**. Forewing. **F**. Apex of hind tibia. **G**. Detail of forewing at level of r-m crossvein. **H**. Apex of foreleg, inner surface. **I**. Pronotum, ventral view, showing open condition of acetabulae. **J**. Foreleg, outer surface. (A, D, I, and J from Wygodzinsky, 1949)

our most numerous species, *T. penai*, 19 out of 107 wings studied (18 percent) were teratological in various ways. In *T. sturmi*, one slight teratology (see key) occurred much more frequently than the "normal" condition, prompting us to use it as a key character. It is necessary to consider these differences when defining genera or species, whether they are genetically controlled, or the result of environmental factors during development.

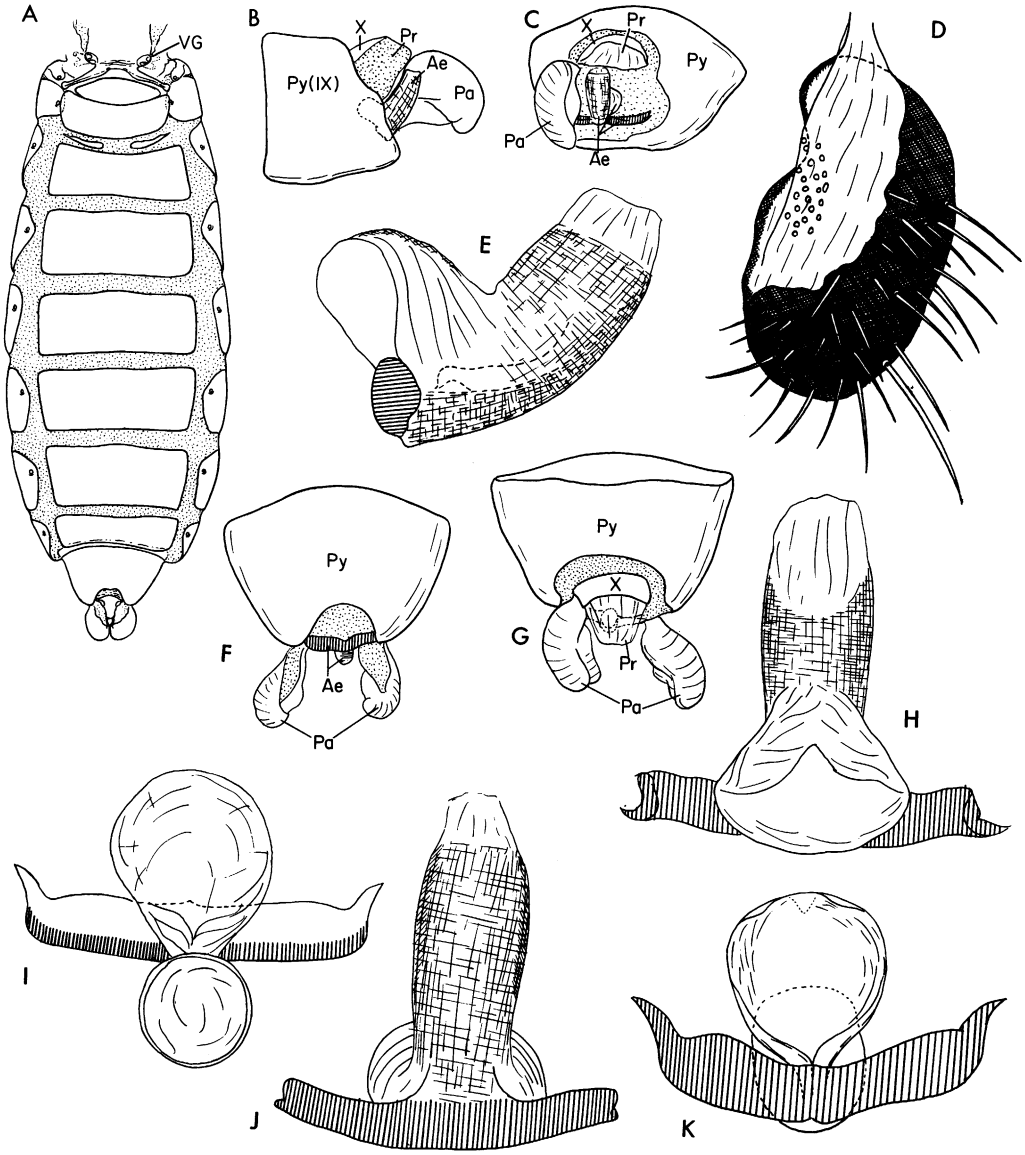


Fig. 35. *Gamostolus subantarcticus*, ♂. **A**. Abdomen, ventral, with part of thorax attached anteriorly. **B**. Pygophore, lateral view, left paramere removed. **C**. Pygophore from behind, slightly lateral, right paramere removed. **D**. Right paramere. **E**. Phallus, lateral. **F**. Genital capsule, ventral. **G**. Genital capsule, dorsal. **H**. Phallus, dorsal. **I**. Phallus, posterior. **J**. Phallus, ventral. **K**. Phallus, anterior. (A, D, I, and J from Wygodzinsky, 1949)

Wygodzinsky and Štys (1970) reported that the scent gland in female *Boreostolus sikhotalinensis* is a median opening at the front of the first abdominal sternum. Examination of the same area in a slide of the female paratype of *B. americanus* reveals no such structure, nor does the scanning electron microscope (SEM) study. Slides of several *Tornocrusus* species show a slight invagination of the cuticle in that area, but SEM studies reveal no corresponding opening. We have since found that all macropterous members of the New

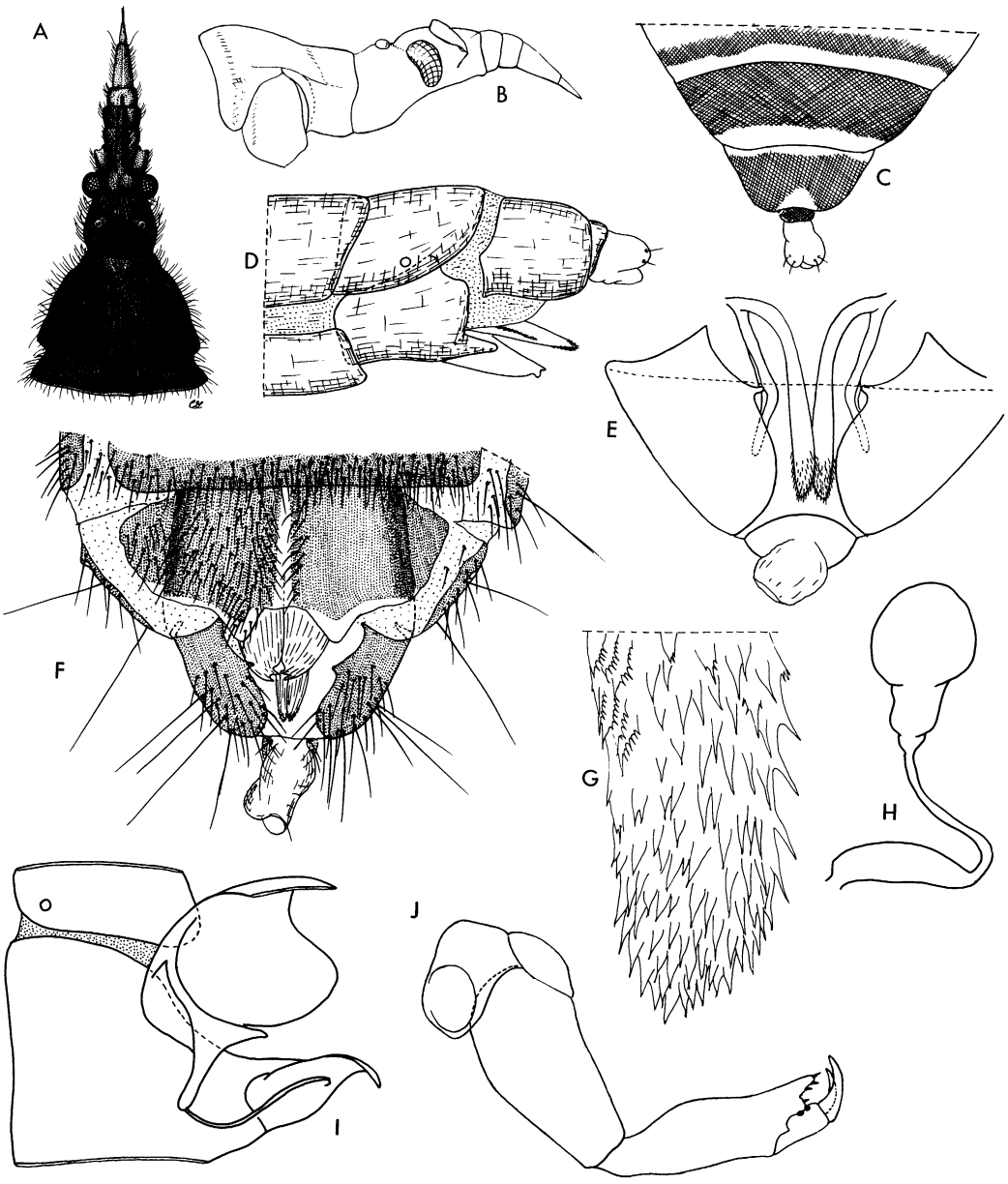


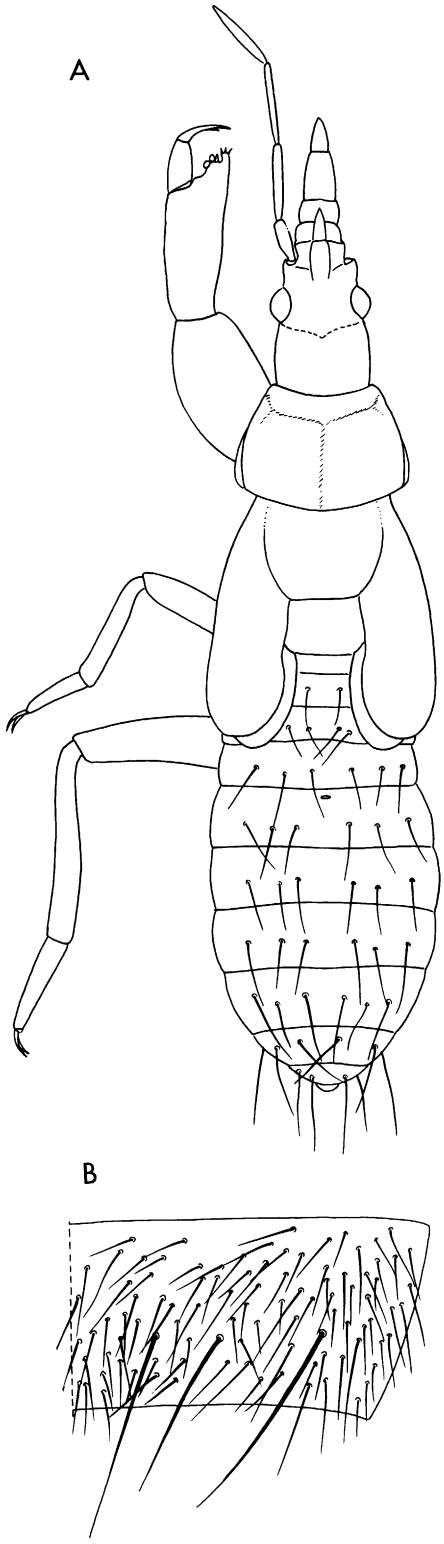
Fig. 36. *Gamostolus subantarcticus*, ♀. **A**. Head and pronotum, dorsal. **B**. Same, lateral. **C**. Apex of abdomen, dorsal. **D**. Same, lateral. **E**. Ninth tergum with second valvulae. **F**. Ventral view of genital area, showing first and second valvula in center. **G**. Detail of apex of second valvulae. **H**. Spermatheca. **I**. Eighth and ninth segments internal view of right side, left side removed. **J**. Foreleg. (A, D, I, and J from Wygodzinsky, 1949)

World Aenictopecheinae have more typical heteropteran metathoracic scent gland auricles located underneath the forewing near its base (see morphology section) and also the paired ventral glands at the thoracico-abdominal junction. Thus the presence, structure, and possible function of the median structure should be reevaluated.

KEY TO SPECIES OF *TORNOCRUSUS*

(The following key contains all species except *aguilari*, known only from a brachypterous female from Guadeloupe, Lesser Antilles.)

1. Male 2
   Female 6
2. Large species, 4.4–4.7 mm in length. Eyes relatively small in dorsal view; ratio eye width to synthlipsis 1:2.4. Pronotum comparatively elongate; ratio length to width 1:1.3. Phallus with a very large, dorsally directed process (figs. 50F, H, I). Color dark brown to piceous ..... *penai*, n. sp.
   Smaller species, 3.8–4.1 mm in length. Eyes slightly larger than above in dorsal view; ratio eye width to synthlipsis 1:2.0–1:2.1. Pronotum wider than above; ratio length to width 1:1.4–1:1.7. Phallus with knob small, or lacking (fig. 48I) 3
3. Parameres roughly triangular (figs. 54C, D). Foretibial spine closest to tarsus (fig. 10; spine "g" of Štys, 1980) with a lateral spur (fig. 53G) ..... *stysi* Kritsky
   Parameres more rhomboid in shape (figs. 48C, D). Fore tibial spine "g" without lateral spur, rounded (fig. 47G) 4
4. Phallus in side view with no dorsal spur or knob (fig. 48I) ..... *occidentalis*, n. sp.
   Phallus in side view with a small to medium-size knob (fig. 46H) 5
5. Phallus in side view with a medium-size, slightly backward-directed knob (fig. 46H). Forewing with m-cu crossvein more basad of cu-pcu (fig. 46C). Legs relatively slender, ratio length to width of both forefemur and foretibia 1:0.32, of hind femur 1:0.14 .... *incaicus*, n. sp.
   Phallus in side view with a small knob (fig. 52D); forewings often with m-cu and cu-pcu crossveins at same level (figs. 51I) ....*sturmi*, n. sp.
6. Large species, 4.6–5.1 mm in length. Color dark brown to piceous. Pronotum relatively long and narrow; ratio length to width 1:1.3. Ocelli fairly close, separated by 2.5–3 times their width 7
   Smaller species, 3.2–4.2 mm in length. Color light to medium brown. Pronotum somewhat wider than above; ratio length to width 1:1.5 to 1:1.7. Ocelli farther apart than above, separated by 3.5 to 4 times their width 8



→

Fig. 37. **A**. *Gamostolus subantarcticus*, 5th instar nymph. **B**. Detail of tergum VI.

TABLE 10
Proportions of *Tornocrusus* Males
(L = length; W = width)

	penai	*occidentalis*	*sturmi*[a]	*incaicus*	*stysi*
Length	4.4–4.7 mm	3.8–4.0	—	4.1	4.0
Head/pronotum	1:1	1:0.8	—	1:0.9	1:0.9
Head L/W across eyes	1:0.8	1:0.8	—	1:0.8	1:0.8
Eye L/anteocular distance	1:0.3	1:0.5	—	1:0.2	1:0.4
Eye W/synthlipsis	1:2.4	1:2.1	—	1:2.1	1:2.0
Hind lobe head L/hind lobe head W	1:2.7	1:3.2	—	1:2.4	1:2.6
Antennal segments I–IV	1:1.7:1.9:1.6	1:1.5:1.7:1.5	—	1:1.9:1.9:1.8	1:1.6:1.7:1.9
Antennal L/head plus pronotum L	1:0.8	1:0.8	—	1:0.8	1:0.8
Mid pronotum W/hind pronotum W	1:1.2	1:1.2	—	1:1.2	1:1.1
Pronotum L/pronotum W	1:1.3	1:1.4	—	1:1.4	1:1.7
L/W forefemur	1:0.43	1:0.43	—	1:0.33	1:0.43
L/W foretibia	1:0.36	1:0.33	—	1:0.33	1:0.37
L/W hind femur	1:0.20	1:0.19	—	1:0.14	1:0.18
No. bristles in foretibial comb	36	32	—	—	—

[a] No measurements. ♂ broken up on slide.

7. Length 5.1 mm. Foretibial bristle comb with 38–40 setae. Eyes in dorsal view large, ratio eye width to synthlipsis 1:3.1. Ocelli separated by three times their width .... *penai*, n. sp.
   Length 4.6 mm. Foretibial bristle comb with approximately 33 setae. Ratio eye width to synthlipsis 1:3.9. Ocelli separated by 2.5 times their width ..... *occidentalis*, n. sp.
8. Very small species, 3.2–3.4 mm. Foretibia with relatively few setae (33–35) in bristle comb. Forewing crossveins "normal" (figs. 45F, 55G) 9
   Medium-size species, 4.2 mm. Foretibia with approximately 40 setae in bristle comb. Forewings sometimes, but not always, with m-cu and cu-pcu crossveins at same level (fig. 51I) .....*sturmi*, n. sp.
9. Eyes, from top, very small; ratio eye width to synthlipis 1:4.4. Outer foretarsal claw one-

TABLE 11
Proportions of *Tornocrusus* Females

	penai	*occidentalis*	*sturmi*	*browni*	*venezolanus*
Length	5.1 mm	4.6	4.2	3.2	3.4
Head L/pronotum L	1:1.1	1.1	1:0.8	1:0.7	1:0.9
Head L/W across eyes	1:0.9	1:0.9	1:0.8	1:0.7	1:0.9
Eye L/anteocular distance	1:0.4	1:0.5	1:0.6	1:0.3	1:0.4
Eye W/synthlipsis	1:3.1	1:3.9	1:4.3	1:4.4	1:3.7
Hind lobe head L/hind lobe head W	1:3.3	1:3.8	1:3.2	1:3.6	1:3.6
Antennal segments I–IV	1:1.5:1.8:1.4	1:1.8:1.8:1.5	1:1.7:1.9:1.7	1:1.7:1.8:1.6	1:1.5:1.7:1.5
Antennal L/head plus pronotum L	1:0.9	1:0.9	1:0.8	1:0.9	1:0.8
Mid pronotum W/hind pronotum W	1:1.2	1:1.2	1:1.2	1:1.1	1:1.1
Pronotum L/pronotum W	1:1.3	1:1.3	1:1.5	1:1.7	1:1.5
L/W forefemur	1:0.50	1:0.50	1:0.43	1:0.53	1:0.56
L/W foretibia	1:0.40	1:0.34	1:0.33	1:0.40	1:0.33
L/W hind femur	1:0.24	1:0.23	1:0.21	1:0.26	1:0.26
No. bristles in foretibial comb	38–40	33	40	35	33

Fig. 38. Distribution of *Tornocrusus*. Described species (●). Undescribed (■).

third length of inner claw. Approximately 35 setae in foretibial bristle comb. Color medium to dark brown ..... *browni*, n. sp.

Ratio eye width to synthlipsis 1:3.7. Outer foretarsal claw one-half length of inner claw. Approximately 33 setae in bristle comb. Color light to medium brown .... *venezolanus*, n. sp.

Tornocrusus aguilari (Villiers), new combination
Figures 38, 44

Lomagostus aguilari Villiers, 1978: 727.

DISTRIBUTION: Known only from Guadeloupe, Lesser Antilles.

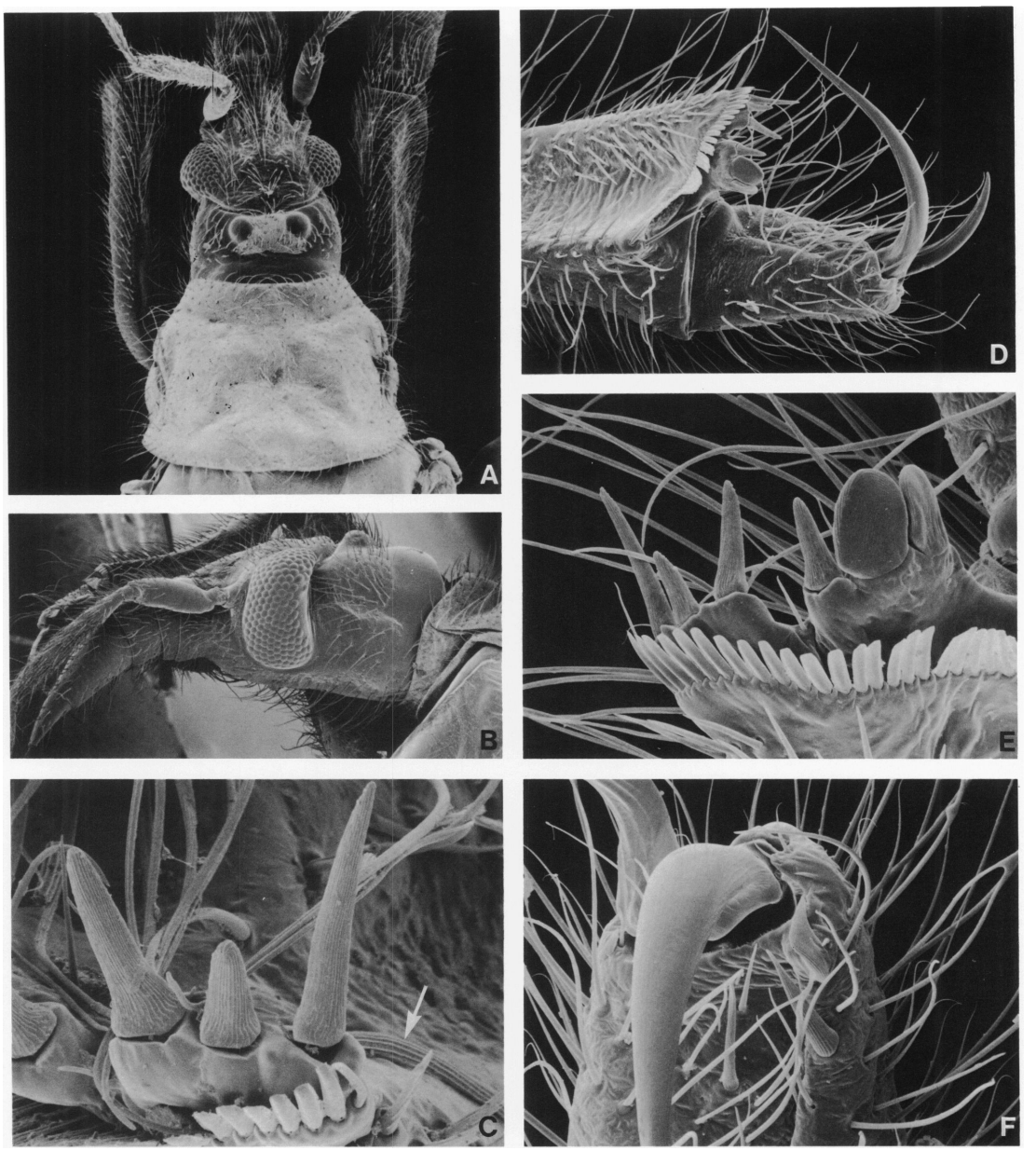


Fig. 39. *Tornocrusus penai*, ♂. **A**. Head and pronotum, dorsal. **B**. Head, lateral. **C**. Detail of outer three foretibial spines, and also spine "a" (arrow). **D**. Apex of foreleg, inner view. **E**. Foretibial spines. **F**. Foretarsal spines.

DIAGNOSIS: *T. aguilari* is the smallest member of the genus at 2.6 mm in length. It is known only from one adult, a brachypterous female (which was erroneously listed as a male in the original description), the proportions of which follow.

ADDITION TO DESCRIPTION: Length 2.6 mm. General body color pale brown, fairly unicolorous, with exception of slightly darker head. Head, legs, antennae, and abdomen shiny; pronotum, rest of thorax, and wings matte. Eyes small, red. Ocelli present, red, separated by 4.3 times their width. Wing bases and intersegmental membranes of abdomen red. Abdomen well sclerotized.

Ratio head length to maximum length of

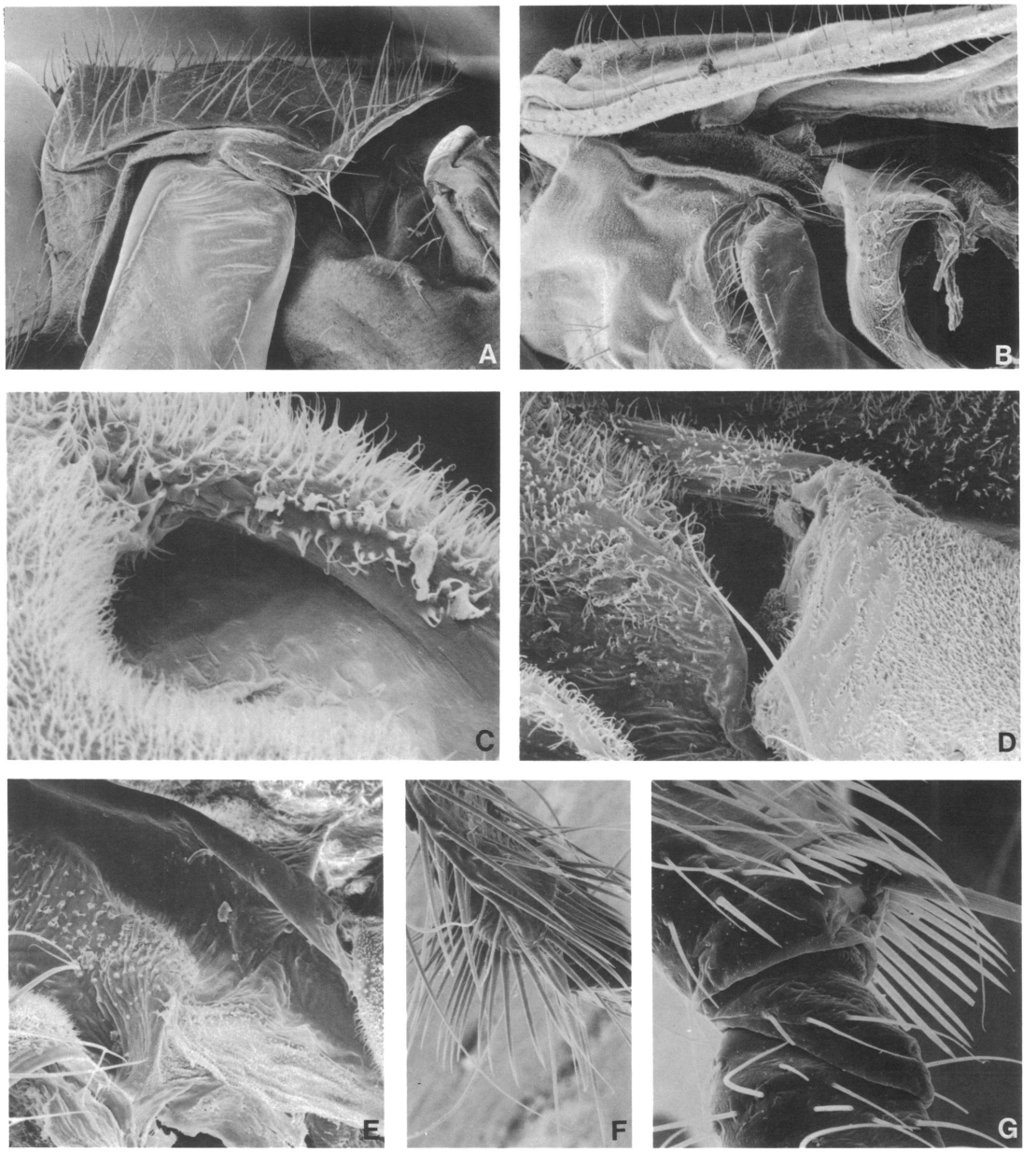


Fig. 40. *Tornocrusus penai*, ♂. **A**, **B**. Lateral views of left prothorax, and meso- and metathorax, respectively. **C**. Close-up of depression corresponding to internal apodeme. **D**. Metathoracic spiracle. **E**. Hind wing coupling groove also forming part of hind acetabulum. **F** and **G**. Continuous hind tibial bristle comb and spine, outer and inner views.

pronotum 1:0.9. Ratio head length to width across eyes 1:0.8. Ratio eye length to anteocular distance 1:0.9; ratio eye width to synthlipsis 1:3.8. Ratio length to width of hind lobe of head 1:3.5. Antenna longer than head plus pronotum (1:0.8); ratio segments I–IV 1: 1.4: 1.6: 1.4.

Ratio width of mid to hind lobe of pronotum 1:1.1.

Ratio length to width of forefemur 1:0.53. Ratio length to width of foretibia 1:0.33. Ratio length to width of hind femur 1:0.25.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, LESSER ANTILLES:

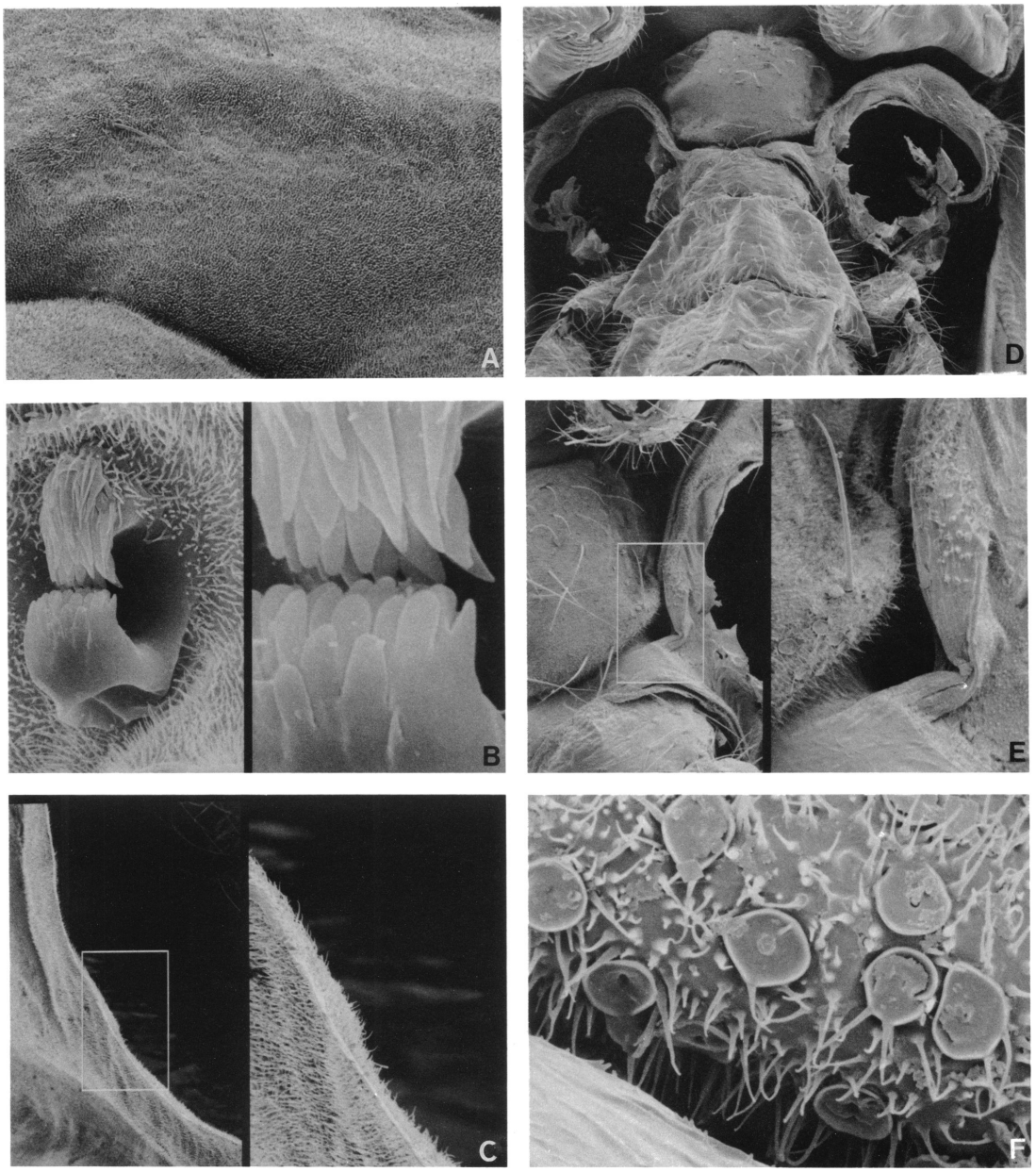


Fig. 41. *Tornocrusus penai*, ♂. **A**. Forewing surface. **B**. Forewing coupling mechanism. **C**. Hind wing edge at level of wing coupling mechanism. **D**. Thoracicoabdominal junction, ventral. **E**. Details of above, showing orifices of thoracicoabdominal scent glands. **F**. Cuticular structures on wall of above.

Guadeloupe Island: La Soufriere, Les Marmites, under stony sulfur deposits, August 15, 1960 (J. d'Aguilar; MNHN); examined.

MATERIAL EXAMINED: Holotype, above.

DISCUSSION: It is with a very slight element of doubt that we move this species from the genus *Lomagostus* to *Tornocrusus*. Thanks to the kindness of Dr. J. Carayon, we have been able to examine the holotype. However, since it is a unique specimen we did not wish to dissect it, and limited our observations to those that could be made under a low-pow-

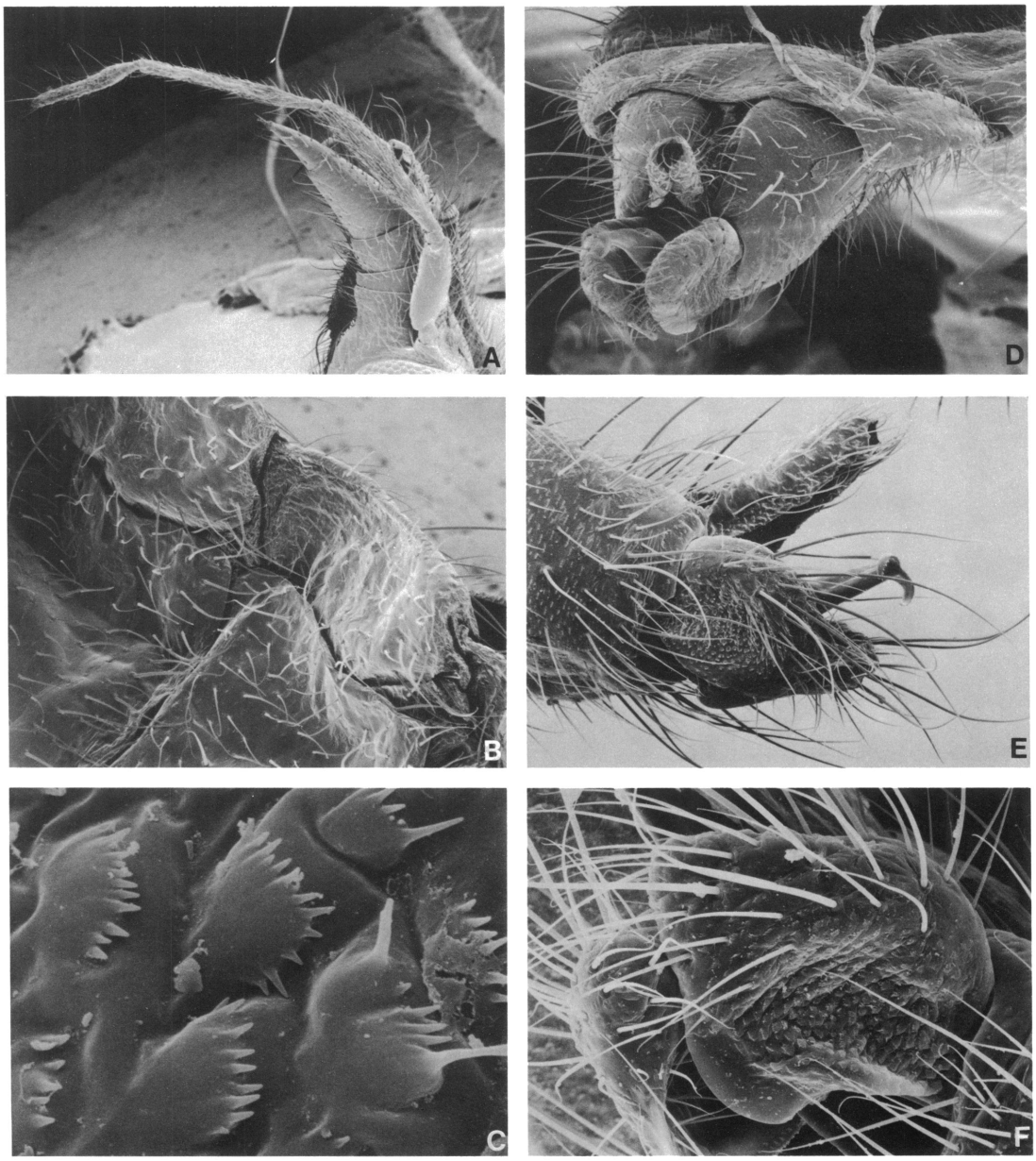


Fig. 42. *Tornocrusus penai*, ♂. **A**. Antenna and rostrum. **B**. Ventral abdominal segments IV and V and corresponding ventral connexival plates. **C**. Detail of cuticular structures on outer surface of paramere. **D**. Genitalia, oblique posterior view. **E**. Genitalia, lateral. **F**. Outer surface of paramere.

ered dissecting microscope. The specimen is definitely a female. Figure 44E is a sketch of the apex of the abdomen.

Our generic determination is made primarily on the basis of foretibial spination (fig. 44D) which is identical to that of other *Tornocrusus* species. Foretarsal spines were not visible enough to be useful.

Placement is slightly uncertain for several reasons. The specimen is a brachypterous female, the first of that wing morph known from the genus *Tornocrusus*. It is possible

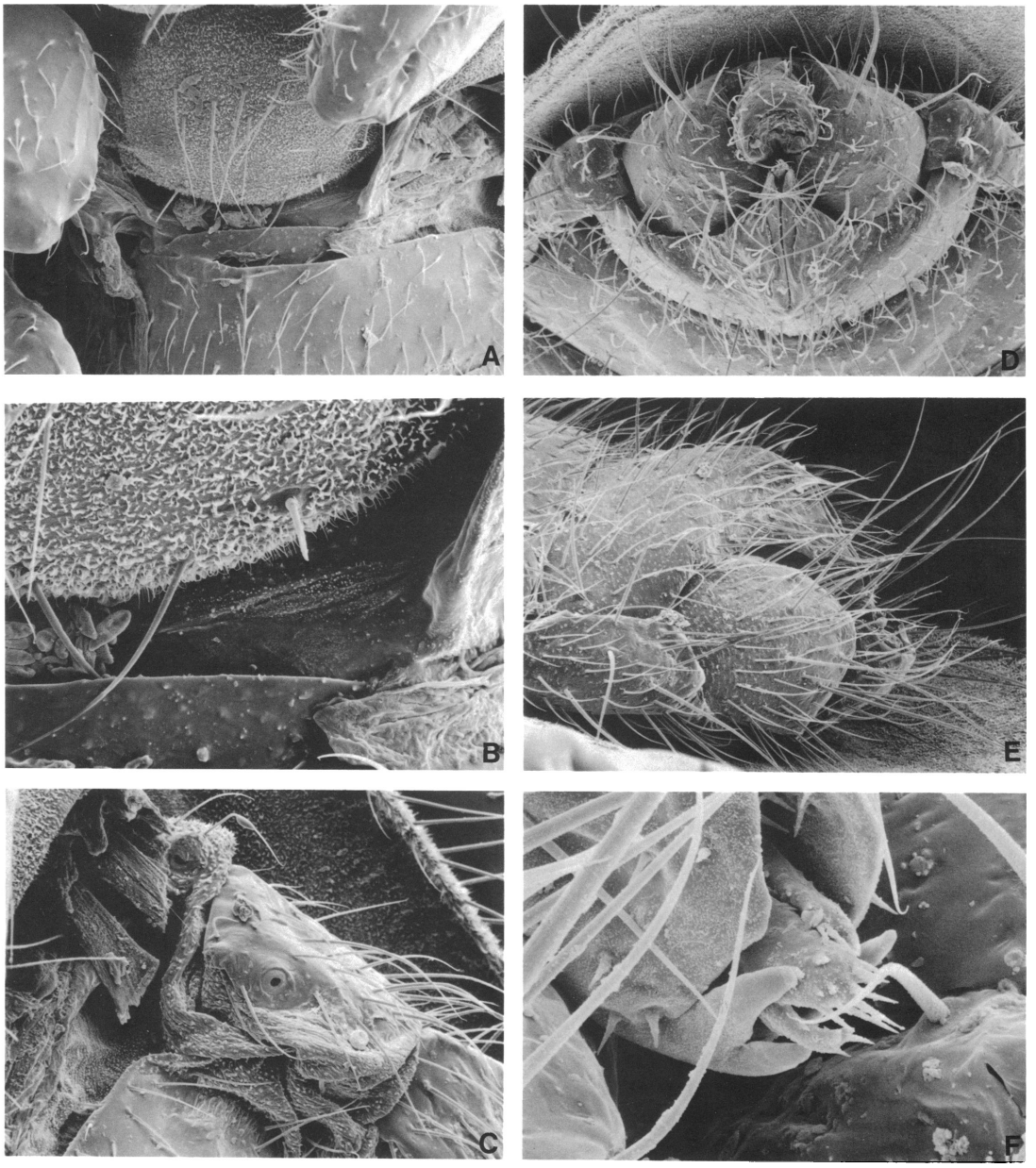


Fig. 43. *Tornocrusus sturmi*, ♀. **A**. Thoracicoabdominal junction, ventral, showing left and right scent gland orifices. **B**. Close-up of left (on right side of photo A) thoracicoabdominal scent gland orifice. **C**. Ventral connexival plate II and spiracle. **D–F**. Genitalia. **D**. Posterior view, showing rods of first valvulae. **E**. Lateral view. **F**. Apices of first valvulae enclosing second valvulae.

that many proportions used in determination of the genus are severely altered, especially those relating to eye size and pronotal shape. Also, due to the sex, we could not compare the more informative male genitalic structures with those of its congeners.

Another factor contributing to our uncertainty is the apparent lack of a basal cell in the forewing, a distinguishing character of *Tornocrusus*. *Lomagostus* lacks the basal cell. However, many of the veins in the small forewing were extremely faint and generally poor-

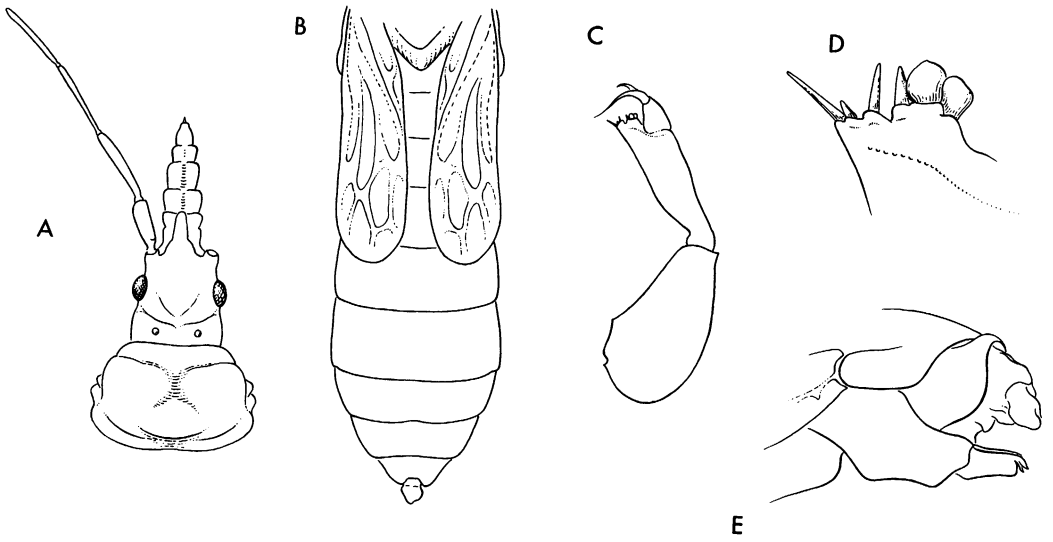


Fig. 44. *Tornocrusus aguilari*, ♀ (holotype). **A**. Dorsal view of head and pronotum. **B**. Dorsal view of brachypterous wings and abdomen. **C**. Foreleg. **D**. Apex of foretibia, inner view. **E**. Lateral view of ♀ genital region.

ly developed. We would hesitate to give much weight to this character at present, since we could not observe the wing under a compound microscope, and do not have a more typical macropterous specimen.

The type species of *Lomagostus* is from Madagascar. Although Madagascar-Caribbean distributions are not unknown, it is improbable that this is the case here, based on the morphological similarities to *Tornocrusus* (especially foretibial spines). Geographically, the closest species of *Tornocrusus* occurs in northern Venezuela, not far from Guadeloupe Island.

Tornocrusus browni, new species
Figures 38, 45

DISTRIBUTION: Brazil; Estado São Paulo.

DIAGNOSIS: *Tornocrusus browni* females can best be distinguished from their congeners by their small size (3.2 mm), and proportions, including: short, wide pronotum (ratio length to width 1:1.7); small eyes (ratio eye width to synthlipsis 1:4.4); ocelli separated by four times their width. They can also be distinguished by the relatively small number of setae in the foretibial bristle combs (35).

DESCRIPTION: Males unknown. Length of female 3.2 mm. General body color medium to dark brown. Head, pronotum, scutellum, remainder of thorax, and abdomen darkest; all appendages and wings lighter. Eyes and forewing bases slightly tinged with red; ocelli ringed with red. Setiferous tubercles and cuticular granules absent. Thorax and wings beset with microtrichiae, giving an overall matte appearance. All other body parts shiny.

Head longer than pronotum (1:0.7). Ratio head length to width across eyes 1:0.7. Ratio length of eyes to anteocular distance 1:0.3. Eyes very small; ratio eye width to synthlipsis 1:4.4. Ratio length to width of hind lobe of head 1:3.6. Eyes in side view remote from levels of both top and bottom of head. Beneath head, distance between eyes slightly greater than 1.5 times eye length. Ocelli separated by 3.5–4.0 times their width. Antennae slightly longer than head plus pronotum (1:0.9). Proportions of segments I–IV 1:1.7:1.8:1.6. Rostrum as in figure 45B.

Pronotum much wider than long; ratio length to width 1:1.7. Ratio width of mid to hind lobes 1:1.1. Scutellum and remainder of thorax as in generic description.

Fore and hind wings fully developed; forewings 2.2 mm in length. Setae sparse, most numerous basally and around costal edge of wing, very sparse on veins, and absent from cell lumens. Hind wings not setose apically.

Abdomen well sclerotized. Segmentation and genitalia as in generic description.

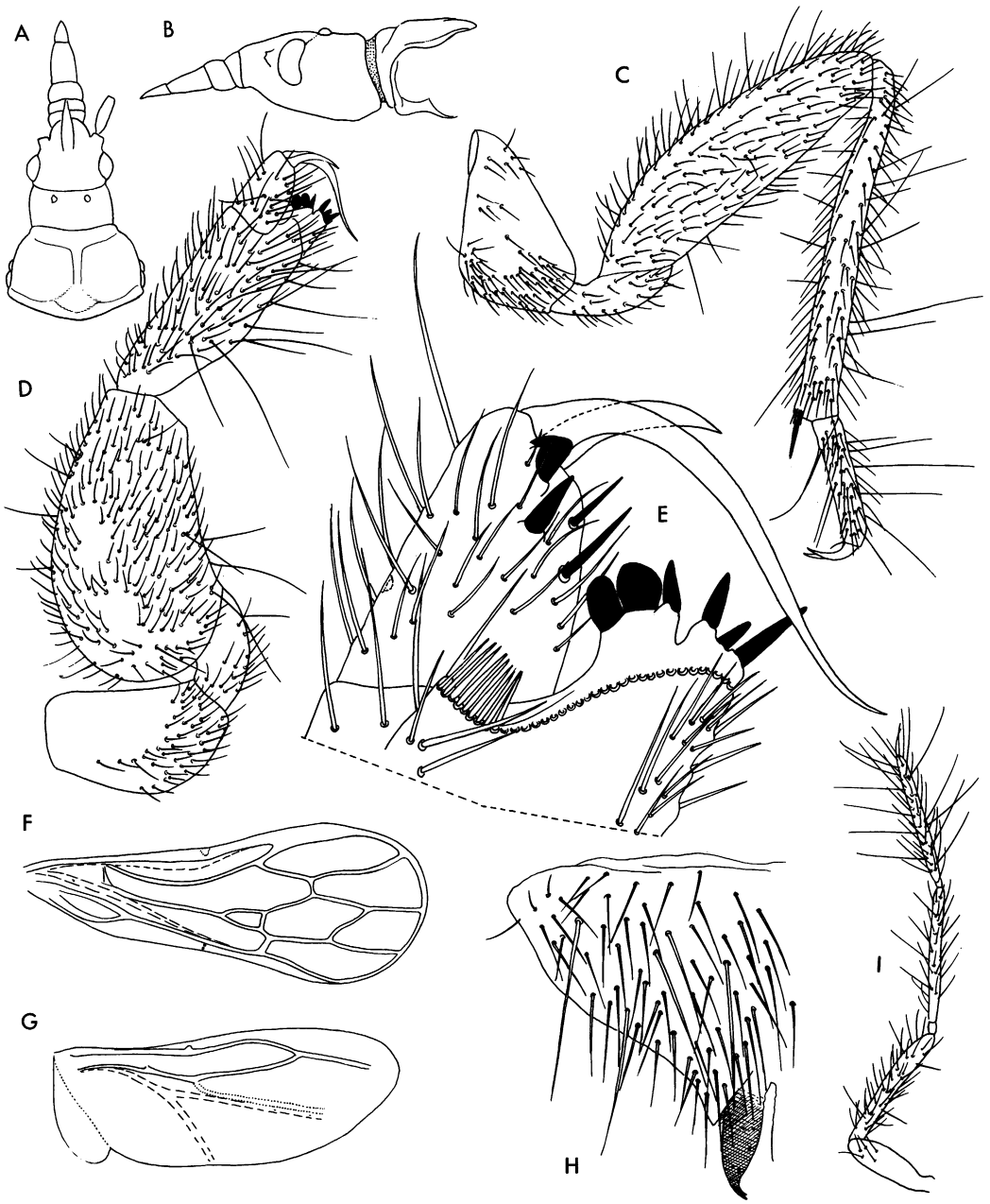


Fig. 45. *Tornocrusus browni*, ♀. **A**. Dorsal view of head and pronotum. **B**. Lateral view of head and pronotum. **C**. Hind leg. **D**. Foreleg, outer view. **E**. Apex of foreleg, inner view. **F**. Forewing. **G**. Hind wing. **H**. Eighth sternum (right side) with first valvula. **I**. Antenna.

Forelegs stout. Ratio length to width of forefemur 1:0.53. Inner surface of article without cuticular granules. Ratio length to width of foretibia 1:0.40. Bristle comb consisting of 35 (±) setae. Tibial and tarsal spines as in generic description. Outer tarsal claw comparatively short, one-third length of inner claw. Ratio length to width of hind femur 1: 0.26. Trichobothria present on femora, tibiae, and tarsi of all legs (figs. 45C, D).

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRAZIL: Estado São Paulo: Jardim Botanico (Agua Funda), wet forest, February, 1967 (W. L. Brown; AMNH).

OTHER MATERIAL EXAMINED: BRAZIL: same data as holotype (AMNH), 1♀ paratype (wings and legs on slide, remainder in alcohol); Estacão Biol. Boraceia, Mun., Salesopolis, wet forest, 850 m, May 24–28, 1971 (W. L. and D. E. Brown; AMNH), 1♀, 2 nymphs.

ETYMOLOGY: *Tornocrusus browni* is named for its collector Dr. W. L. Brown.

DISCUSSION: Females of this genus are difficult to distinguish from one another. The female from Salesopolis is considerably lighter in color than the holotype, but quite similar in all other respects, especially proportions. In case associated males of this species are subsequently found, and they prove to be of more than one species, the above description is based on the holotype, with details of the foreleg taken from the slide of the paratype. Information from the Salesopolis specimen is not included.

Tornocrusus incaicus, new species
Figures 38, 46

DISTRIBUTION: Peru.

DIAGNOSIS: *Tornocrusus incaicus* males (females unknown) can be distinguished from their congeners by the shape of the phallus in side view, which has a backward-directed, medium-size dorsal process.

DESCRIPTION: Length of male 4.1 mm. General body color dark brown. Pronotum, scutellum, remainder of thorax and wings with a matte surface. All other body parts shiny. Eyes, ocelli, forewing bases, and intersegmental membranes of abdomen tinged with red. Head, rostrum, and abdomen dark brown; legs and antennae slightly lighter.

Ratio head length to pronotum length 1:0.9. Ratio head length to width across eyes 1:0.8. Ratio eye length to anteocular distance 1:0.2; ratio eye width to synthlipsis 1:2.1. Ratio hind lobe head length to hind lobe head width 1:2.4. Ocelli separated by 2 times their width. Antennae longer than head plus pronotum (1:0.8). Ratio segments I–IV 1:1.9:1.9:1.8.

Pronotum as in figure 46A. Ratio width of mid to hind pronotal lobes 1:1.2. Pronotum of moderate width; ratio length to width 1:1.4.

Male genitalia as in figures 46F, G–M. Parameres roughly rhomboid (fig. 46J). Phallus T-shaped (figs. 46I, K) with a large opening in its central part (fig. 46I), the edge (in side view) forming a medium-size, slightly backward-directed process (fig. 46H).

Legs slender. Ratio length to width of both forefemur and tibia 1:0.33. Foretibial and tarsal spines as in figure 46D. Outer claw of foretarsus long, ⅝ length of inner claw. Ratio length to width of hind femur 1:0.14.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, PERU: Cuzco Dept.: Machu Picchu, November 30, 1965 (H. and M. Townes; UMMZ).

ETYMOLOGY: Named after the Inca Indians of Peru.

Tornocrusus occidentalis, new species
Figures 38, 47, 48

DISTRIBUTION: Colombia.

DIAGNOSIS: *Tornocrusus occidentalis* can be distinguished by the unique shape of the male genitalia and the body proportions below.

DESCRIPTION: Length of male 3.8–4.0 mm, of female 4.6 mm. General body color dark brown. Antennae, head, rostrum, legs, and abdomen shiny brown with a yellowish tinge; legs, antennae and rostrum frequently lighter than head. Pronotum, scutellum, underside of thorax, and wings dark brown with a more reddish tinge than foregoing and also with a dull matte surface sharply contrasting with shine of head and legs. Abdomen shiny dark brown and fully sclerotized. Eyes, ocelli, wing bases, and stigmal areas frequently tinged with red. Setae slender and simple, longest and most numerous on legs, antennae, rostrum, and abdomen; short and sparse on head, thorax, and wings.

Sexual dimorphism not pronounced except in structures of terminalia; males and females differing most in the slightly larger size, stouter leg proportions, and slightly smaller eyes of the female. Ratio head length to pronotum length 1:0.8 in males, 1:1 in female (we were

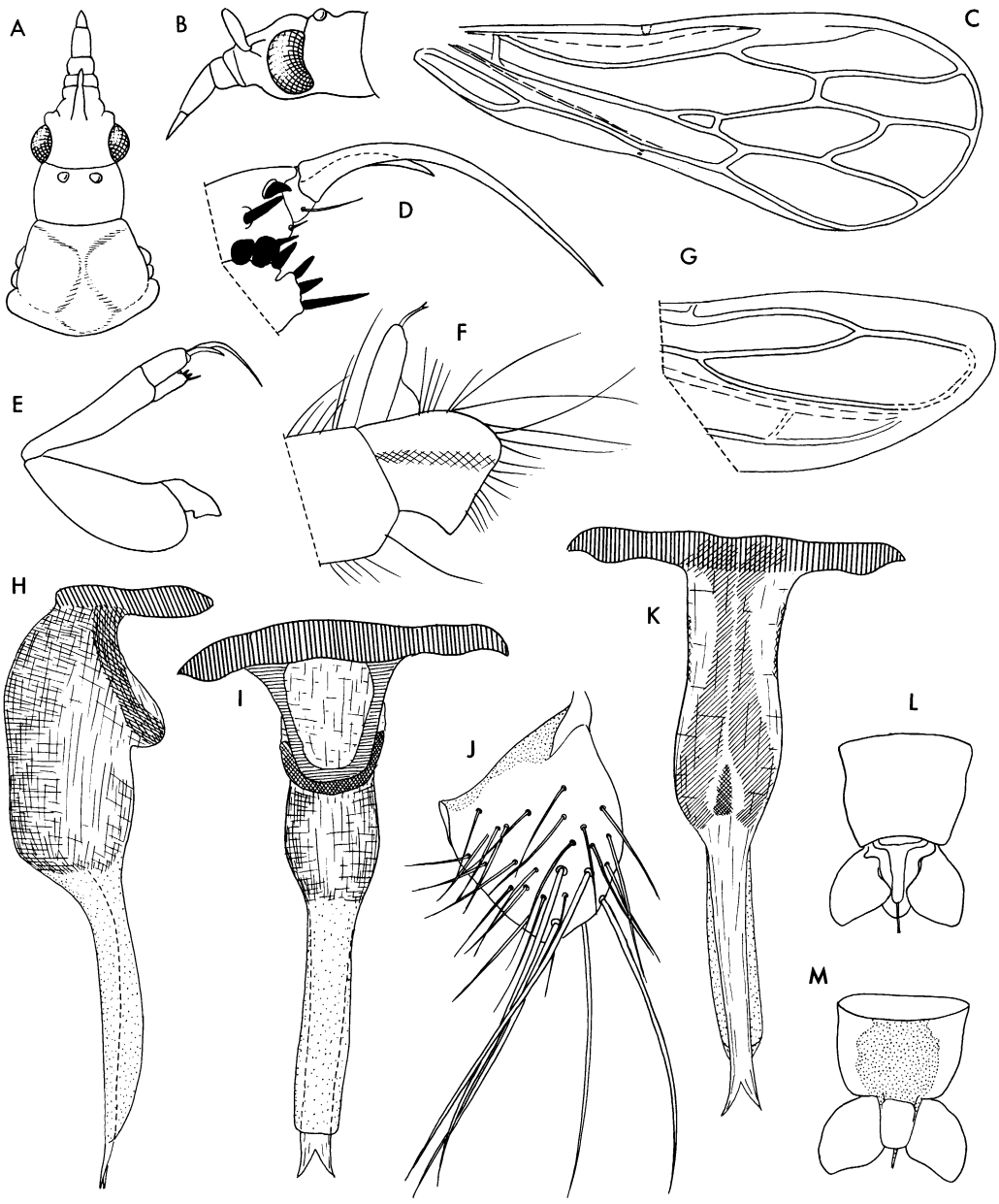


Fig. 46. *Tornocrusus incaicus*, ♂. **A**. Head and pronotum, dorsal. **B**. Lateral view of head. **C**. Forewing. **D**. Apex of foreleg, inner view. **E**. Foreleg. **F**. Lateral view of genital region. **G**. Apical half of hind wing. **H**. Phallus, lateral. **I**. Phallus, dorsal. **J**. Paramere. **K**. Phallus, ventral. **L**. Pygophore, ventral. **M**. Same dorsal.

able to measure only one female). Ratio head length to width across eyes 1:0.8 in males, 1: 0.9 in female. Ratio length of eyes to anteocular distance 1:0.5 in both sexes; ratio eye width to synthlipsis 1:2.1 in males, 1:3.9 in female. Ocelli situated toward center of head and separated by 1.5 times their own diameter in males, 2.5 times in female. Antennae

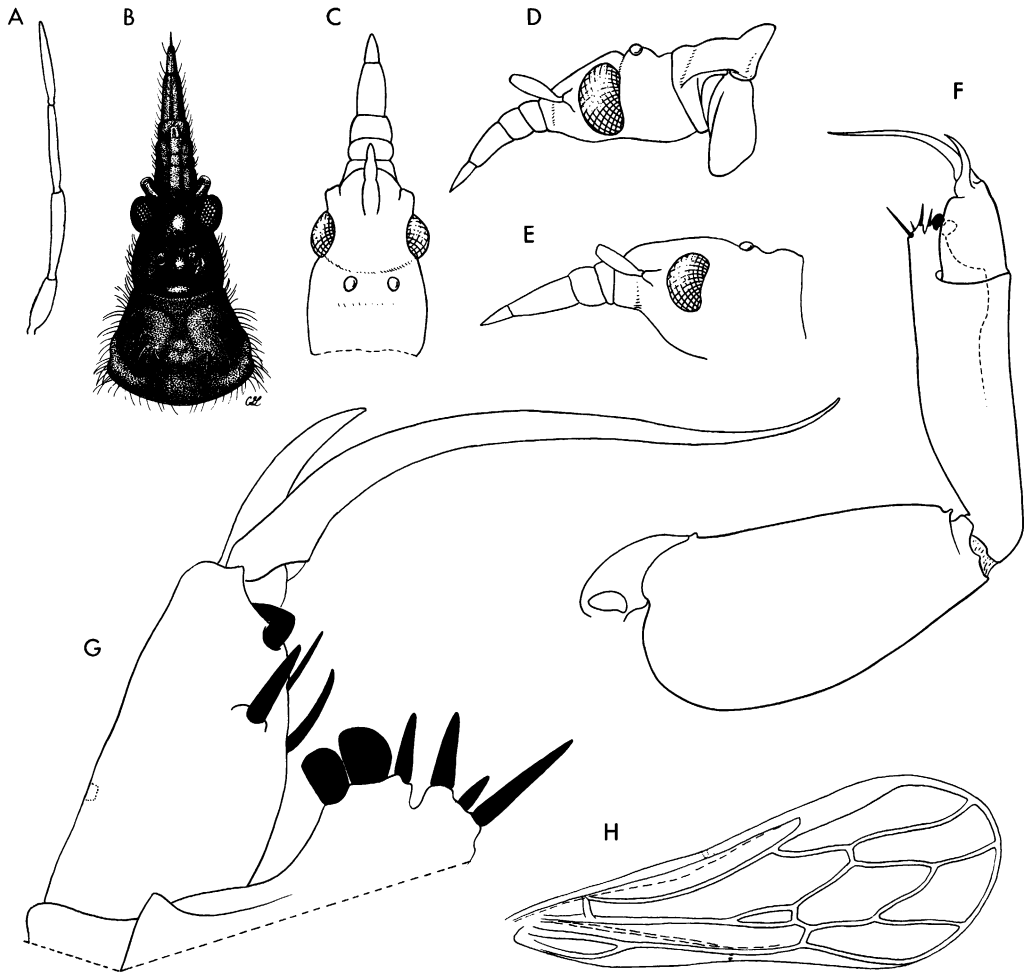


Fig. 47. *Tornocrusus occidentalis*. **A**. Antenna. **B**. Head and pronotum, ♂, dorsal. **C**. Head, ♀, dorsal. **D**. Lateral view of head and pronotum, ♂. **E**. Head, lateral, ♀. **F**. Foreleg, outer view, ♂. **G**. Apex of foreleg, inner view, ♂. **H**. Forewing.

longer than head plus pronotum (1:0.8 in males, 1:0.9 in female). Last three segments subequal in length; proportions of segments I–IV 1:1.5:1.7:1.5 in males, 1:1.8:1.8:1.5 in female. Rostrum as in figures 47D, E.

Pronotum as in generic description. Ratio width of mid to hind lobes 1:1.2 in both sexes. Proepimera and proepisterna reduced, but visible from above.

Fore and hind wings fully developed in both sexes. Lumens of cells without setae.

Abdomen as in generic description. Male genitalia with parameres roughly rhomboid (figs. 48A–F). Posteroventral edge nearly straight, lower corner spur-shaped (sometimes obscured by membrane); anteroventral edge with a central point (figs. 48C, D). Phallus T-shaped in dorsal or ventral view (figs. 48G, H). Basal half of trunk of T expanded and well sclerotized; apical half less sclerotized with a bifurcating tip. Phallus in side view with a large well-developed ventral keel along basal half of trunk (fig. 48I), but with no dorsal knob. Female genitalia as in generic description.

Forelegs as in generic description. Ratio length to width of forefemur 1:0.43 in males, 1:0.50 in female. Cuticular granules absent

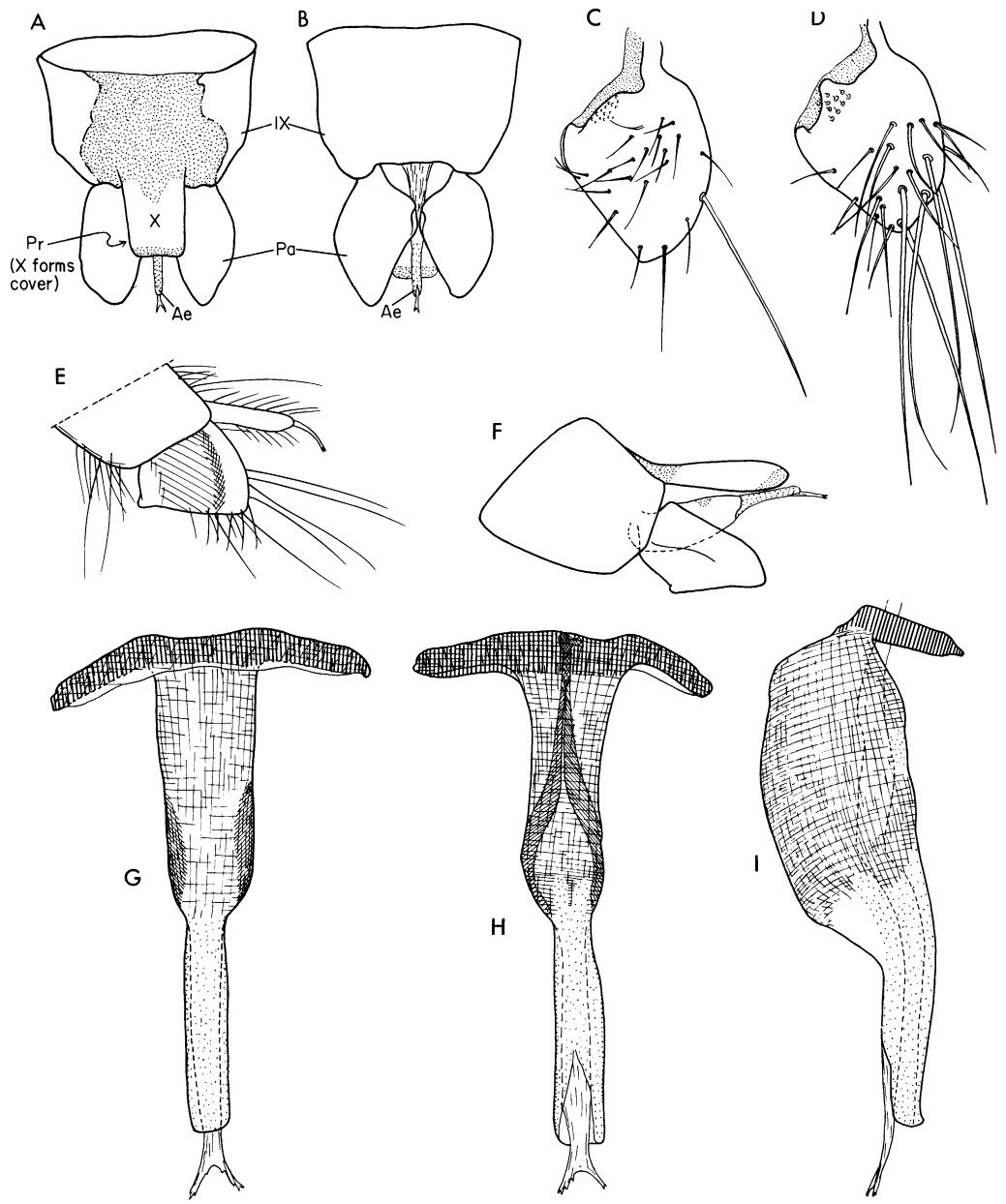


Fig. 48. *Tornocrusus occidentalis*, ♂. **A**. Genital region, dorsal. **B**. Genital region, ventral. **C**. Paramere, dorsal. **D**. Paramere, ventral. **E**, **F**. Lateral views of genital region. **G**. Phallus, dorsal. **H**. Phallus, ventral. **I**. Phallus, lateral.

from forefemur, but a few minute multipointed tubercles barely visible on inner surface. Ratio length to width of foretibia 1:0.33 in males, 1:0.34 in female. Foreleg spines as in figure 47G. Foretibial bristle comb with 32–33 setae. Outer claw of foretarsus one-third length of inner claw. Ratio length to width of hind femur 1:0.19 in males, 1:0.23 in female.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, COLOMBIA: Valle: 13 mi W of Cali, March 20, 1955 (E. I. Schlinger and E. S. Ross; CAS).

PARATYPES: Same data as holotype, 2♂, 1♀ (CAS); 1♂ (AMNH).

ETYMOLOGY: From the Latin, meaning "of the West."

Tornocrusus penai, new species

Figures 38, 39–42, 49, 50

DISTRIBUTION: Ecuador.

DIAGNOSIS: *Tornocrusus penai* males can be distinguished from their congeners by their large size; by the nearly rhomboid shape of the parameres, which have their posteromedial edges convex; by the phallus viewed laterally, which has a large dorsally directed central process. Females can be distinguished by their large size and their proportions as listed below.

DESCRIPTION: (Since we have only one female specimen, our description of females of this species is less detailed and reliable than that of the males.)

Length of males 4.4–4.8 mm, of female 5.1 mm. General body color very dark brown to piceous. Head, pronotum, forefemur, antennae, and rostrum piceous; rostrum (and sometimes antennae) with terminal article darker than remainder. Foretibia and tarsus vary from mottled medium and dark brown to entirely piceous. Mid- and hind legs and wings lighter brown. Slight tinge of red on some or all of the following: claws of forelegs, base of antennae, eyes, ocelli, wing bases, and abdominal membranes. Setae sparse on pronotum, scutellum, and wings; of medium length and more numerous on legs, antennae, rostrum, and sides of head. Setiferous tubercles absent with exception of four or five slightly swollen bases of trichobothria on forefemur. All body parts except thorax and wings shiny, usually with a slightly granular texture; entire thorax both dorsally and ventrally with a dull velvety texture. Wings varying from dull matte surface to slightly shiny; membrane translucent, veins slightly darker brown.

Female stouter than male.

Head length nearly equal to pronotum length, 1:1 in males, 1:1.1 in female. Ratio head length to head width across eyes 1:0.8 in males, 1:0.9 in female. Eyes slightly smaller in female (side view). Ratio eye length to anteocular distance 1:0.3 in males, 1:0.4 in female; ratio eye width to synthlipsis 1:2.4 in males, 1:3.1 in female. Ratio length to width of hind lobe of head 1:2.7 in males, 1:3.3 in female. Eyes in side view not approximating top or bottom of head in either sex, although more closely approaching lower border in males. Eyes from below not nearly touching, approximately one eye length apart in males, 1½ in female. Ocelli situated toward center of head in males, separated by about twice their width. In females, ocelli farther apart, about three times their width. Rostrum as in figures 39B, 49A and C.

Antenna slightly longer than head plus pronotum, 1:0.8 in males, 1:0.9 in female. Proportions of segments I–IV 1:1.7:1.9:1.6 in males, 1:1.5:1.8:1.4 in female. Setae of two lengths, longer setae sparser, standing out from segment nearly at right angles, and not present on segment I. Shorter setae more closely adpressed to body of antenna and present on all articles.

Pronotum weakly three-lobed, unarmed. Sides diverging caudad only slightly. Forelobe in form of broad collar demarcated posteriorly by 1 + 1 sulci, which are distinct laterally, but obsolescent medially, leaving a central bridge extending well back into the midlobe. Midlobe with a central callosity, in some specimens containing a deep concavity (probably due to drying and shrinkage), in others wholly convex. Central callosity obscuring division between mid and hind lobes, but with 1 + 1 shallow sulci laterally, making division more obvious. Hind lobe very short. Ratio width of mid to hind lobes of pronotum 1:1.2 in both sexes.

Surface of scutellum convex, smooth, and relatively featureless in well-preserved specimens, but frequently asymmetrically wrinkled in poorly preserved material.

Proepimeron and proepisternum reduced, forming a narrow band aligned with the edge of the pronotum and leaving an extremely large, posteriorly open acetabula. Forecoxae extremely large.

Fore and hind wings fully developed in both sexes. Forewings 3.4–3.7 mm in length with

normal veins and setae as in figures 49A, I. Eighteen percent of forewings in specimens studied with abnormal venation (19 out of 107 wings). Setae sparse, most numerous on wing margins, costa and wing bases; setae simple and of medium length. Costal fracture occurring at level of base of basal cell. Wing coupling mechanism as in figure 41B.

Hind wings approximately two-thirds length of forewings. Hind wings not setose apically, but may bear large microtrichiae. Veins as in figure 49F. Cubital furrow (after Štys, 1980), transparent, branching, not quite attaining edge of wing in both branches. Posteriorly, a faint vein (possibly the postcubitus) extending from wing base and intersecting apically with posterior branch of cubital furrow. Both anal veins represented as slight thickenings at wing base.

Abdomen well sclerotized in both sexes and heavily beset with setae. Connexival plates not divided into dorsal and ventral rows, and not clearly separable from tergites except by their flexion in nondistended state. Sternites separate from connexival plates I–VIII, although the demarcations often difficult to see (they are most visible in specimens in alcohol). Spiracles on ventral side of connexival plates I–VIII or possibly in intersegmental membranes (not always distinguishable).

In male, segment VIII entire, normally developed. Segment IX, the pygophore, large, only slightly invaginated into eighth segment. Dorsal surface membranous, with rudiments of dorsal bridge appearing as sclerotized lateral arms extending towards one another, but not connecting (fig. 50B). Parameres subrhomboid with posterolateral and posteromedial edges convex (figs. 50J, L). Phallus T-shaped, characterized by a central, dorsally projecting spur quite prominent in side view (figs. 50F, H, I). Tip of phallus bifid.

Female genitalia as in generic description.

Forelegs stout. Ratio length to width of forefemur 1:0.43 in males, 1:0.50 in female. Inner surface of forefemur without cuticular granules, although sometimes with four or five trichobothrial insertions slightly enlarged. Ratio length to width of foretibia 1: 0.36 in males, 1:0.40 in female. Foretibia sculptured, three-dimensional apically, with a dorsally directed ridge along apical half (fig. 39D); tibial spines as in figure 39E. Foretibial bristle comb with approximately 36 setae in males, 38–40 in female. Foretarsus with four spines as in figure 39F; inner claw long and slender, outer claw half as long. Mid legs as in generic description. Hind legs of male as in figures 40F, G, 50C; ratio length to width of hind femur 1:0.20 in males, 1:0.24 in female.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, ECUADOR: Napo-Pastaza: Sebundoy (0°30'N: 77°30'W), between Santa Barbara and La Bonita, 2600 m, September 11–15, 1977 (L. E. Peña; AMNH).

PARATYPES: same data as holotype, 71♂ pinned (some used for SEM observation), 1♀ pinned, 46♂ in alcohol (AMNH).

ETYMOLOGY: This species is named for Mr. Luis E. Peña, the collector.

DISCUSSION: We have also seen a group of eight closely related specimens from Ecuador (E of Papallacta, between Quito and Baeza, 2900 m, January 15, 1977, collector unknown), which vary somewhat from the above. They are lighter brown and their phalli lack the prominent central dorsal projection.

Tornocrusus sturmi, new species

Figures 38, 43, 51, 52

DISTRIBUTION: Colombian cordillera.

DIAGNOSIS: *T. sturmi* can be distinguished from its congeners by the shape of the phallus in side view, which bears a small knob; by the shape of the parameres, which are slightly more triangular than those of other species; and by the proportions described below. Many specimens also have a characteristic forewing vein configuration. The m-cu and cu-pcu crossveins are often at the same level (fig. 51I).

DESCRIPTION: (All of the following measurements and proportions are from the female holotype, which is pinned. The single male specimen is slide mounted in many pieces and is impossible to measure.)

Length 4.2 mm. General body color medium brown. Head and thorax slightly darker than abdomen and appendages. Eyes, ocelli, forewing bases, and intersegmental membranes of abdominal tergum tinged with red. Entire prothorax, central disk of scutellum, remainder of meso- and metathorax, and wing

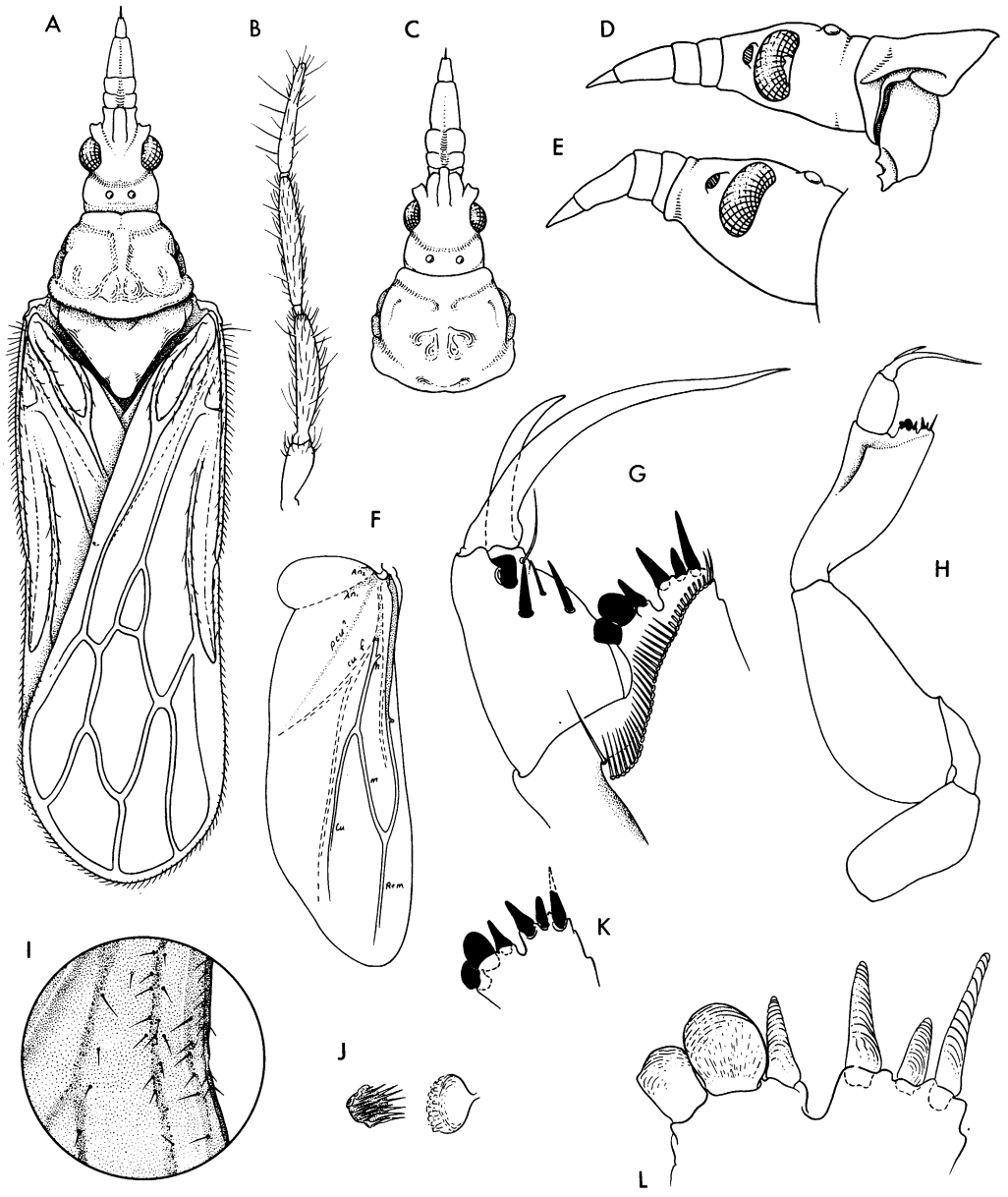


Fig. 49. *Tornocrusus penai*. **A**. Dorsal view, ♂. **B**. Antenna. **C**. Dorsal view of head and pronotum, ♀. **D**, **E**. Lateral views of head and pronotum, ♂ and ♀, respectively. **F**. Hind wing. **G**. Apex of foreleg, inner view. **H**. Foreleg, inner view. **I**. Detail of forewing at level of costal fracture. **J**. Wing coupling mechanism. **K**, **L**. Foretibial spines, outer and inner views, respectively.

surfaces beset with microtrichiae, giving their surfaces a matte texture. Forewing membranes light dusky brown; veins lighter yellow-brown. Cuticular granules and setiferous tubercles absent from all body parts and legs. Trichobothria present on all legs as in generic description, their bases very slightly expanded.

Head longer than pronotum (1:0.8). Ratio head length to width across eyes 1:0.8. Ratio eye length to anteocular distance 1:0.6; ratio eye width to synthlipsis 1:4.3. Ratio length

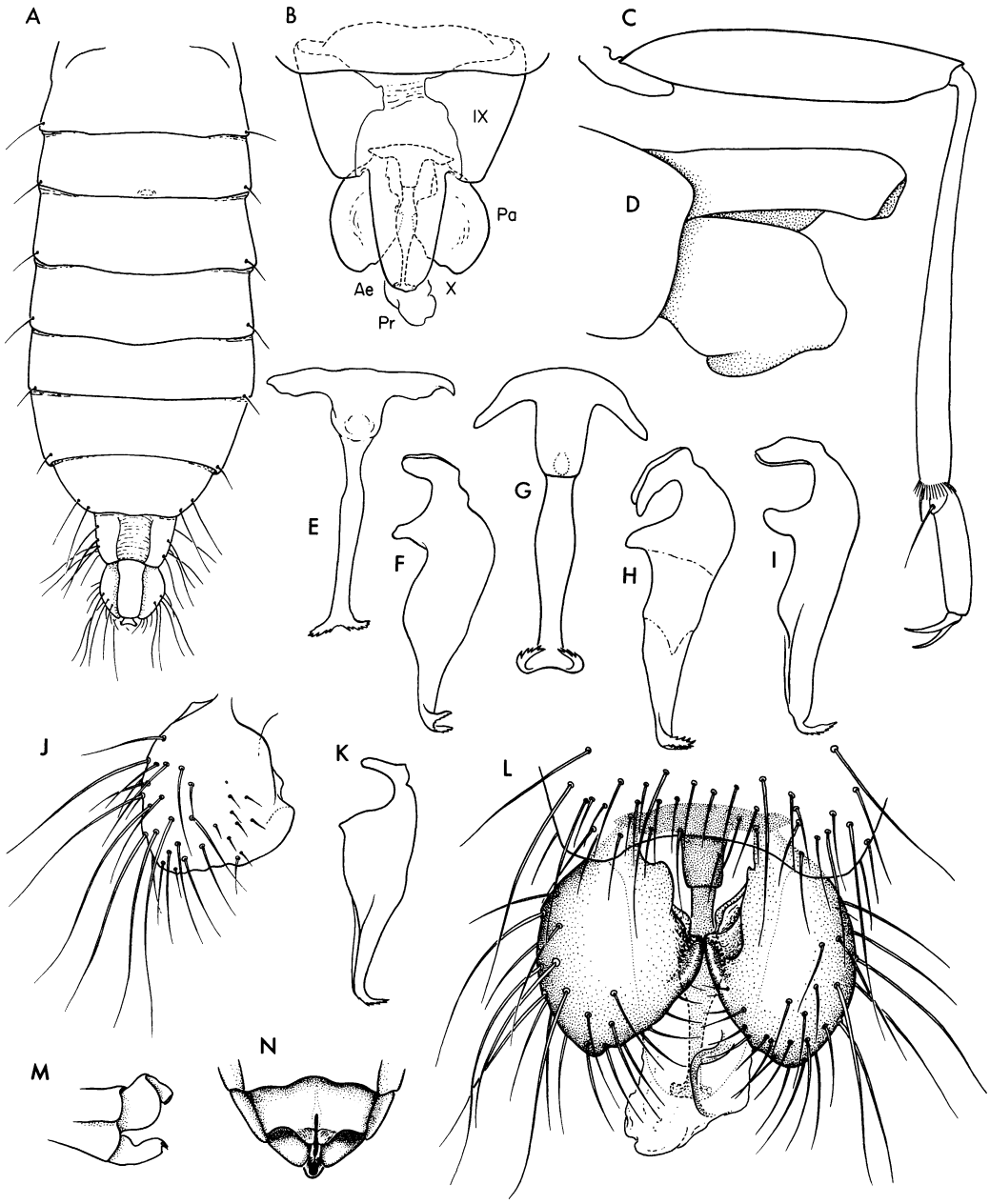


Fig. 50. *Tornocrusus penai*. **A–L.** ♂. **M, N.** ♀. **A.** Dorsal view of abdomen and genital region. **B.** Dorsal view of genital region. **C.** Hind leg. **D.** Lateral view of genital region. **E–I.** Variation in shapes of phalli, from 1 lot. **E.** Dorsal view. **G.** Ventral view. **F, H, I.** Lateral view. **J.** Right paramere, ventral. **K.** Phallus of nr. *penai*, lateral view, with smaller dorsally-directed knob. **L.** Ventral view of genital region. **M.** Lateral view of ♀ genital region. **N.** Ventral view of ♀ genital region.

to width of hind lobe of head 1:3.2. Eyes in side view extremely small, only two-fifths height of head and not nearly reaching level of either top or bottom of head. Eyes widely separated below, the distance between them 2.3 times their length. Ocelli separated by

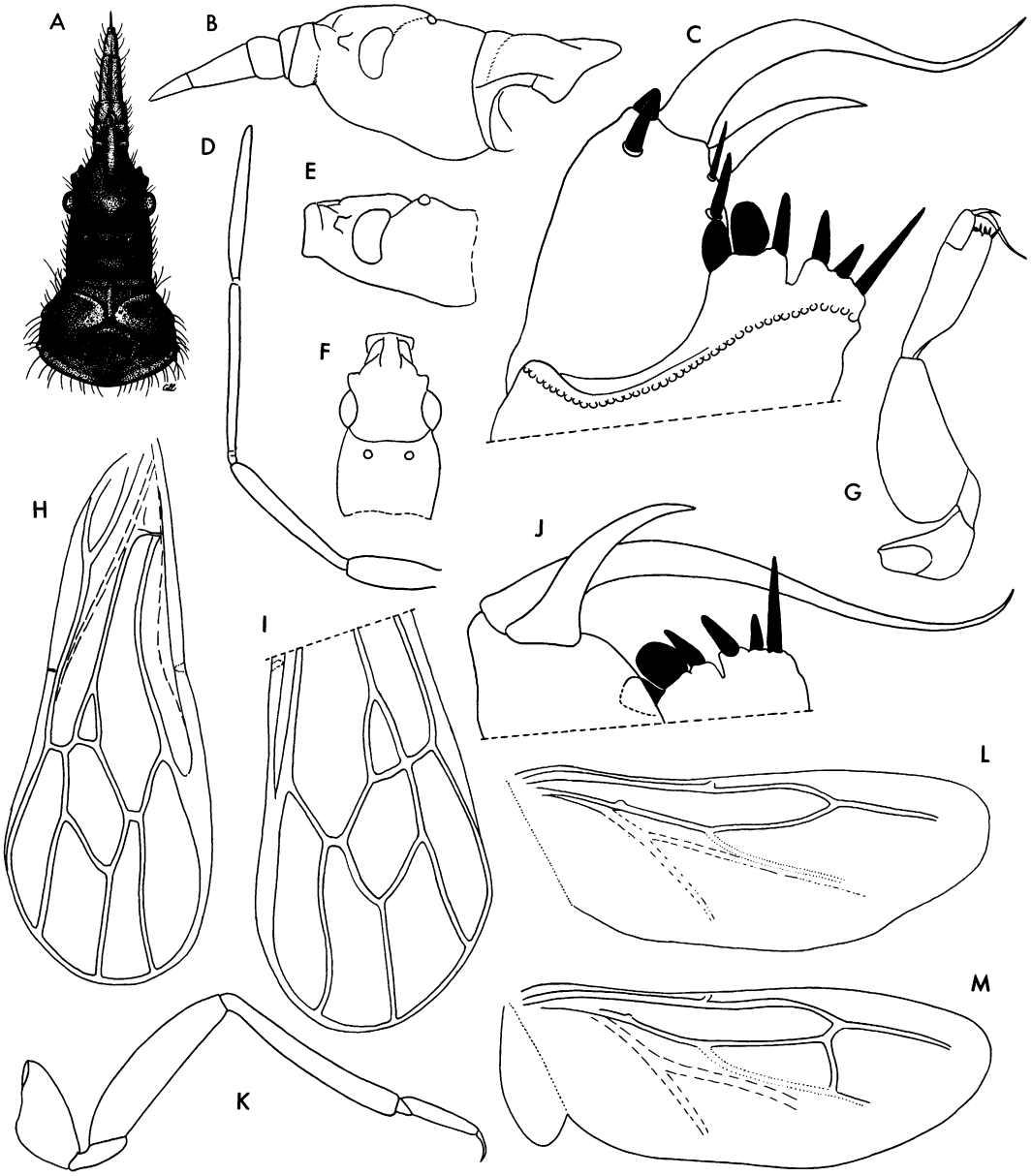


Fig. 51. *Tornocrusus sturmi*. **A**. Dorsal view of head and pronotum, ♀. **B**. Lateral view of head, ♀. **C**. Apex of foreleg, inner view, ♀. **D**. Antenna, ♀. **E**, **F**. Lateral and dorsal views of head, ♂. **G**. Foreleg, ♀, outer view. **H**, **I**. Forewings, ♀. **J**. Tarsal claws of foreleg, outer view. **K**. Hind leg, ♀. **L**. "Normal" hind wing, ♀. **M**. Teratological hind wing with m-cu crossvein present, ♀.

four times their width. Antenna longer than head plus pronotum (1:0.8). Proportions of segments I–IV 1:1.7:1.9:1.7.

Pronotum of medium proportions, the ratio of its length to width 1:1.5. Ratio of mid to hind lobe 1:1.2. Sides of thorax as in generic description.

Fore and hind wings fully developed in both sexes. Venation as in figures 51H, I, L, M (see discussion).

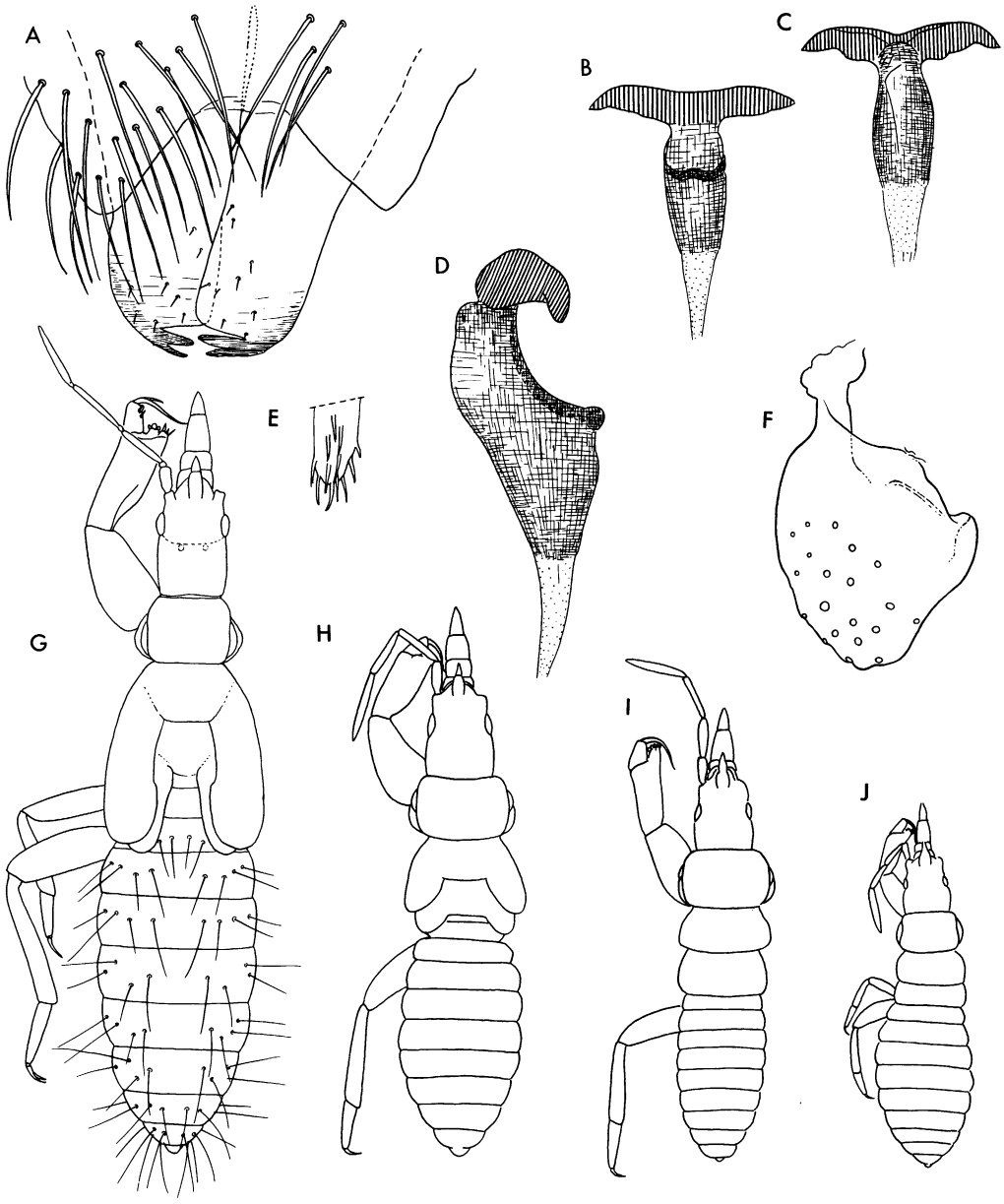


Fig. 52. *Tornocrusus sturmi*. **A**. ♀ genitalia, ventral view, showing first valvifers and first valvulae. **B**. Base of ♂ phallus, dorsal. **C**. Base of phallus, ventral. **D**. Base of phallus, lateral. **E**. Tip of second valvula. **F–J**. Nymphs, probably 5th, 3rd, 2nd, and 1st instars, respectively.

Abdomen well sclerotized in both sexes. In male, phallus T-shaped in ventral view (fig. 52C), heavily sclerotized along the cross bar of the T, and moderately sclerotized for basal two-thirds of length of stem. Opening present dorsally on basal third of stem and well sclerotized along its edge (fig. 52B); in side view forming a small knoblike process. Parameres (fig. 52F) very roughly triangular. In female, first valvulae with two teeth apically (fig. 43F); tip of second valvulae beset with microtrichiae (figs. 43F, 52E).

Ratio length to width of forefemur 1:0.43. Cuticular granules absent in both sexes. Ratio

length to width of foretibia 1:0.33. Approximately 40 setae in bristle comb of female. Outer claw of foretarsus one-third length of inner claw. Ratio length to width of hind femur 1:0.21. Trichobothria present on all legs.

Fifth instar nymph as in figure 52G. Forewing pads not meeting medially, but separated by a distance approximately equal to their width. Hind wing pads extending slightly beyond forewings. Earlier instar nymphs as in figures 52H–J.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, COLOMBIA: Nariño; Cumbal, 3200–3400 m, July 9–23, 1956 (Sturm; AMNH).

PARATYPES: Same data as holotype, 1♂ (on 2 slides), 2♀. COLOMBIA: **Cundinamarca**: Monterredondo, between Bogotá and Villevicencio (H. Sturm; AMNH), 1♀.

OTHER MATERIAL EXAMINED: Same data as holotype, 2 nymphs (on slides), 16 nymphs (in alcohol).

ETYMOLOGY: This species is named for its collector, Dr. H. Sturm.

DISCUSSION: Of seven forewings available for study from the type locality, only two are normal for the genus. The other five differ in having the m-cu and cu-pcu crossveins at the same level, making the basal cell larger than usual for the genus. This condition also exists in both wings of the Monterredondo specimen. Since the wings of our specimens are predominantly of the aberrant form, we will assume that in this species it is the most frequently expressed wing form, and use it as a specific character. We do this reluctantly in light of the high degree of wing vein teratologies in the rest of the genus and family, but we will take the chance until more material is collected.

The hind wings also show abnormalities, one of the paratype's wings having an extra crossvein.

Tornocrusus stysi Kritsky
Figures 38, 53, 54

Tornocrusus stysi Kritsky, 1977b: 161–168. — Štys, 1980: 304–305.

DISTRIBUTION: Costa Rica.

DIAGNOSIS: *T. stysi* is the only member of this genus that has a lateral projection on the foretibial spine nearest the tarsus (spine "g"; Štys, 1980, fig. 53G).

ADDITION TO DESCRIPTION: We add the following information to Kritsky's (1977) description in order to be consistent with our other material. All measurements and proportions were taken from the holotype male which is mounted on two slides.

Length 4.0 mm. Color dark brown with the following areas tinged with red: foreleg claws, eyes, ocelli, wingbases, costal margin of wing, and intersegmental membranes of abdomen.

Head length slightly longer than pronotum length (1:0.9). Ratio head length to width across eyes 1:0.8. Ratio eye length to anteocular distance 1:0.4; ratio eye width to synthlipsis 1:2.0. Ratio length to width of hind lobe of head 1:2.6. Antenna longer than head plus pronotum (1:0.8). Proportions of segments I–IV 1:1.6:1.7:1.9.

Pronotum as in figure 53A. Ratio width of mid to hind lobes 1:1.1. Scutellum with posterolateral edges sinuous near apex but not notched (fig. 53A and see Discussion).

Normal venation of forewings as in figure 53A. Setae of medium length on costa, irregularly arranged at base of vein and slightly longer and more regularly arranged toward apex. Setae short and sparse on bases of all other veins; very few or none beyond level of costal fracture. Wing coupling device as in figure 53F. Hind wing as in figure 53D.

Ratio length to width of forefemur 1:0.43; of foretibia 1:0.37, of hind femur 1:0.18. Foretibial spine "g" with lateral process (fig. 53G).

Parameres as in figures 54C, D. Posteromedial edge S-shaped, concave at apex. Phallus as in figure 54A (shape not completely discernible from slide).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male (on 2 slides), COSTA RICA: Alajuela, Chomogo area, 1620 m, 10°18'W: 84°47'N, June 13, 1973 (Erwin and Hevel Central American Expedition; USNM); examined.

DISCUSSION: See generic discussion concerning observances that differ from original description, and hence demand that the generic diagnosis be revised slightly.

Tornocrusus venezolanus, new species
Figures 38, 55

DISTRIBUTION: Northern Venezuela.

DIAGNOSIS: *T. venezolanus* females (males unknown) are difficult to distinguish from

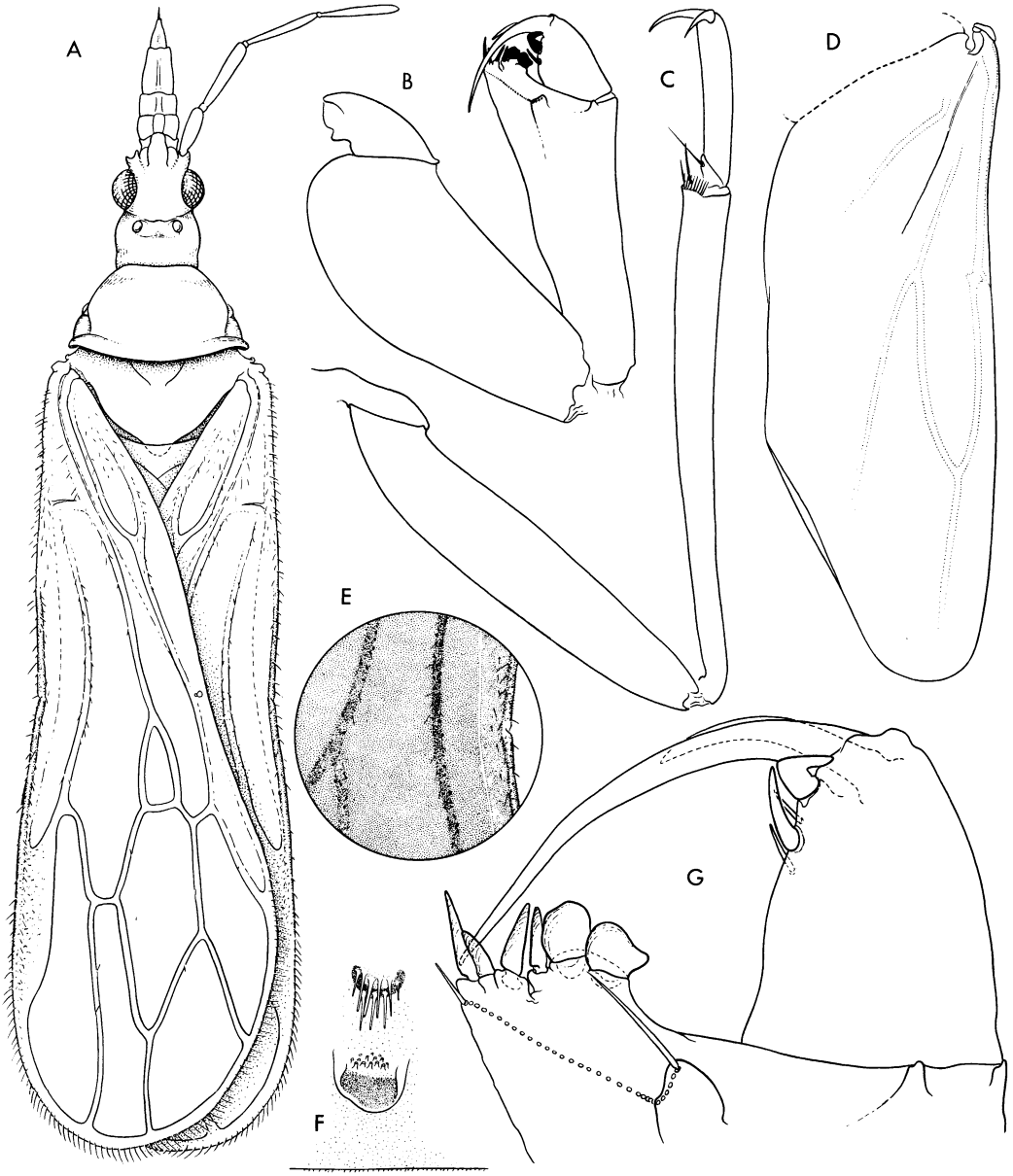


Fig. 53. *Tornocrusus stysi*, ♂. **A**. Dorsal view. **B**. Foreleg, inner view. **C**. Hind leg. **D**. Hind wing. **E**. Detail of forewing at level of costal fracture. **F**. Wing coupling mechanism. **G**. Apex of foreleg, inner view.

other females of this genus. They can best be separated by their small size, their light to medium brown color, the small number of setae in the foretibial bristle comb (ca. 33), the relatively long outer tarsal claw (one-half length of inner claw), and other subtle proportions listed below.

DESCRIPTION: Males unknown. Length of female 3.4 mm. General body color light to medium brown. Head slightly darker than rest of body. Eyes and ocelli tinged with red. Entire pronotum, scutellum, rest of thorax and wings with a matte surface. Remainder of body shiny.

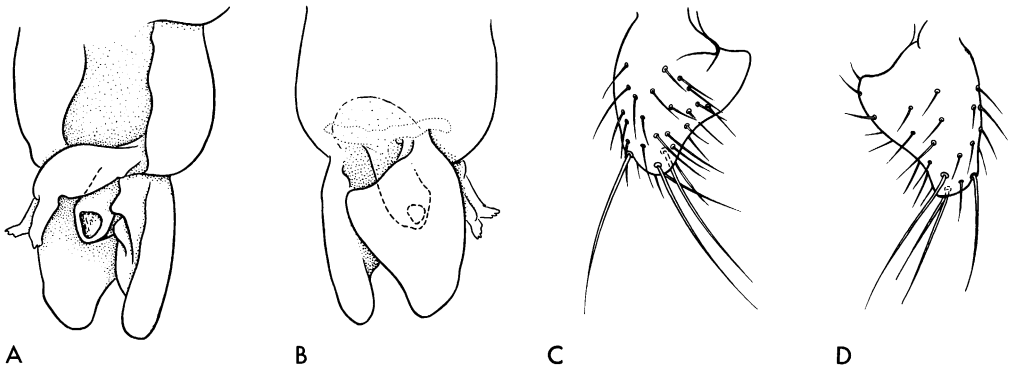


Fig. 54. *Tornocrusus stysi*, ♂ genitalia (holotype). **A**. Dorsolateral view of genital region, showing pygophore, phallus, proctiger, and parameres. **B**. Ventrolateral view of same area. **C**. Left paramere, dorsal. **D**. Left paramere, ventral.

Head very slightly longer than pronotum (1:0.9). Ratio head length to width across eyes 1:0.9. Ratio length of eyes to anteocular distance 1:0.4; ratio eye width to synthlipsis 1: 3.7. Ratio length to width of hind lobe of head 1:3.6. Beneath head, distance between eyes 1⅔ eye length. Ocelli separated by 4 times their width. Antennae longer than head plus pronotum (1:0.8). Proportions of segments I–IV 1:1.5:1.7:1.5.

Pronotum wider than long, ratio length to width 1:1.5. Ratio width of mid to hind lobes 1:1.1.

Forewings and hind wings fully developed. Setae sparse on forewings, most numerous on basal veins and costal edge, very scarce on disc of wing, and absent from cell lumens. Forewing veins slightly darker than membrane. Hind wing veins basally much darker than membrane.

Abdomen well sclerotized, as in generic description.

Forefemur very stout; ratio length to width 1:0.56. Cuticular granules absent. Foretibia relatively slender; ratio length to width 1: 0.33. Bristle comb consisting of approximately 33 setae. Tibial and tarsal spines as in generic description. Outer tarsal claw rather long, ½ length of inner claw. Ratio length to width of hind femur 1:0.26. Trichobothria present on all legs.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, VENEZUELA: Estado Aragua: Rancho Grande, 1100 m, rainforest, June 23–27, 1971 (W. L. and D. E. Brown; AMNH).

PARATYPE: VENEZUELA: **Estado Aragua**: Rancho Grande, 1100 m, rainforest, March, 1950 (Marcuzzi; AMNH), 1♀ (part on slide).

ETYMOLOGY: *T. venezolanus* is from Latin, meaning "pertaining to, or belonging to Venezuela."

ENICOCEPHALINAE

SYSTELLODERINI

Systelloderes Blanchard

Systelloderes Blanchard 1852: 224. — Jeannel 1942: 302. — Usinger 1945: 339. — Woodward, 1956: 417. — Villiers, 1969: 195. — Štys, 1970b: 226; 1978 (1977): 249. — Kritsky, 1978a: 65. (Type species: *Systelloderes moschatus* Blanchard. Fixation by monotypy.)

Compsoderes Jeannel 1943: 116.

Hymenodectes Uhler 1892: 180. — Ashmead 1892b: 329.

Systelloderus Stål 1866: 166. — Walker 1873: 22. — Lethierry and Severin 1896: 67. — Usinger 1932: 150.

DISCUSSION: *Systelloderes* is the only genus in the newly resurrected tribe Systelloderini (see section on Genitalia, Homologies, and the Phylogeny of the New World Taxa). It is by far the largest genus in the New World, with 19 described species and dozens of undescribed taxa (see preface). *Systelloderes* can be recognized by the autapomorphic fusion of the ninth and tenth abdominal terga, which form the roof of the phygophore (fig. 60D). As a practical matter, it can be most easily distinguished by the presence of a well-de-

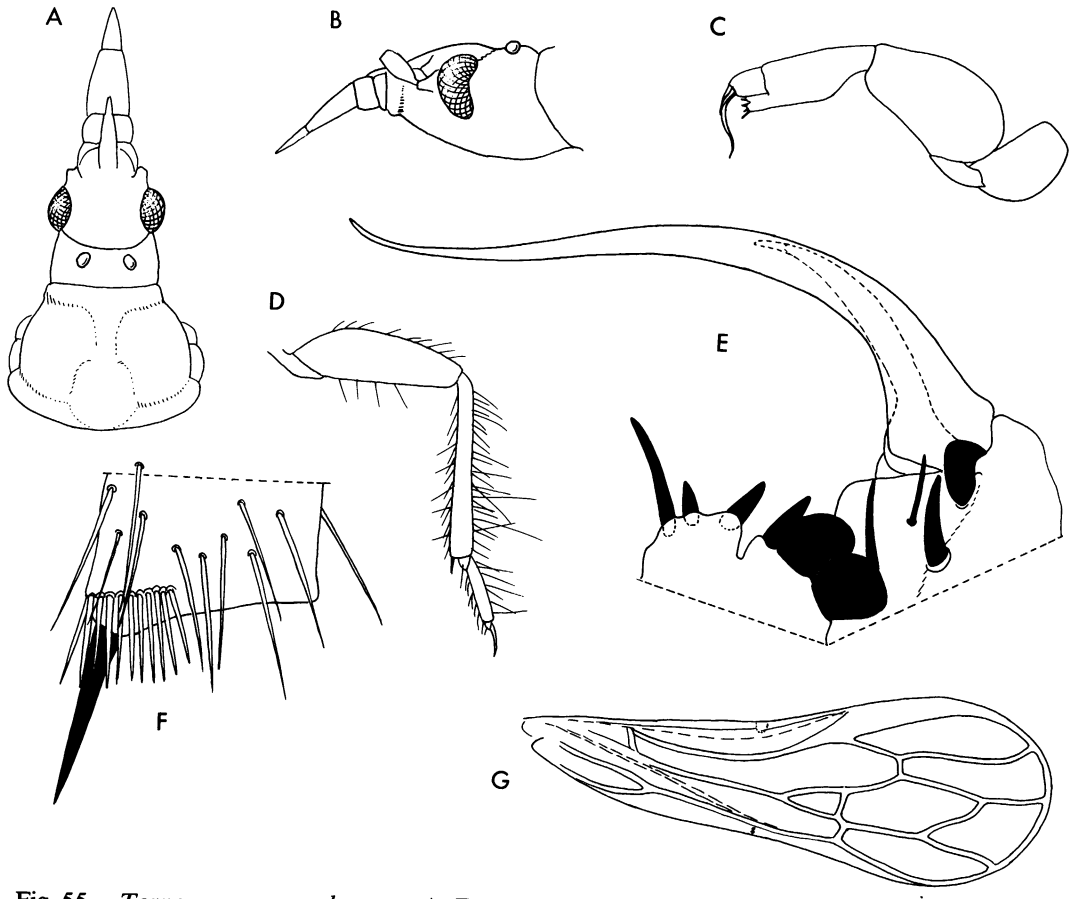


Fig. 55. *Tornocrusus venezolanus*, ♀. **A**. Dorsal view of head and pronotum. **B**. Lateral view of head. **C**. Foreleg, outer view. **D**. Hind leg. **E**. Apex of foreleg, inner view. **F**. Detail of hind leg, showing the single spine and continuous bristle comb. **G**. Forewing.

veloped supradistal plate (figs. 60A, B, D, E; central plate above the guide), a plesiomorphy that has been retained in *Systelloderes* and lost in the Enicocephalini.

We have delineated over 40 species of *Systelloderes* in the New World, which fall into two groups based on the length of tibial spine V and other characters. Species with a long tibial spine are most common in North America, but rarer in South America. Swarms studied by the senior author were usually found to be di- or trispecific, and often contained both a short- and a long-spined form. *Systelloderes* species are frequently found at higher elevations and the ranges of most species are probably very restricted. Wide-ranging species such as the North American *S. biceps* are most likely an exception.

Further treatment of *Systelloderes* will not be attempted here for reasons explained in the Preface. The scanning electron micrographs are included for comparative purposes and for documenting the reasons for resurrecting the tribes Systelloderini and Enicocephalini.

DISTRIBUTION: Known to occur from southern Canada to southern Chile.

List of Described New World Species

angustatus Champion, 1898 (Guatemala)
biceps (Say), 1832 (North America) = *terrenus* Drake and Harris, 1927
crassatus Usinger, 1932 (S. California)
culicis (Uhler), 1892 (Utah)
doriai Villiers, 1968b (Costa Rica)
dorsalus Kritsky, 1978a (Jamaica)
grandes Kritsky, 1978a (Oregon)
guigliae Villiers, 1968b (Venezuela)
harroyi Villiers, 1952a (Venezuela)
inusitatus Drake and Harris, 1927 (Mississippi)

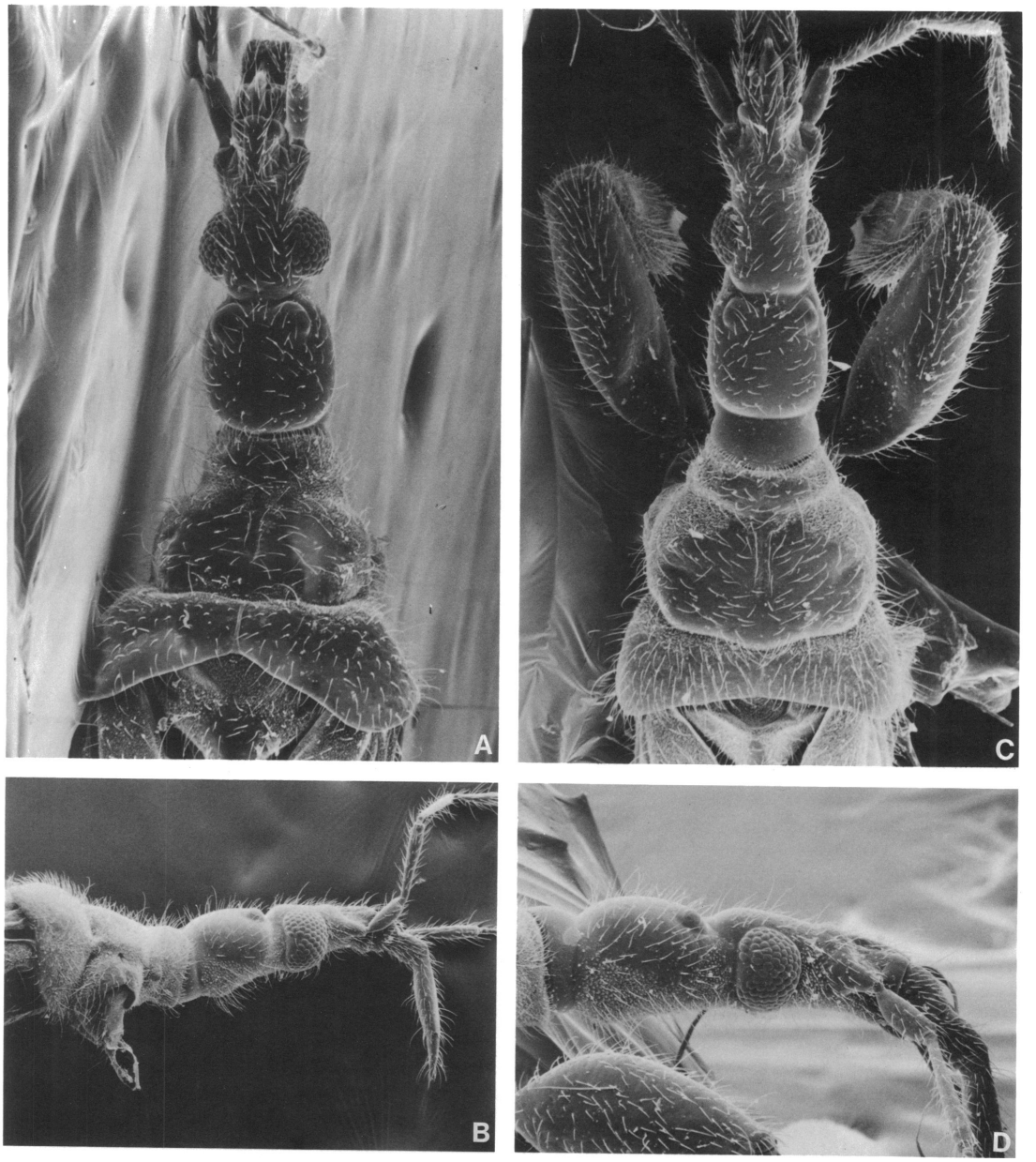


Fig. 56. *Systelloderes culicis*. **A**, **B**. ♂. **A**. Head and pronotum, dorsal. **B**. Same, lateral. **C**, **D**. ♀. **C**. Head and pronotum, dorsal. **D**. Head, lateral.

iowensis Drake and Harris, 1927 (Iowa)
jamaicensis Kritsky, 1978a (Jamaica)
lateralus Kritsky, 1978a (Virginia)
longiceps Jeannel, 1944 (1943) (Peru)
moschatus Blanchard, 1852 (Chile)
nitidus Usinger, 1932 (Honduras)
spurculus Stål, 1860 (S. Brazil)
tenuis Jeannel, 1944 (1943) (Costa Rica)
tortonesei Villiers, 1968b (Bolivia)

ENICOCEPHALINI

Brevidorsus Kritsky

Brevidorsus Kritsky, 1977b: 161, 164–168. — Štys, 1978 (1977): 252.

TYPE SPECIES: *Brevidorsus arizonensis* Kritsky. Fixation by original designation.

DISTRIBUTION: Sonoran. This genus occurs

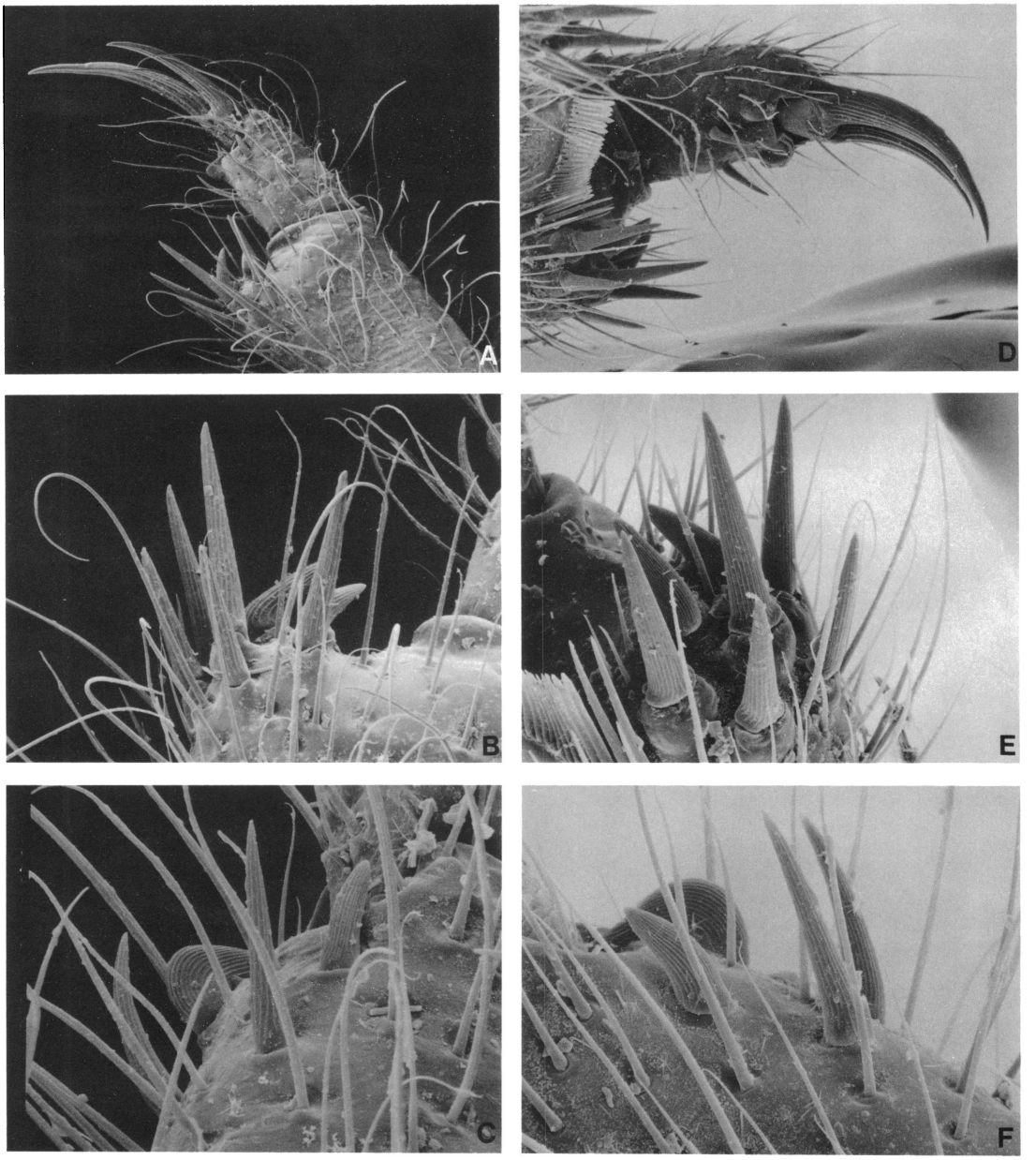


Fig. 57. *Systelloderes culicis*. **A–C**. ♂. **A**. Apex of foreleg. **B**. Foretibial spines. **C**. Foretarsal spines. **D–F**. ♀. **D**. Apex of foreleg. **E**. Foretibial spines. **F**. Foretarsal spines.

from southern Arizona south to Baja California and northwestern Mexico (fig. 61).

DIAGNOSIS: *Brevidorsus* males (females unknown) differ from related genera by the distinctive shape of their tenth and eleventh terga (fig. 64L), the open discal cell of the forewings (fig. 64K), the development of a single anal vein that ends before reaching the wing edge, the lack of foretarsal spines, and the unequal length of tarsal claws (fig. 64G).

ADDITION TO DESCRIPTION: Male. Small size (2.7–3.8 mm). General color light brown.

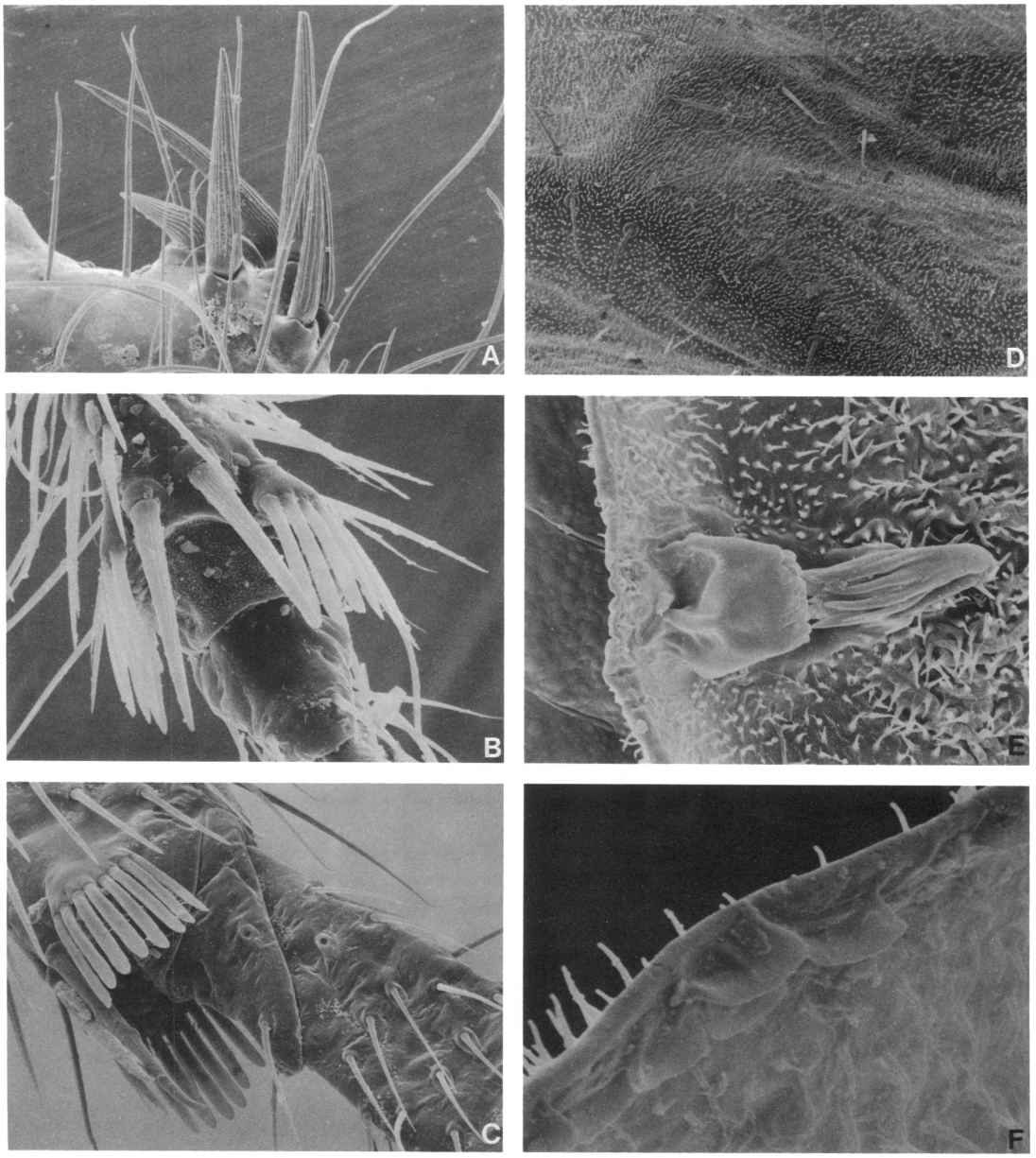


Fig. 58. *Systelloderes* spp. **A**. Foretibial spines of *Systelloderes*. **B–F**. *S. culicis*. **B**. Hind leg bristle comb and spines, ♂. **C**. Same, ♀. **D**. Forewing surface. **E**. Forewing coupling mechanism, ♂. **F**. Hind wing edge at level of wing coupling mechanism, ♂.

Body surface somewhat shining, lacking setiferous tubercles. All setae simple, slender. Macropterous.

Head with constriction behind eyes well developed (fig. 62A). Eyes very large; synthlipsis narrower than eye width. Ocelli medium size and widely separated, projecting laterally beyond edges of head. Antennae with second segment longest, third and fourth subequal in length. Rostrum not very slender (fig. 64B). Hind lobe of head transverse, shorter than wide, its sides rounded.

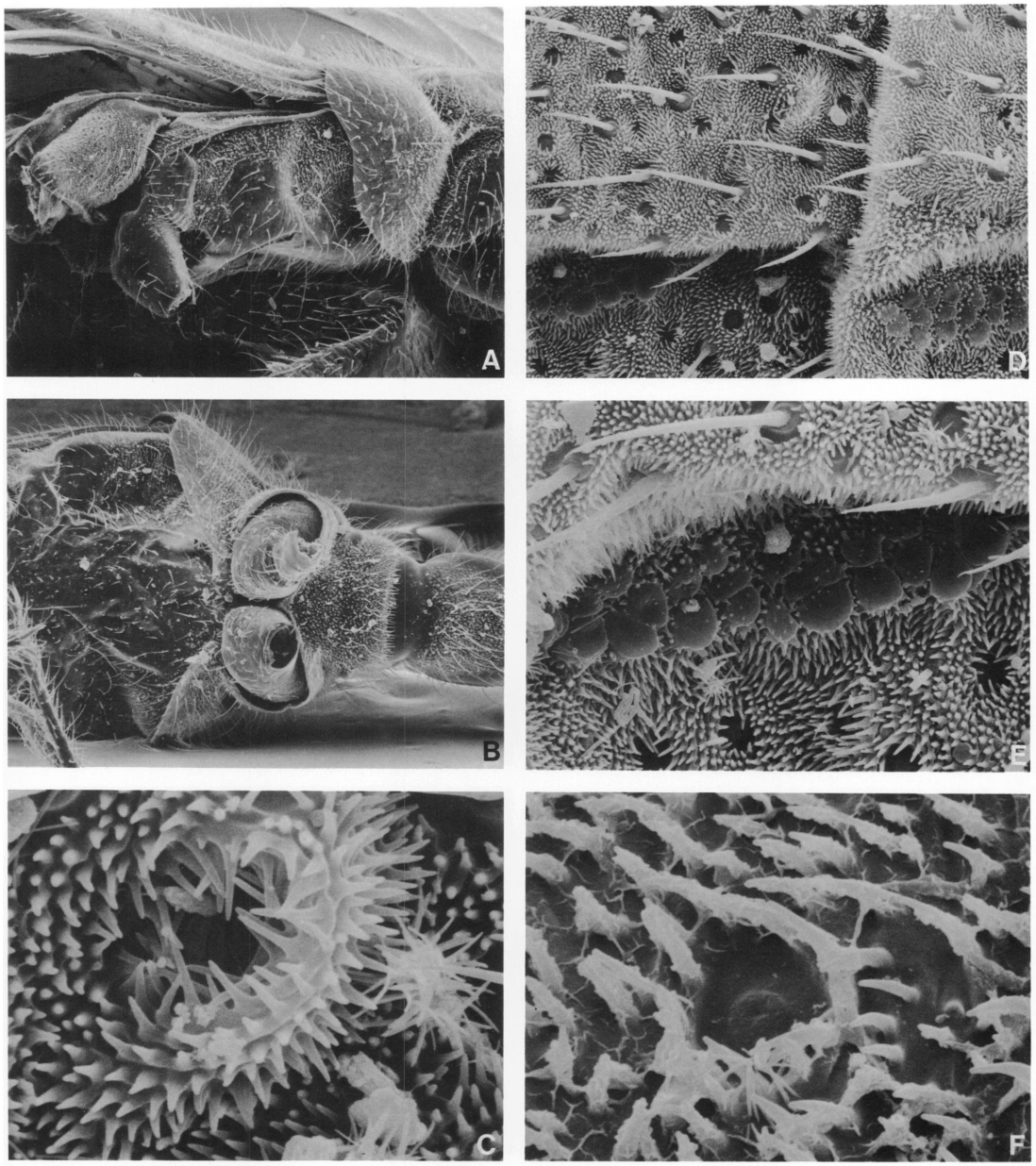


Fig. 59. *Systelloderes culicis*. **A**. Thorax, lateral, ♀ (note slender fore and hind wing-to-body coupling groove). **B** Thorax, ventral, ♂, showing open acetabula. **C**. Spiracle on ventral connexival plate V, ♀. **D**. Ventral connexical plates and sterna III and IV, ♀. **E**. Detail of papillae between plates, above, ♀. **F**. Detail of "bare" spot in photo D.

Pronotum unarmed (fig. 62A). Median lobe with a faint median longitudinal impression; disc laterally lacking sculptural elements. Hind lobe of pronotum very short, almost ribbon-shaped, its posterior border emarginate. Mesonotum widely exposed. Anterior acetabula open behind. Meso- and metathorax and abdomen very poorly sclerotized, shrunken in air-dried specimens.

Forelegs of average proportions (fig. 64D).

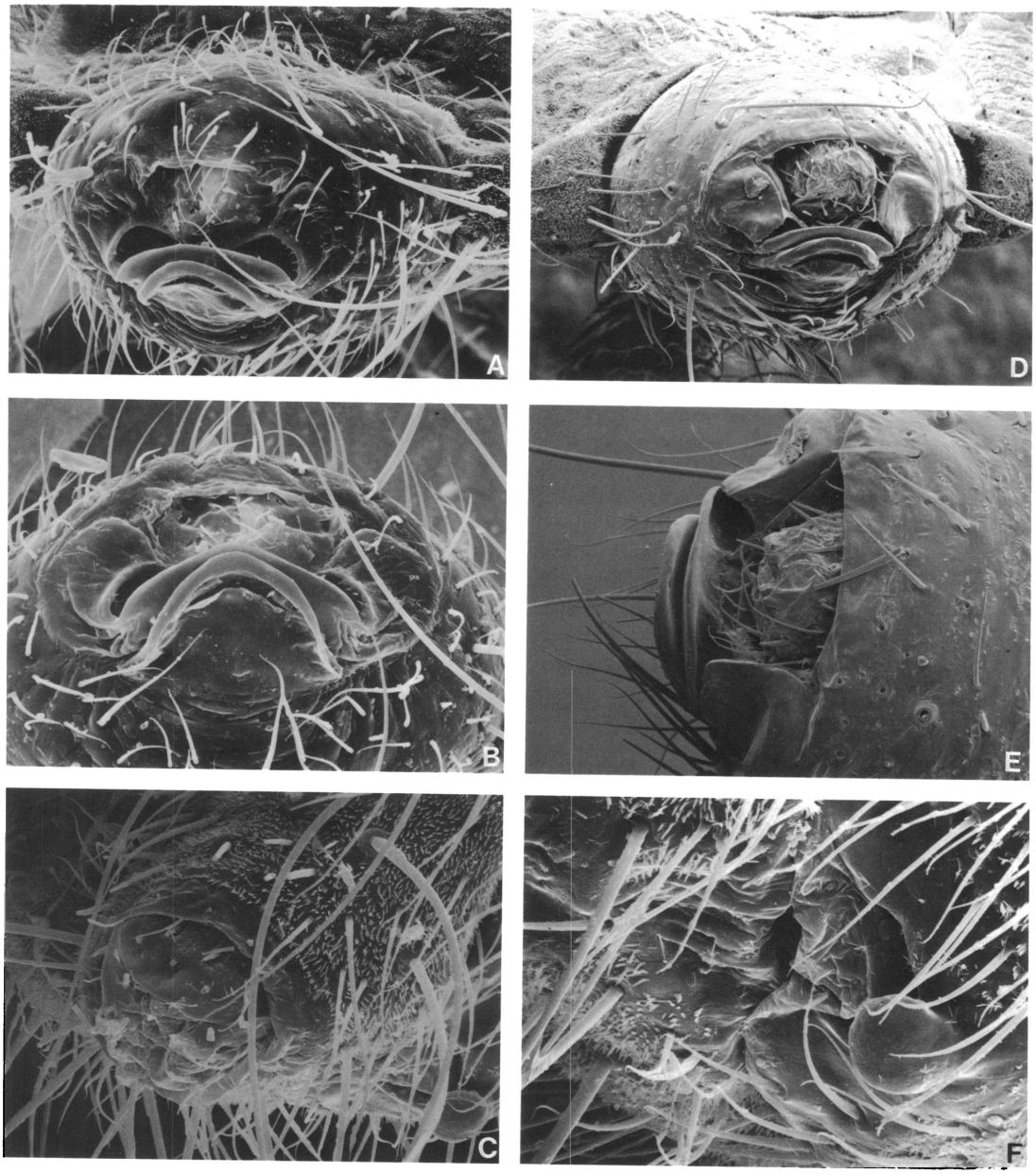


Fig. 60. *Systelloderes* spp. **A**, **B**. *S. culicis*, ♂ genital capsule, posterior and posteroventral views, respectively. **C**. *S. culicis*, ♀, apex of abdomen, showing proctiger (center) and median tab on ventrite VIII (lower right). **D**, **E**. *Systelloderes*, ♂, genital capsule, posterior and dorsolateral views, respectively. **F**. *S. culicis*, ♀, detail of vestigial first and second valvulae and median tab.

Coxae and femora with minute pointed cuticular tubercles arranged in groups (fig. 64E). Trochanter lacking process. Inner apical angle of tibia with two large straight spines, and two to four shorter, spinelike setae (figs. 64C, G–I). Tarsus approximately as long as width of apical portion of tibia; spines absent (fig. 62C, D). Tarsal organ almost dorsally situated. Tarsus with two claws, outer one only two-thirds as long as inner one, the latter over

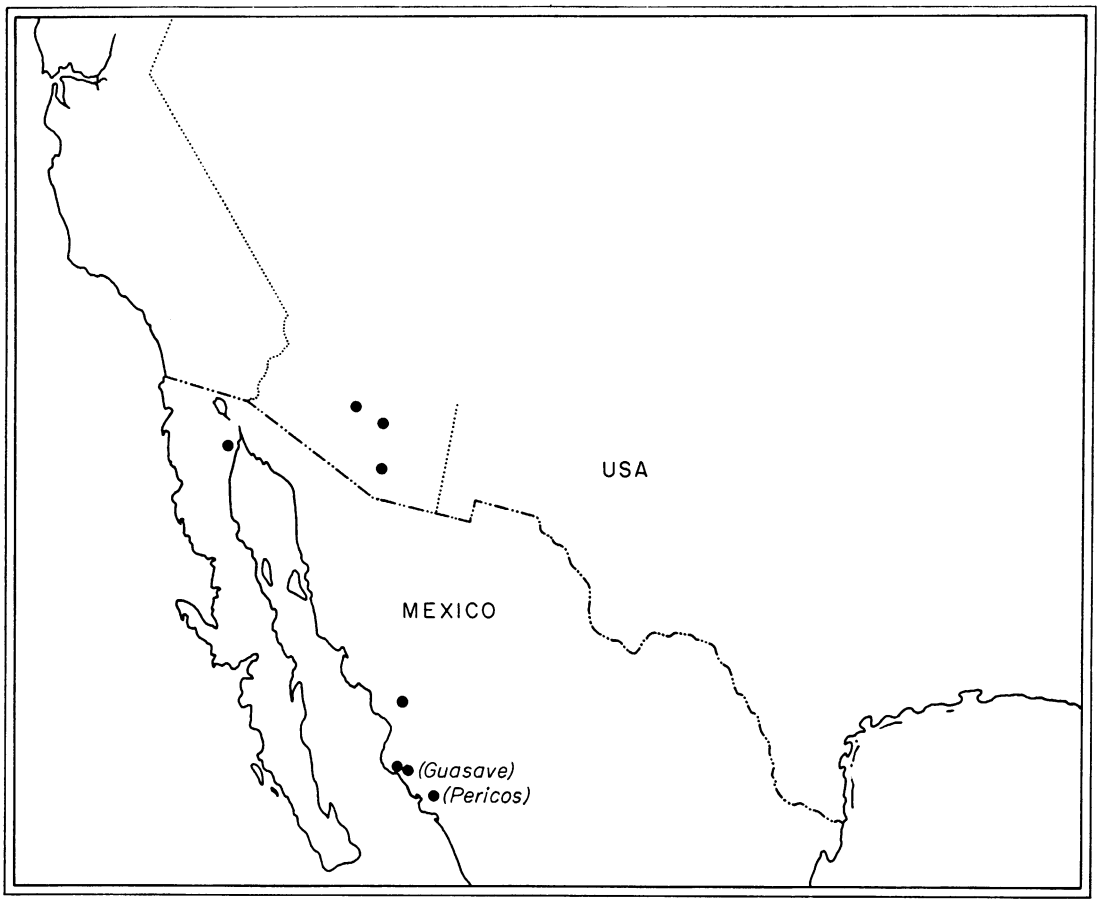


Fig. 61. Distribution of *Brevidorsus*. *B. arizonensis* (●).

half as long as tarsus (fig. 62D). Mid and hind tarsi two-segmented; apex of tibiae with two large spines and two narrowly separated bristle combs (fig. 63A; usually appear as one under compound microscope).

Forewings lacking basal cell; discal cell open (fig. 64K). Stigmal cell elongate. Apex of Cu not attaining wing margin. Only one anal vein developed (PCu), not extending beyond level of cu-pcu crossvein. Setae arranged in one or two irregular rows on most veins, mostly in a single row on R, and much more numerous on costal margin. Lumens of cells with large numbers of short setae (fig. 63D). Forewing coupling device C-shaped, with arm of "C" closest to wing edge longer than inner arm (fig. 63E); apices of arms beset with long, slender projections, equal in length on both sides. Hind wing edges with foliaceous structures at level of forewing coupling device (fig. 63F).

Abdomen very poorly sclerotized, but with both dorsal and ventral connexival plates discernible and separated from tergites and sternites. Spiracles present on ventral connexival plates II–VII.

Tenth tergum well developed, with 1 + 1 setae, and with a distinctive posteromedial tongue-shaped tab, probably tergum 11 (fig. 63C). Guide subrectangular, slightly rounded apically (fig. 63B).

Female unknown, probably wingless.

DISCUSSION: For a discussion of possible females of this genus, see Discussion under *Urnacephala*.

Brevidorsus arizonensis Kritsky
Figures 61–64

Brevidorsus arizonensis Kritsky, 1977b: 164, 167.

DISTRIBUTION: Sonoran. This species occurs from southern Arizona south to Baja California and northwestern Mexico.

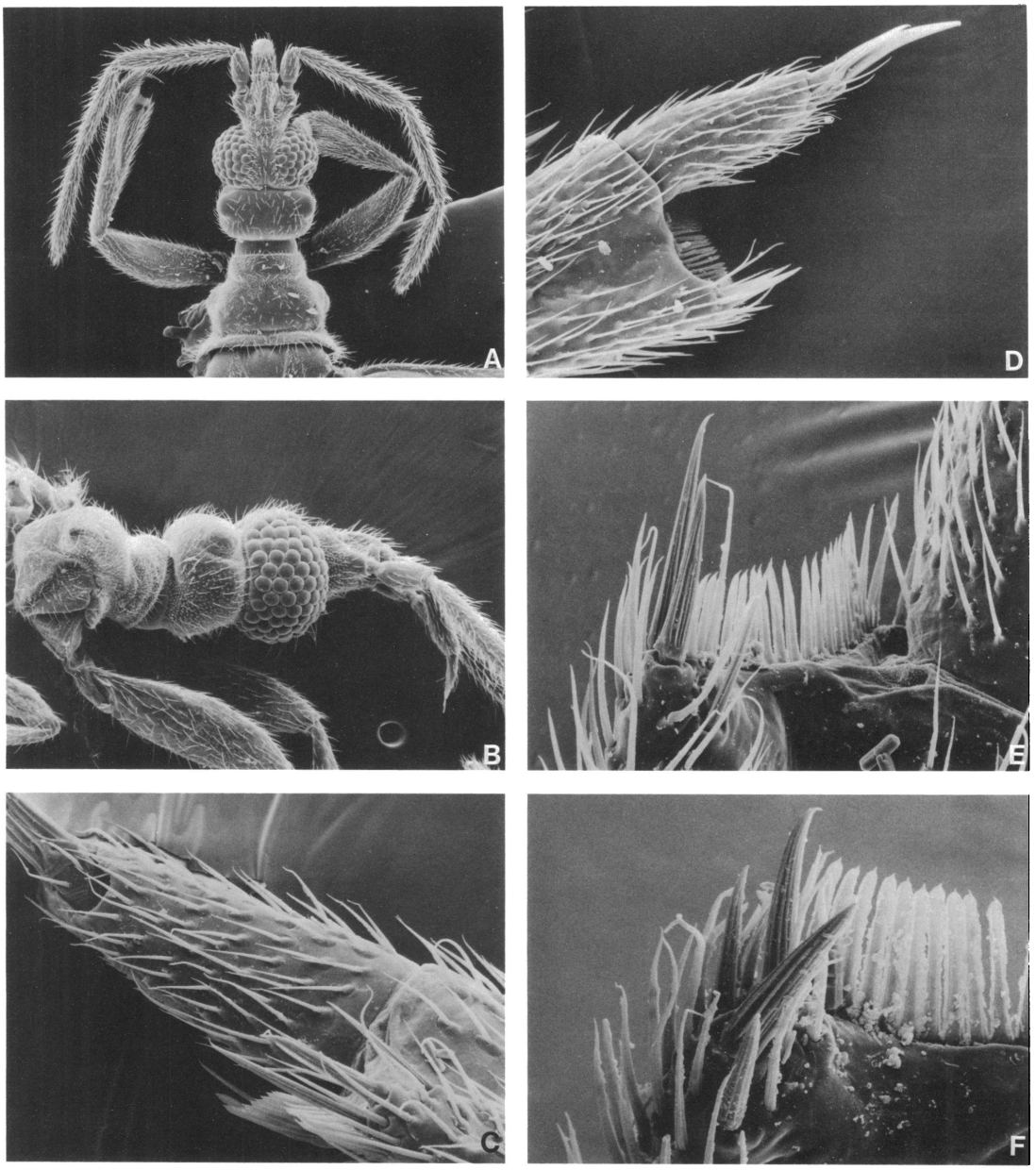


Fig. 62. *Brevidorsus arizonensis*, ♂. **A**. Head and pronotum, dorsal. **B**. Same, lateral. **C**. Foretarsus with setae only, no spines. **D**. Apex of foreleg. **E**, **F**. Variations in foretibial spine configurations and numbers.

DIAGNOSIS: *Brevidorsus arizonensis* can be distinguished by the proportions listed below.

ADDITION TO DESCRIPTION: Females unknown. Length of male 2.7–3.8 mm. Head dark brown, sharply contrasting with light, delicate, transparent body. Body surface somewhat shiny, lacking setiferous tubercles. All setae slender, simple. Macropterous.

Distal end of foretibia with two heavy spines plus two to four shorter and thinner setalike spines (fig. 64C, G–I). Forefemora and coxae with minute toothed cuticular structures arranged in small arcs (fig. 64E).

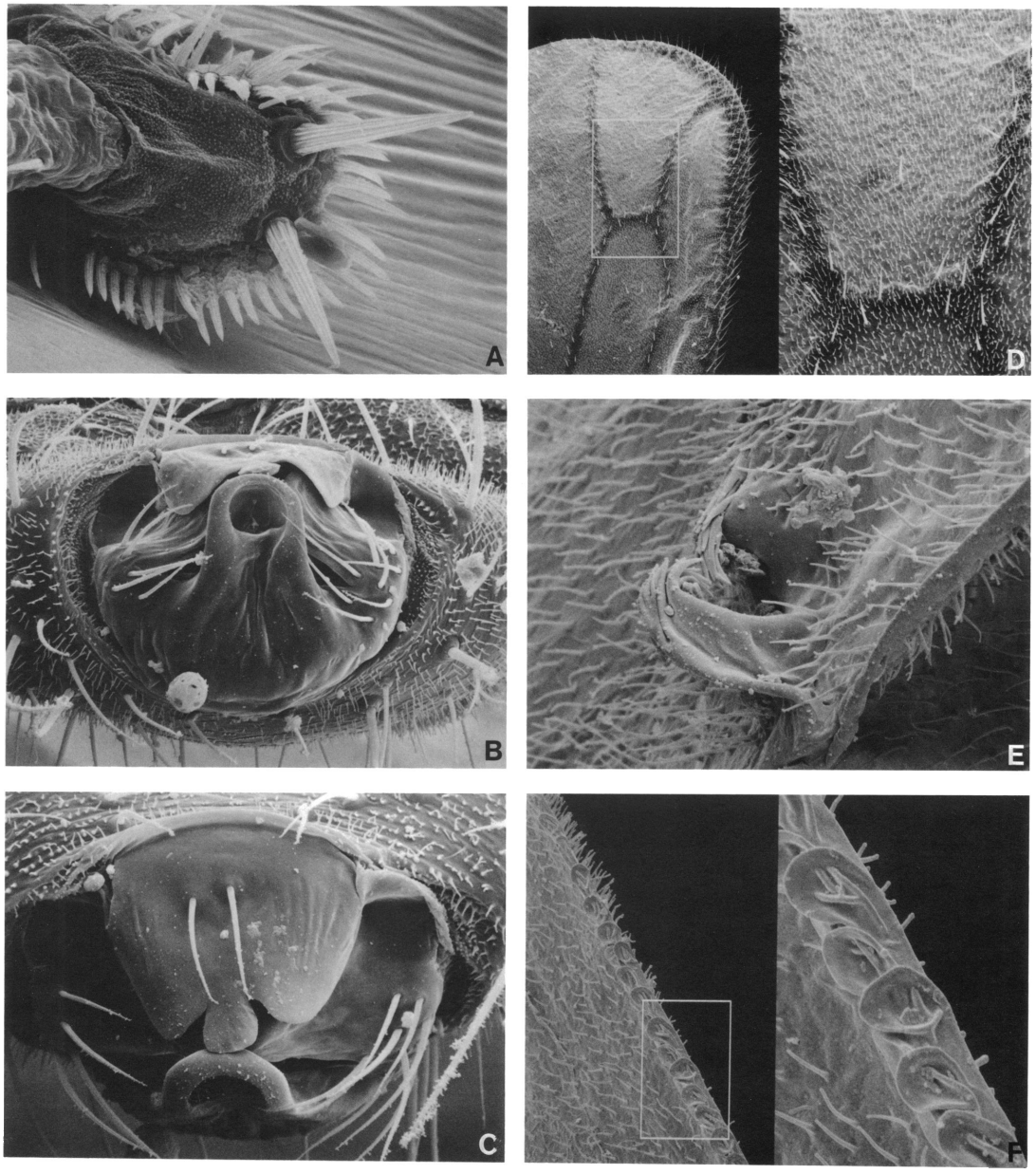


Fig. 63. *Brevidorsus arizonensis*, ♂. **A**. Hind tibia, end-on view, showing bristle combs and spines. **B**, **C**. Genital capsule, posterior and dorsal views, respectively. **D**. Forewing. **E**. Wing coupling mechanism. **F**. Hind wing edge at level of wing coupling mechanism, showing foliaceous structures.

Proportions as in table 12.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, USA: Arizona: *Pinal Co.*: Boyce Thompson Arboretum near Superior, light trap in rain, July 24, 1948 (H. K. Gloyd; INHS); examined.

MATERIAL EXAMINED: MEXICO. – **Baja California Norte**: 80 mi S of Mexicali, June 4, 1961 (H. F. Howden; CNC), 1♂. **Sinaloa**: 11 mi S of Guasave, December 16, 1963 (Tauber and Tosch; AMNH), 1♂; 26 mi N of Pericos, August 13, 1960 (Arnaud, Ross, and

TABLE 12
Proportions of Groups of *Brevidorsus arizonensis*

	Guasave	Bahia San Carlos	Tucson, other Sinaloa
Length	3.8 mm	3.8 mm	2.6–3.0 mm
Head L/pronotum L	1:0.7	1:0.6	1:0.7
Head L/W across eyes	1:0.7	1:0.6	1:0.7
Head W across eyes/hind lobe head W	1:0.8	1:0.9	1:0.9
Eye L/anteocular distance	1:0.4	1:0.6	1:0.5
Eye W/synthlipsis	1:0.3	1:0.5	1:0.4
Hind lobe head L/hind lobe head W	1:1.9	1:2.1	1:2
Antennal segments I–IV	1:3.8:3.2:3.2	1:3.5:2.9:2.9	1:3:2.7:2.7
Antennal L/head plus pronotum L	1:0.7	1:0.6	1:0.7
Mid lobe pronotum W/hind lobe W	1:1.5	1:1.3	1:1.3
L/W forefemur	1:0.26	1:0.26	1:0.27
L/W hind femur	1:0.21	1:0.26	1:0.24
L/W foretibia	1:0.24	1:0.23	1:0.27

Rentz; CAS), 4♂; 1 mi S of Pericos, June 11, 1954 (A. A. Alcorn; UK), 1♂. **Sonora**: Alamos, February 22, 1963 (P. H. Arnaud; CAS), 1♂; Bahia San Carlos, March 2, 1963 (P. H. Arnaud; CAS), 4♂. USA. – **Arizona**: *Pinal Co.*, Boyce Thompson Arboretum near Superior; at light, August-September, 1949 (H. K. Gloyd; INHS) 1♂, paratype; Superior, at light, July 16–August 5, 1948 (H. K. Gloyd; UAR); 152♂ (several used for SEM). *Pima Co.*: Tucson, July 14, 1958 (M. Adachi; UAR), 1♂; at light, August 4, 1958 (M. Adachi; UAR), 1♂. *Maricopa Co.*: Phoenix, July 6, 1946 (R. A. Flock; AMNH), 1♂.

DISCUSSION: One of our specimens, from Guasave, Sinaloa, Mexico, is longer than the rest (3.8 mm). Both this specimen and a smaller one from Pericos, Sinaloa, have dark heads anterior to the eyes and dark antennal segments I and II. There is also considerable variation among our specimens regarding the ratio of head width across eyes/hind lobe head width.

These differences seem to form a mosaic-like distribution of characters that cannot be resolved on the basis of locality and are never clear-cut enough to form distinctly separable species. The Guasave specimen is most consistently different from the rest, but overlaps the other specimens in most characters at some point. We therefore will consider all of the above differences intraspecific variation until more material can be studied.

Chiricocoris, new genus

TYPE SPECIES: *Chiricocoris dybasi*, new species.

DISTRIBUTION: Panama; Chiriqui province (fig. 65).

DIAGNOSIS: Males unknown. Females can be distinguished by their very robust overall aspect, the extremely thick forelegs (fig. 69D) the great extension in length of the midlobe of pronotum with the accompanying reduction of the hind lobe (fig. 66A), the posteriorly closed anterior coxal cavities (fig. 69E), and the presence of a large conical projection at the anteroventral angle of the foretarsus (fig. 69C). The forewings have neither basal nor discal cells.

DESCRIPTION: Males unknown. Female: Enicocephalinae. Medium size species (5–6 mm). General body surface dull, lacking simple or setiferous cuticular tubercles. All setae simple, slender. Macropterous.

Head elongate (fig. 66A). Constriction behind eyes distinct. Antennae with second and fourth segments subequal in length, third somewhat longer. Rostrum stout (figs. 66B, C).

Pronotum unarmed (fig. 66A); median lobe with a simple median longitudinal impression. Hind lobe of pronotum very short, almost ribbon-shaped, its posterior border straight; metanotum not exposed. Anterior acetabula closed behind (fig. 69E). Scutellum

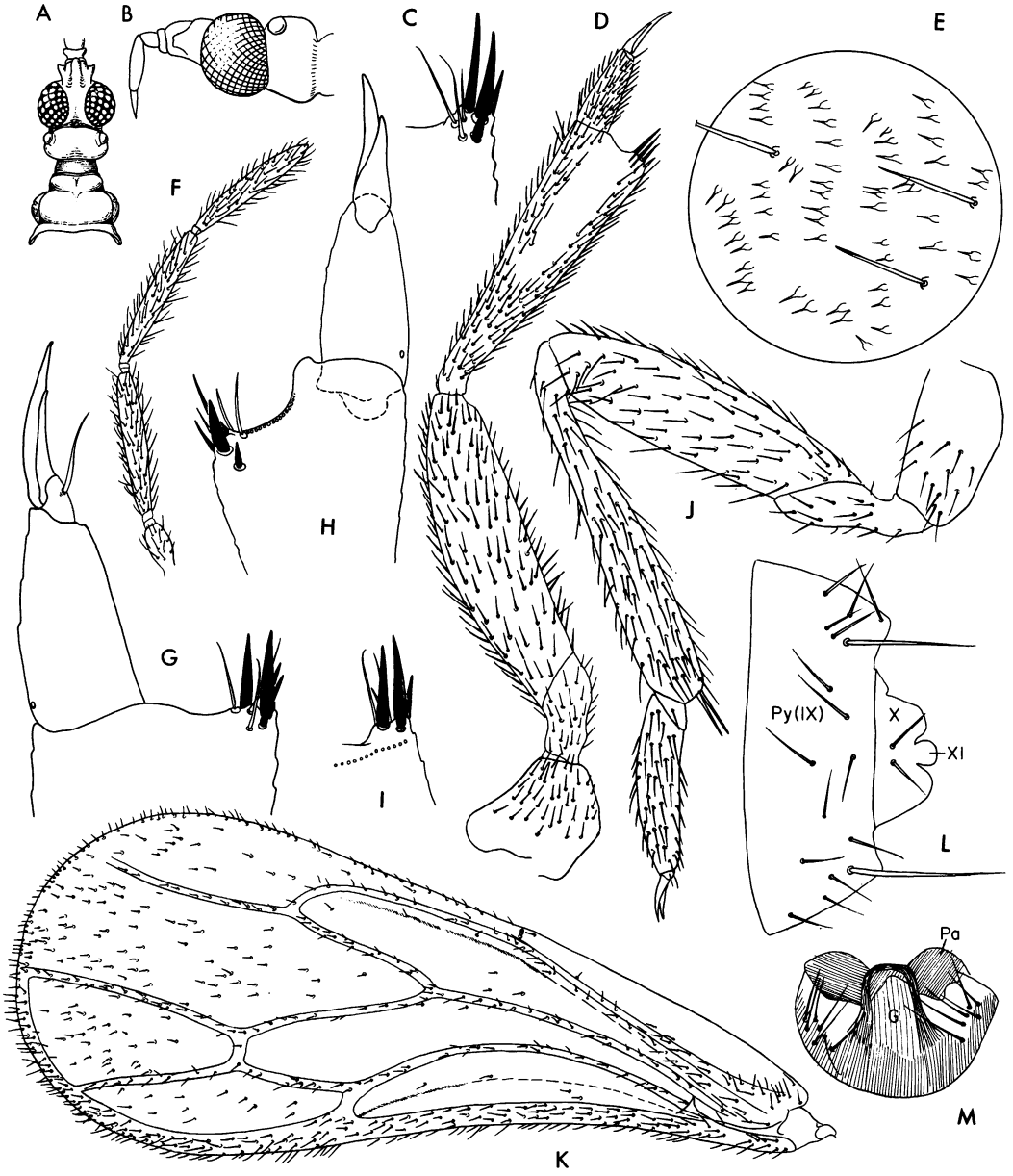


Fig. 64. *Brevidorsus arizonensis*, ♂. **A**. Head and pronotum, dorsal. **B**. Lateral view of head. **C**. Detail of foretibial spines, outer view. **D**. Foreleg. **E**. Detail of inner ventral surface of forefemur showing cuticular microstructures. **F**. Antenna. **G**. Apex of foreleg, outer surface. **H**. Apex of foreleg, inner surface (foreshortened, from holotype). **I**. Detail of foretibial spines, inner view. **J**. Hind leg. **K**. Forewing. **L**. Pygophore and tergites X and XI, dorsal view. **M**. Genital area, ventral view.

broadly triangular (fig. 69A). Meso- and metathorax in side view with shallow, moderately developed groove (above metathoracic synpleuron) that receives costal edge of forewing when at rest.

Forewings lacking basal and discal cell (fig. 70C). Stigmal cell extending beyond apex of stigma. Setae arranged in two irregular series on most veins, but only a single row on R + M, and numerous irregular series on costal

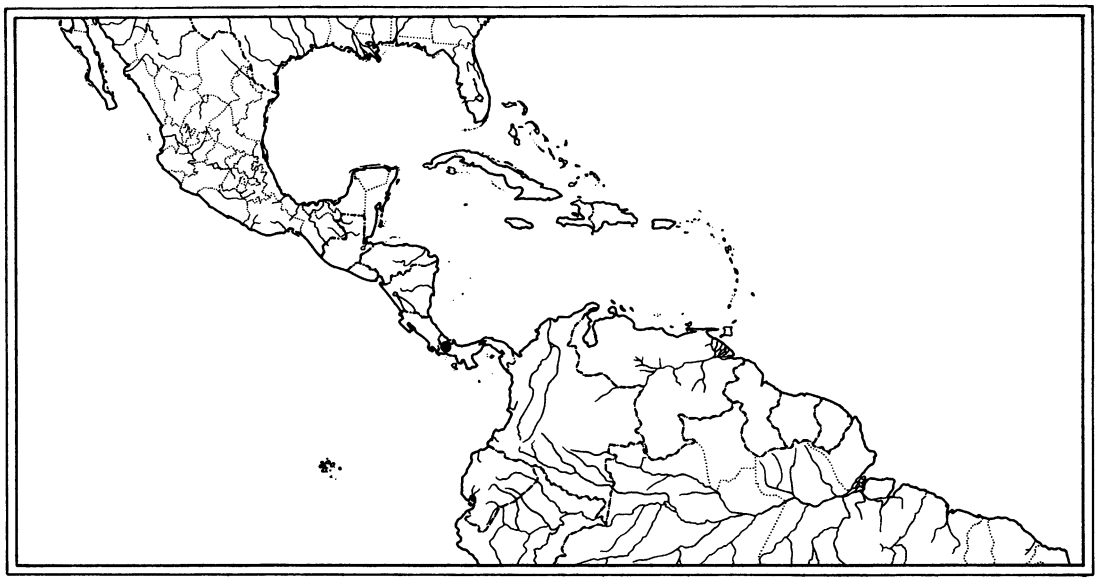


Fig. 65. Distribution of *Chiricocoris*. *C. dybasi* (●).

margin. Membrane of cells lacking setae (fig. 66D). Wing coupling device C-shaped, with both arms of "C" terminating in groups of large microtrichial projections of approximately equal length on each side (fig. 66F).

Hind wings with apical portion of "cell," beyond insertion of free posterior vein, over four times as long as wide (fig. 70E). Setae completely absent. Wing edge rolled inward at level of wing coupling device, but lacking foliaceous structures (fig. 66E).

Abdomen with regularly arranged sclerotized patches both dorsally and ventrally (fig. 70F). Sclerotized areas bearing many bare evaporatory (?) spots, each with a central hole (figs. 68B, C). Spiracles on ventral connexival plates II–VIII (fig. 68D).

Front legs extremely stout (fig. 69D). Articles lacking tubercles or scalelike cuticular structures. Trochanter without process. Femur angularly salient at dorsal basal angle. Inner apical angle of tibia with seven spines (figs. 67B, C). Spines I–IV and VII simple; V elongate, curved; VI in form of a short stout hook. Tarsus with four spines (fig. 67F). Spine III sickle-shaped, the others subconical, I short, II and IV relatively long. Anteroventral angle of tarsus with conspicuous conical projection (fig. 67F), appearing to be a fifth spine. Tarsal organ dorsolateral. Foretarsus with two claws, the outer one shorter than the inner one (fig. 67A). Apex of mid and hind tibiae with two bristle combs and two large spines (fig. 67D).

Fifth instar nymph (fig. 70I). Shape slender. Eyes well developed. Antennae slender. Neck distinct, mesothoracic wing pads meeting medially, longer than wide, rounded posteriorly. Abdomen membranous; terga III–VII with ordinary setae and with macrochaetae (1 + 1 submedian and 1 + 1 sublateral).

ETYMOLOGY: Derived from Chiriqui, the Panamanian province from which it is known.

Chiricocoris dybasi, new species

Figures 65–70

DISTRIBUTION: Panama; known only from Chiriqui Province.

DIAGNOSIS: *Chiricocoris dybasi* can be recognized by the proportions given below.

DESCRIPTION: (Where there is a range of measurements, those of the holotype appear first.)

Males unknown. Length of female 5.5–6.0 mm. General body color brown. Head shiny chestnut brown with eyes and areas surrounding ocelli red. Remainder of body dark, dull, velvety brown, sharply contrasting with shine of head. Hind lobe of pronotum slightly darker, scutellum and Sc of forewing slightly

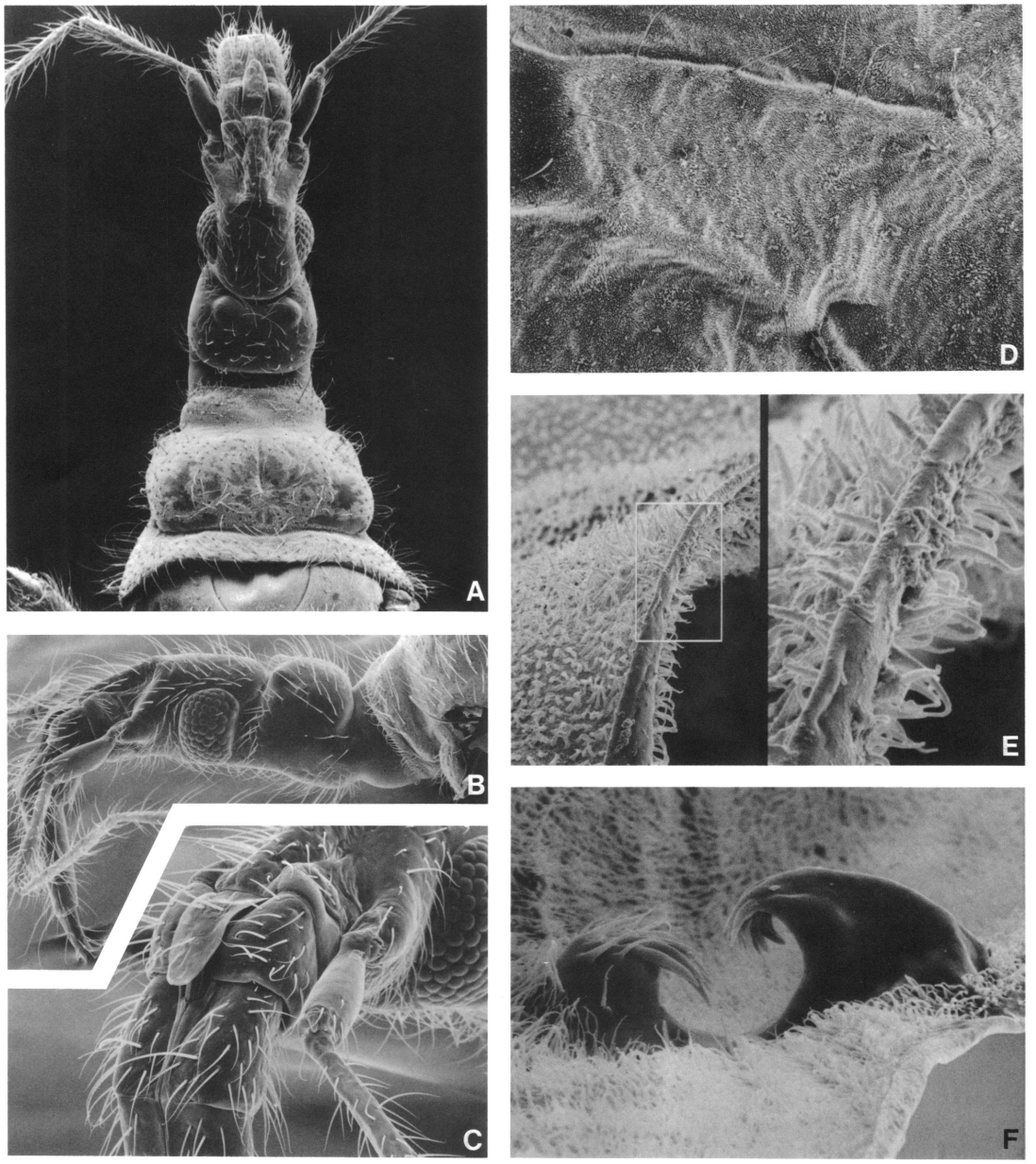


Fig. 66. *Chiricocoris dybasi*, ♀. **A**. Head and pronotum, dorsal. **B**. Head, lateral. **C**. Rostrum. **D**. Forewing surface. **E**. Hind wing edge at level of wing coupling mechanism. **F**. Wing coupling mechanism on hind edge of forewing.

lighter than rest. Antennae, rostrum, and legs light yellow-brown. Foretibia with a faint darker brown band around center of article; foretarsus brown. Abdomen beige, strongly tinted with rose in the membranous areas and bearing brown sclerotized plates regularly arranged on each segment (fig. 70F).

Head longer than pronotum [1:0.7 (0.8)]. Ratio head length to width across eyes 1:0.4 (0.5). Ratio length to width of hind lobe of head 1:1.4 (1.5). Eye length equal to anteocular distance; ratio width of eyes to synthlipsis 1:3.0 (2.9). Rostrum as in figures 66B, C.

Antennal segments I–IV 1:1.9 (1.8):2.7

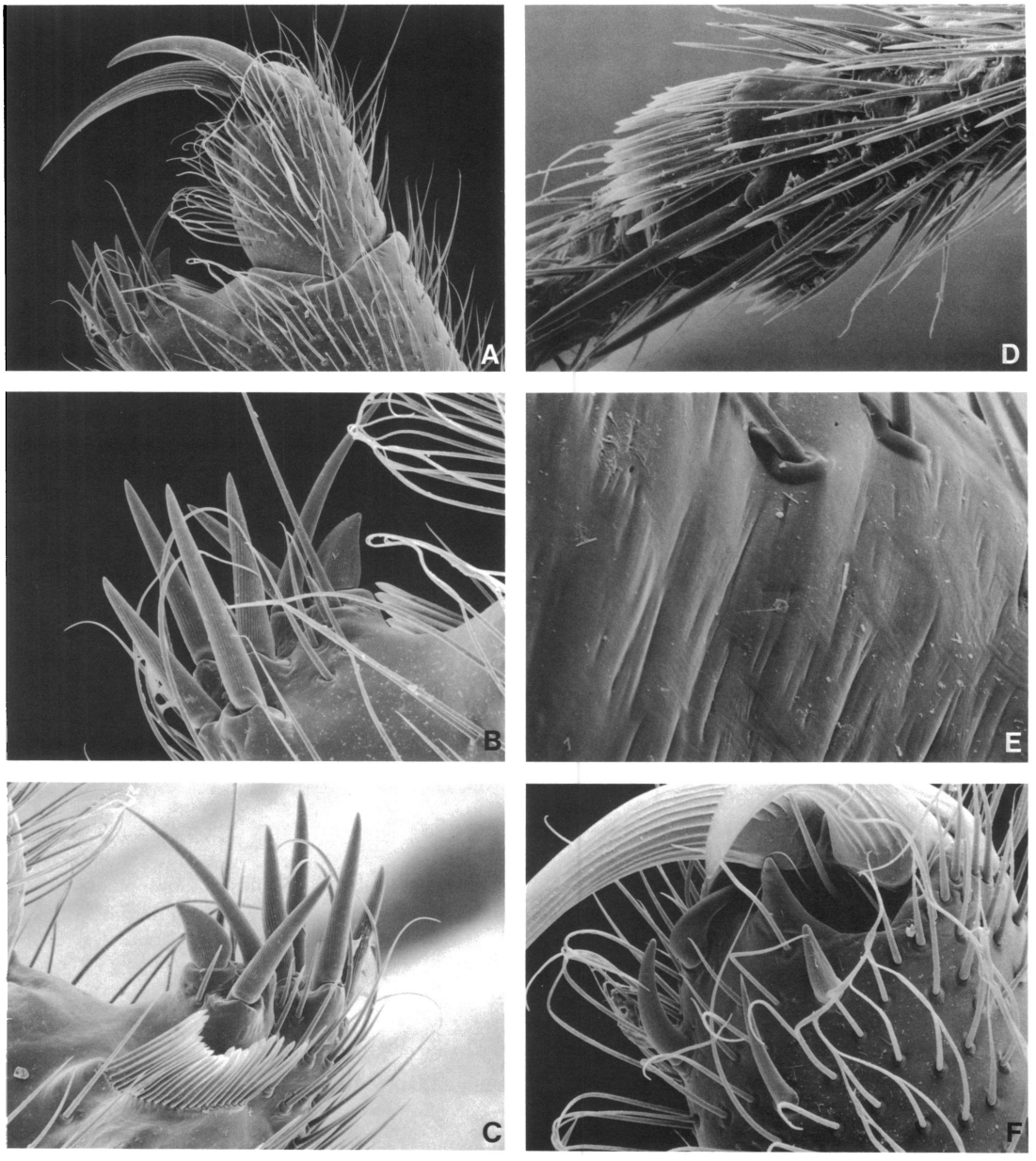


Fig. 67. *Chiricocoris dybasi*, ♀. **A**. Apex of foreleg. **B**. Foretibial spines, outer view. **C**. Same, inner view, showing bristle comb. **D**. Apex of hind tibia. **E**. Inner surface of forefemur. **F**. Foretarsal spines and also apical conical projection.

(2.4):2.0 (2.1); combined, approximately equal to head plus pronotum.

Pronotum as in figure 66A; proportional width of mid to hind lobes 1:1.4 (1.3).

Forewing veins as in generic description. Setae very sparse and randomly scattered on all veins of disc, more numerous around edges. Forewings not attaining level of apex of abdomen. Hind wing as in figure 70E.

Abdomen clothed with scattered medium size setae interspersed with larger setae in a regularly arranged pattern. Abdomen weakly sclerotized. Both sterna and terga with 1 + 1 lateral sclerotized patches (figs. 68A, B),

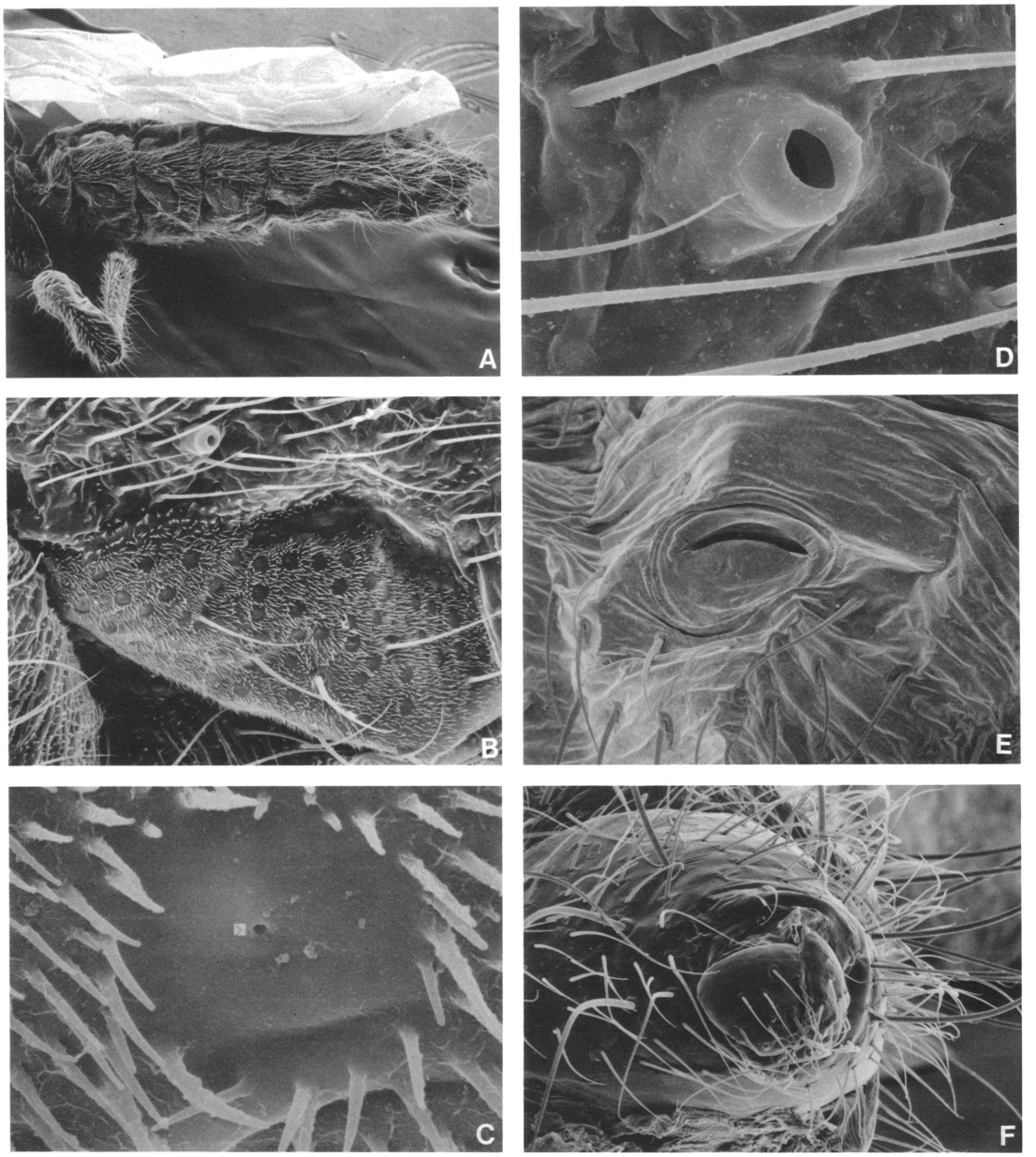


Fig. 68. *Chiricocoris dybasi*, ♀. **A**. Abdomen, lateral. **B**. Detail of sclerotized patch on abdominal sternum. **C**. Detail of a circular "bare" spot on photo B. **D**. Abdominal spiracle. **E**. Dorsal abdominal scent gland orifice. **F**. Genital capsule, posterolateral.

located on terga I–VIII, and sterna I–VII. Sternum VIII completely sclerotized. Abdominal segment IX sclerotized above, membranous below. All sclerotized abdominal patches on segments I–VIII with circular bare spots, each with a central hole (fig. 68C; possibly evaporatory or secretory structures). Spiracles on segments I–VIII, expanded (fig. 68D)

Forelegs stout. Forefemur devoid of cuticular tubercles; ratio length to width 1:0.48 (0.53). Foretibia bearing seven spines, as in

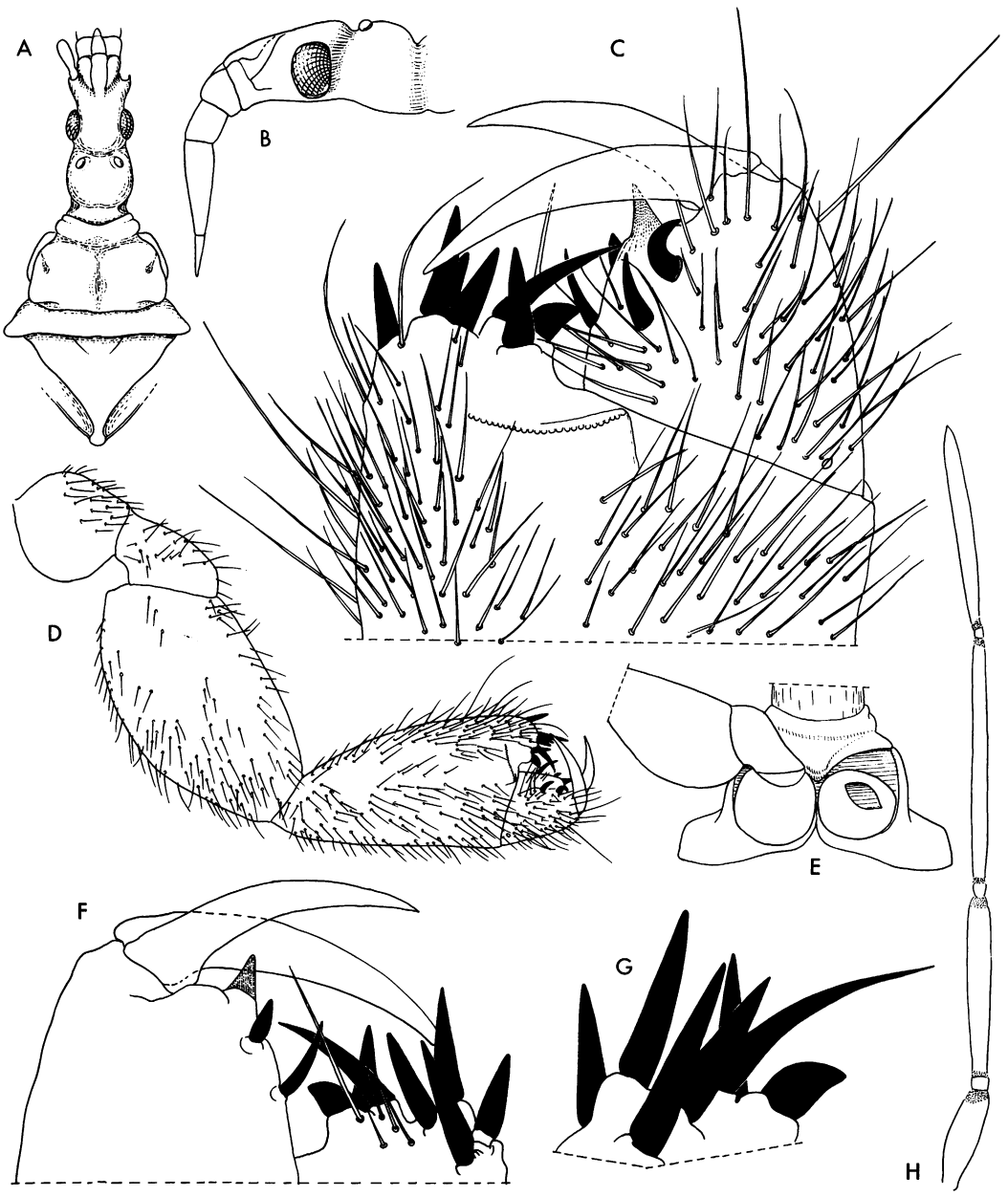


Fig. 69. *Chiricocoris dybasi*, ♀. **A**. Head, pronotum, and scutellum, dorsal. **B**. Lateral view of head. **C**. Apex of foreleg, inner surface. **D**. Foreleg. **E**. Ventral view of prothorax, showing closed condition of acetabula. **F**. Apex of foreleg, outer surface (note characteristic tarsal protuberance). **G**. Detail of foretibial spines, inner view. **H**. Antenna.

figures 69C, F, G; ratio length to width 1:0.26 (0.33). Foretarsus with four spines as in figure 69C; a distinctive conical protection present just below tarsal claws (figs. 67F, 69C). Outer claw shorter than inner.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, PANAMA: Chiriqui Province: 'Barca Area,' Finca Lerida near Boquete, 5600 ft (1713 m), March 15, 1959 (G. A. Solem; FMNH).

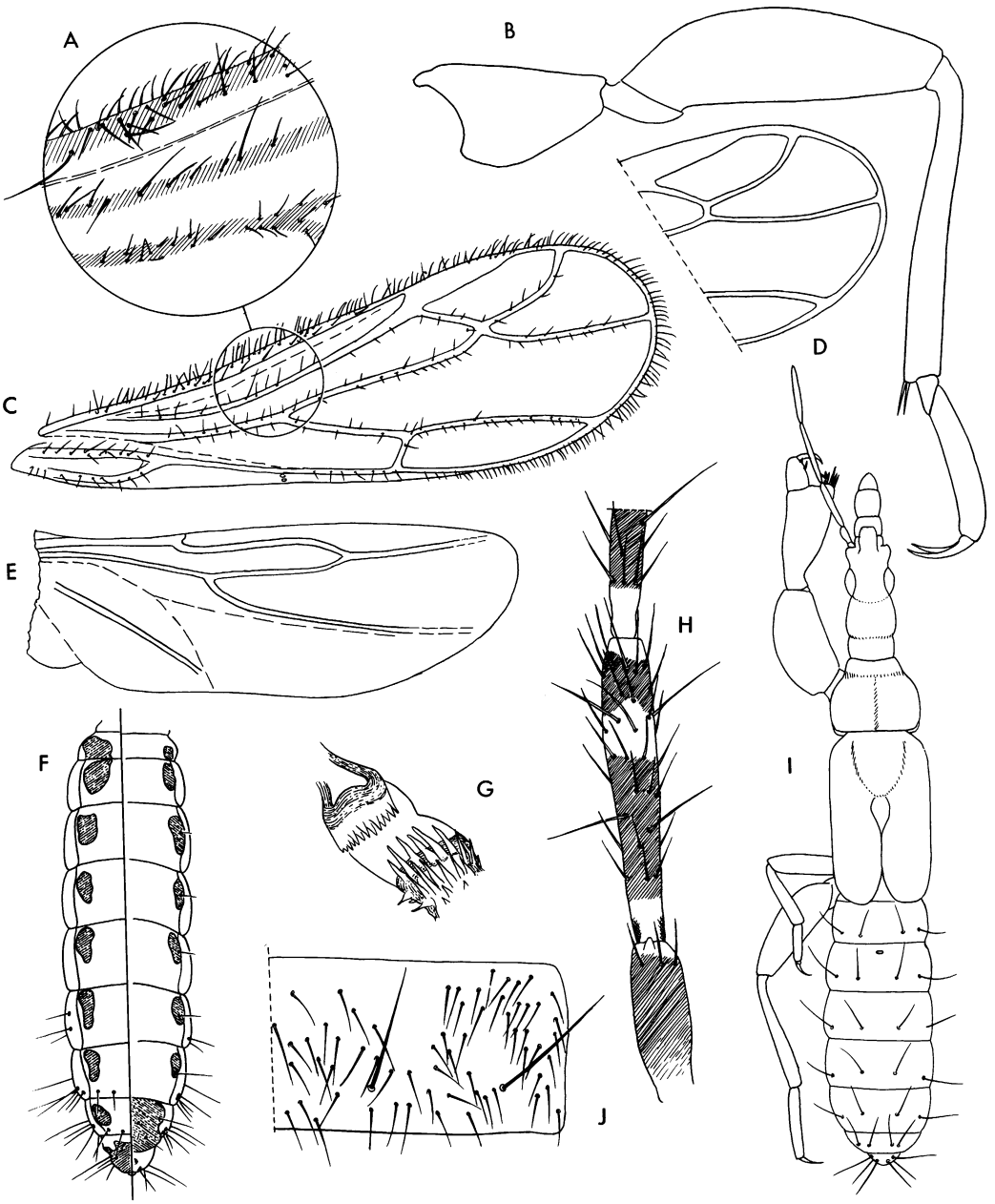


Fig. 70. *Chiricocoris dybasi*. **A–G**. ♀. **A**. Detail of forewing. **B**. Hind leg. **C**. Right forewing. **D**. Detail of apex of left forewing. **E**. Hind wing. **F**. Abdomen, left = dorsal, right = ventral. **G**. Wing coupling mechanism. **H–J**. Fifth instar nymph. **H**. Coloration of base of antenna. **I**. Dorsal view. **J**. Detail of tergum VI.

PARATYPES AND NYMPHS: PANAMA: **Chiriqui Province**: W of Finca Palo Santo near Nueva California, 4900 ft (1498 m), March, 1959 (Henry S. Dybas; FMNH), 1♀ (slide); Finca Palo Santo near Nueva California, 4900 ft (1498 m), March 9, 1959 (G. A. Solem; FMNH), 1♀; 'Barca Area,' Finca Lerida near Boquete, 5650 ft (1728 m), March 14, 1959, forest floor litter (Henry S. Dybas; FMNH) 4 nymphs (1 slide); same forest floor litter

and wood chips in logging area (Henry S. Dybas; FMNH) 4 nymphs; same litter and chips at base of cut stump (Henry S. Dybas; FMNH), 2 nymphs; W of Finca Palo Santo near Nueva California, 4900 ft (1498 m), March 9, 1959, forest floor litter in deep ravine (Henry S. Dybas; AMNH), 1 nymph.

ETYMOLOGY: Named for the late Henry S. Dybas, who collected most specimens of this species.

Enicocephalus Westwood

Enicocephalus Westwood, 1837: 22. — Usinger, 1945: 334. — Štys, 1978 (1977): 245 (summary of history of genus). — Kritsky, 1979: 91 (*Chinella* synonymized).

Henicocephalus Agassiz, 1846: 178 (objective synonym; unjustified emendation of *Enicocephalus*). — Bergroth, 1889: 319. — Lethierry and Severin, 1896: 67. — Usinger, 1932: 150, 153. — Jeannel, 1942 (1941): 323. — Štys, 1978 (1977): 245.

Chinella Usinger, 1945: 337 (erected for *E. pilosus* Champion and *emarginatus* Champion). — Kritsky, 1979: 91 (synonymy of *Chinella*).

TYPE SPECIES: *Enicocephalus flavicollis* Westwood. Fixation by original designation.

DISTRIBUTION: Five of the six previously named species of this genus are found in the Antilles; the sixth was described from Bolivia. We now show that the genus also occurs in Central America, and that there are many species in South America, extending as far south as the state of Santa Catarina in Brazil (fig. 71).

DIAGNOSIS: Outer claws of foreleg extremely small or obsolescent (fig. 72G); tarsal spine III half-moon shaped; tibia with five apical spines, the innermost one (VI) long and slender, curved toward remaining spines, generally with a subbasal hump (fig. 73A, B).

Males winged; females winged or with wings caducous. Wings without setae in lumens of cells (fig. 73D).

REDESCRIPTION:: Small to medium size species (3.5–8.0 mm). Body slightly shining to dull. Setiferous tubercles absent. Cuticular granules and evaporatory structures present in various configurations on many parts of body (fig. 72A, C–E). All setae simple, slender. All known species macropterous, but wings frequently caducous in females.

Head with deep constriction behind eyes (figs. 72A, C). Postocular portion of head subglobular to distinctly transverse, with convex sides. Eyes sexually dimorphic; eyes of males larger than those of females, attaining level of under surface of head in some cases and almost meeting below in some males. Antennae with first segment shortest, third segment longest, second and fourth somewhat shorter than third (except in *dominicus* and *ningulus*). Third and fourth segments not conspicuously thinner than second (fig. 72B). Rostrum four-segmented, in some cases reaching, but never surpassing, hind lobe of head (fig. 72D).

Pronotum unarmed (fig. 72A, C). Midlobe with a median longitudinal impression on anterior half, widened posteriorly into a deep simple fovea, not reaching back to suture dividing mid and hind lobe. Sides of disc of median lobe with 1 + 1 simple longitudinal impressions. Hind border of pronotum shallowly emarginate to deeply incised. Scutellum with elevated portion constricted subapically, transversely dilated at apex. Anterior acetabula open behind. Pronotum unkeeled laterally (fig. 74A). Meso- and metanotum as in figure 74B, each with a dorsolateral groove, serving as wing-to-body coupling guides for fore and hind wings, respectively. Thorax variously beset with cuticular granules and evaporatory structures.

Forelegs sexually dimorphic, slightly stouter in females than in males. Coxae, trochantera and femora in many species with more or less numerous minute tubercles on lower surface. Inner apical angle of foretibia with five spines (fig. 73A, B). Spines I, III, IV, and V straight, forming a cluster. VI curved towards other spines, in most cases with a subbasal hump or projection on convex surface. Foretarsus longer than wide; tarsal organ situated on outer surface of tarsus close to its dorsum. Tarsus with four spines (fig. 72G). Spine III half-moon shaped, closely adpressed to tarsus. Spines I, II and IV spiniform; II and IV long and slender, slightly curved, narrowly pointed distally; I short and stout. Foretarsus with two claws (fig. 72G), the inner one large, the outer one very small, closely adpressed to the inner one, visible only at high magnification. Apex of mid and hind tibiae with two spines and two bristle combs (fig. 73C). Mid and hind tarsi two-segmented. Claws of identical size.

Forewings with basal and discal cells. Stig-

mal cell extending beyond apex of stigma about as long as discal cell. Setae of approximately uniform size (fig. 73D), arranged in two series on most veins, including apical marginal vein, but more numerous on costal margin and R+M; in only one species (*wygodzinskyi*) setae on R+M arranged in two rows. Cells lacking setae. Forewing coupling mechanism with two arms (fig. 73E), the arm closest to the wing edge very elongate and curling up and over the other arm; shorter arm barely standing out from wing surface. Hing wing edge foliaceous and rolled inward at level of forewing coupling mechanism (fig. 73F).

Apical portion of "cell" of hind wing, beyond insertion of posterior free vein, about four times as long as wide. Anal lobe with free apical portion. Hind wing either without setae, or with setae on base of anterior vein and/or along apical margin of wing.

Abdomen of male sclerotized. Spiracles on ventral connexival plates II–VIII. Guide fused to pygophore, truncate or rounded apically (figs. 74E, 84D, 88M, N). Genitalia small in most species, but very large and beset with specialized setae in *wygodzinskyi*. In female, abdomen membranous but with regularly arranged sclerotized spots and sclerotized genital area (fig. 75E, K). Spiracles on ventral connexival plates II–VIII (fig. 74C). Abdomen in both sexes beset with cuticular granules and evaporatory structures.

Fifth instar nymph (fig. 75L). General shape stout. Eyes well developed. Antennae slender. Neck distinct. Mesothoracic wing pads meeting medially, longer than wide, rounded posteriorly. Abdomen membranous but in many species with sclerotized areas; if so, segments of abdominal dorsum with 1 + 1 small submedian and 1 + 1 or 2 + 2 sublateral sclerotized plates. Abdominal terga with ordinary setae and short hairlike cuticular processes.

DISCUSSION: We agree with Kritsky (1979) that *Chinella* is a synonym of *Enicocephalus*. Usinger (1945) separated *Chinella* from *Enicocephalus* based upon lack of a cu-1a crossvein in the forewing. We consider this condition to be teratological and have seen it elsewhere in the genus *Enicocephalus*. We have also synonymized the two species which Usinger placed in *Chinella* (see discussion under *E. pilosus*) after closely examining the types of both. Our examination of new material resembling *E. pilosus* in all other respects reveals at least some normal forewings in these specimens. Therefore, we can see no reason why *Enicocephalus* and *Chinella* should be maintained as separate genera. All specimens have the typical claw arrangement of *Enicocephalus*, with a large inner claw and a much reduced outer claw on the front leg.

KEY TO SPECIES OF *ENICOCEPHALUS*

1. General body color light scarlet, scarlet, or ruby, but wings in all cases, and legs in some cases, brown or piceous, or body predominately brown, but in such cases hind lobe of head, neck, fore and hind lobes of pronotum definitely scarlet or ruby 2
   General body color either uniform brown, or with fore and midlobes of pronotum bright orange, sharply contrasting with brown hind lobe and rest of body. Abdomen in some cases scarlet (*exophthalmus*) 6
2. Veins of disc of forewing dark as rest of wing. Forefemora with either minute ventral tubercles (fig. 92E, H) or with minute hairlike processes among larger setae (fig. 78F). Male genitalia not conspicuous. In male, anteocular distance shorter than length of eye (fig. 4B) 3
   Veins of disc of forewing all red, strongly contrasting with dark membrane; forefemora lacking minute tubercles and without minute hairlike processes among larger setae (fig. 99D); guide of male large and complex (fig. 100); in male, anteocular distance larger than length of eye ..... *wygodzinskyi* Villiers
3. Subcosta conspicuously red from its base to level of center of stigmal cell; antennae of male (female unknown) 1.5 times as long as head and pronotum combined, second antennal segment less than twice as long as first, and third almost six times as long as first (fig. 78A); forefemur lacking minute tubercles, but with minute hairlike processes among the larger setae (fig. 78F) ..... *dominicus* Bruner
   Subcosta red at base only, or in some cases reddish to center of wing; antennae shorter than head and pronotum combined; second antennal segment approximately twice as long as first (fig. 76A); forefemora with minute ventral tubercles but lacking minute hairlike processes among larger setae (fig. 98E) 4

4. Head and pronotum uniformly red; apex of forewings narrowly bordered with white (fig. 76N); outer claw of foreleg not exceedingly small (fig. 76I) ..... *cubanus* Bruner
   Head, or head and pronotum not uniformly red; apex of forewings not bordered with white; outer claw of forelegs exceedingly small (fig. 92K, 98C) 5
5. Forelobe of head darkened, but entire pronotum scarlet; eyes of male large and bulging, as long as hind lobe of head, and as wide as, or wider than, synthlipsis (fig. 98A); eyes of males in side view extending from below level of under surface of head to level of upper surface (fig. 98B) (females unknown) ..... *usingeri* Maldonado
   Forelobe of head and disc of midlobe of pronotum darkened; eyes of male of normal size, distinctly shorter than hind lobe of head and never as wide as synthlipsis (fig. 92C); eyes of male in side view smaller, reaching level of under surface of head but remote from upper surface (fig. 92G) ..... *semirufus* Barber
6. Overall color of body brown or piceous, at most forelobe and rarely midlobe of pronotum tinged with orange, but never strongly contrasting with hind lobe; wings rarely caducous (except *sturmi*) (abdomen sometimes scarlet in *exophthalmus*) 7
   Fore and midlobes of pronotum orange colored, sharply contrasting with brown or piceous head and hind lobe of pronotum; wings frequently caducous 12
7. Length 7–8 mm; wings caducous; tibial spine VI lacking distinct subbasal hump (fig. 93H, I); hind wings setose apically (fig. 94C); dorsal anterolateral and posterolateral spots of abdomen of female separate (fig. 94A) ..... *sturmi*, n. sp.
   Length 5 mm or less; wings not caducous; tibial spine VI with distinct subbasal hump (fig. 84B); hind wings setose apically or not; in known females, dorsal anterolateral and posterolateral spots of abdomen fused (fig. 86J) 8
8. Hind margin of pronotum deeply incised, cutting into hind lobe by half its length or more (figs. 84A, 87B). Cuticular granules present in narrow band along inner (ventral) surface of forefemur (fig. 84C) 9
   Hind margin of pronotum shallowly incised, never reaching midpoint of hind lobe (figs. 79B, 86A). Cuticular granules either absent from forefemur altogether, or grading into spicules and not confined to a narrow band on inner surface (figs. 79D–F) 10
9. Male very small, approximately 3.2 mm in length. Guide long and slender, at least 4 times as long as wide and spoonshaped at apex (fig. 84D). Setae of forefemur not interspersed with smaller hairlike processes (fig. 84C). Outer foretarsal claw ¼–⅓ length of inner claw ..... *neblinensis*, n. sp.
   Male slightly larger than above, 3.8–4.0 mm, female 4.5 mm in length. Guide shorter, no more than 2.5 times as long as wide and slightly truncate at apex (fig. 88M). Setae of forefemur interspersed with shorter hairlike processes (fig. 88G). Outer foretarsal claw nearly ½ length of inner claw ..... *pilosus* (Champion)
10. Male medium size, 4.3–4.7 mm in length. Body brown, but tinged with scarlet to ruby on eyes, around ocelli, on forelobe of pronotum, and on abdomen. Eyes of male bulging excessively, their width greater than synthlipsis (fig. 79B) and in side view extending entire height of head (fig. 79C). Forefemur with cuticular granules grading into spicules, the patch extending more than half the width of the article (figs. 79D–F) ..... *exophthalmus*, n. sp.
    Male and female smaller, not exceeding 4.0 mm in length. Color orange brown, brown, or piceous, but not tinged with red. Eyes of normal size. Cuticular granules absent from forefemur, although patches of spicules may be present (fig. 85J) 11
11. Overall color brown. Foretibia of male from 5–6 times as long as wide. Outer foretarsal claw short, about ¼ length of inner claw ..... *taeuberi* Jeannel
    Overall color piceous. Foretibia of male only about 4 times as long as wide. Outer foretarsal claw larger, 2/5–½ length of inner claw 12
12. Central portions of forefemur darkened. Submedian spots absent from ventral surface of female abdomen (fig. 86K) ..... *ningulus*, n. sp.
    Forefemur uniformly light in color. Submedian spots present on ventral surface of female abdomen (fig. 83K) ... *lenkoi*, n. sp.
13. Males 14
    Females 15
14. Legs uniform yellowish brown, foretibia over 4 times as long as maximum width ..... *flavicollis* Westwood
    Legs, especially forelegs, usually with centers of femora somewhat darkened; central portion of foretibia darker than ends; foretibia not over 4 times as long as maximum width ..... *tupi*, n. sp.
15. Size of female from tip of tylus to abdominal apex greater than 5 mm; foretibia distinctly

Fig. 71. Distribution of *Enicocephalus*. Described species (●). Undescribed (■).

banded (fig. 90B); forefemur with smaller hairlike processes among larger setae, and minute tubercles (not grading into toothed microtrichiae) in a wide band, about half as wide as article (fig. 91B) .... *schuhi*, n. sp.

Size of female less than 5 mm; foretibia banded or not; forefemur with or without smaller hairlike processes among larger setae, but tubercles in a narrower band along ventral edge of article (although toothed microtrichiae may extend further (figs. 97A, B, F, K) 16

16. Abdomen lacking any rows of sclerotized spots ventrally or sometimes with one poorly sclerotized row (fig. 97M); forefemur with smaller hairlike processes among larger setae (fig. 97F); foretibia faintly banded or dusky all over ..... *tupi*, n. sp.

Abdomen with three dorsal and three ventral rows of extremely distinct sclerotized spots 17

17. Anterior acetabula darkened; foretibia uniformly orange colored; anteocular portion of head dark below; eyes of female in lateral aspect relatively small, their length much less than anteocular distance (fig. 81B); foretibia as long as forefemur; forefemur 3.1 times as long as wide; anterolateral spots of dorsal surface of abdomen approximately twice as wide as submedian spots (fig. 81H); smaller hairlike processes present among larger setae of forefemur (fig. 81D) .... *guarani*, n. sp.

Anterior acetabula orange colored, as rest of propleuron; foretibia orange-yellow but with central band conspicuously darkened; anteocular portion of head orange colored below; eyes in lateral view equal to or slightly longer than anteocular distance; forefemur 2.7 times as long as wide; foretibia slightly shorter than femur; anterolateral spots of dorsal surface of abdomen much less than twice as wide as submedian spots (fig. 75E); no smaller hairlike processes among larger setae of forefemur (fig. 75D) .... *boraceianus*, n. sp.

Enicocephalus boraceianus, new species
Figures 71, 75

DISTRIBUTION: Southern Brazil.

DIAGNOSIS: *Enicocephalus boraceinanus* seems closest to *E. guarani* but differs from the latter by its orange-colored acetabula, brown banded foretibia, absence of small hairlike cuticular processes among the larger setae of the forefemora, and other details mentioned in the key.

DESCRIPTION: Males unknown. Length of female 4.6 mm, wingless. General body color piceous. Head, including tylus, piceous above, light orange-yellow below. Rostrum stramineous. Antennal segments I and II light yellowish brown, III and IV whitish. Fore and midlobe of pronotum bright orange-yellow; hind lobe piceous. Foreacetabula light orange-yellow. Foretibia stramineous with conspicuously darkened band around central half. Forefemur and entire mid and hind legs stramineous. Abdomen whitish with sclerotized genital area and regularly arranged sclerotized spots; dorsal anterolateral spots less than twice as wide as submedian spots (fig. 75E).

Head slightly shorter than pronotum (1: 1.3) (figs. 75A, C). Ratio head length to width across eyes 1:0.7. Ratio length to width of hind lobe of head 1:1.8. Ratio eye length to anteocular portion 1:0.9. Ratio width of eyes to synthlipsis 1:2.0. Eyes small in side view, not attaining level of under surface of head and remote from top. Antennal segments I–IV 1:1.6:1.8:2.1; combined length substantially shorter than head plus pronotum (1: 1.5). Rostrum as shown in figure 75C.

Pronotum as shown in figure 75A, with very deep posterior incision. Proportional width of mid to hind lobe 1:1.2.

Wings caducous, not present on specimen examined.

Forelegs as shown in figure 75D, F. Ratio length to width of forefemur 1:0.34. Setae on forefemur of uniform length, not interspersed with shorter hairlike processes. Granulose area present on inner edge of forefemur, granules gradually changing into minute spines toward center of femur and extending less than halfway across width of article on dorsal and ventral surfaces. Foretibia as shown in figures 75F, H, I; ratio length to width 1:0.31; tibial spine VI with a distinct subbasal hump. Foretarsi as in figures 75H, I; tarsal spine III half-moon shaped. Outer claw approximately one-third length of inner claw. Ratio length to width of hind femur 1:0.29.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRAZIL: Sao Paulo: Boraceia Biological Station, Municipio Salesopolis, 850 m, wet mountain forest, February, 1967 (W. L. Brown; AMNH).

ETYMOLOGY: Named for Boraceia in the state of São Paulo, where it was collected.

DISCUSSION: We have a specimen from Venezuela similar to *boraceianus* in its lack of smaller hairlike processes among the larger setae of the forefemur, and also in its yellow-orange acetabula. It differs from *boraceianus* in its larger size, unicolorous orange forelegs, and orange hind pronotal lobe.

Enicocephalus cubanus Bruner
Figures 71, 76, 77

Enicocephalus cubanus Bruner, 1924b: 54. — Usinger, 1945: 335. — Alayo, 1967: 10. — Kritsky, 1979: 94.

Henicocephalus cubanus: Jeannel, 1942 (1941): 360.

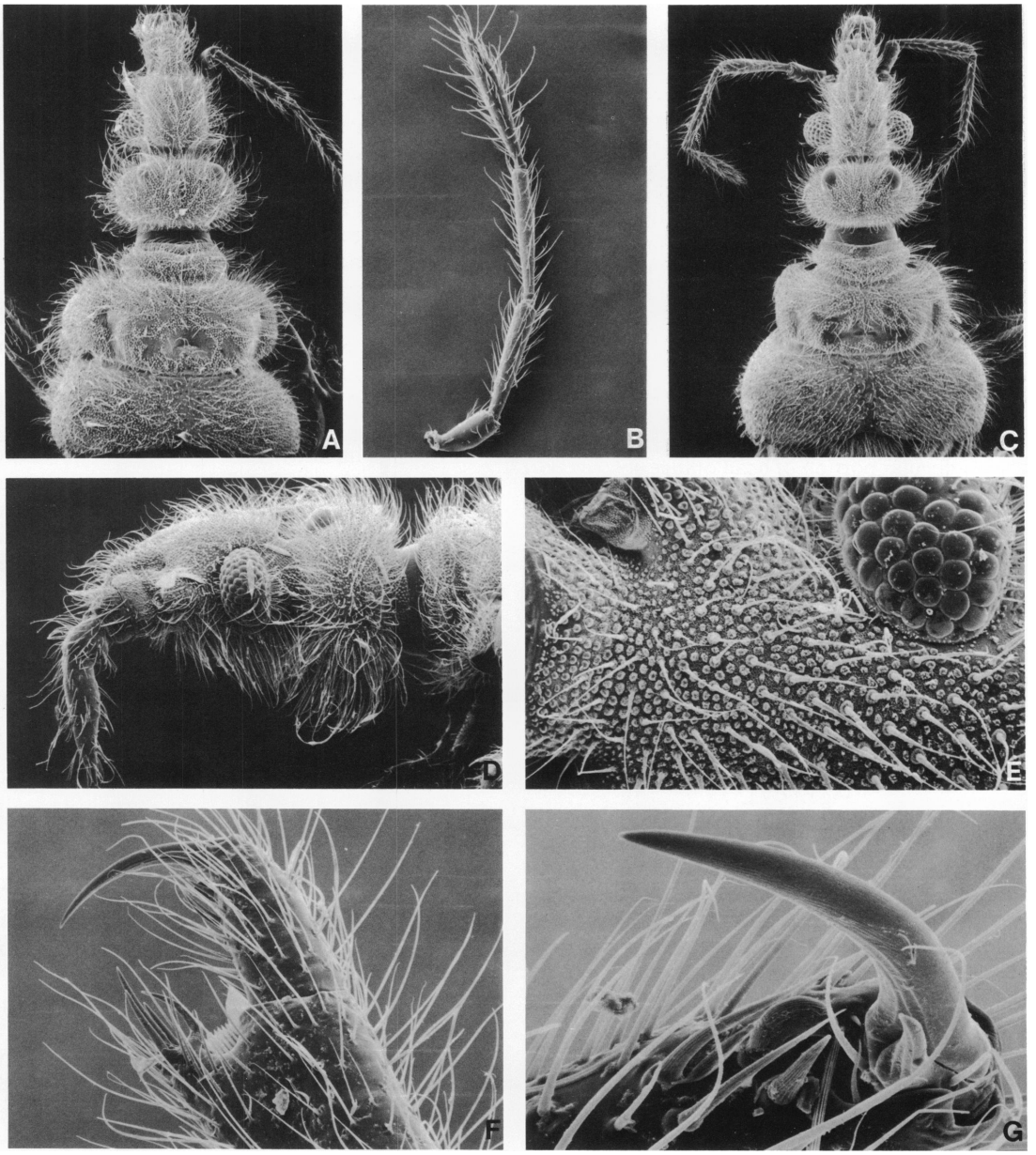


Fig. 72. *Enicocephalus ningulus*. **A**, **C**. Head and pronotum, ♀ (A), ♂ (C). **B**. Antenna, ♂. **D**. Lateral view of head, ♀. **E**. Cuticular granules on ventral (gular) surface of head. **F**. Foretibial spines, ♂. **G**. Foretarsal spines, ♂.

Enicocephalus marimutti Kritsky, 1979: 95. NEW SYNONYMY.

Enicocephalus yvonneae Kritsky, 1979: 95. NEW SYNONYMY.

DISTRIBUTION: Caribbean.

DIAGNOSIS: This is the only scarlet species with piceous forewings in which the apex of the forewings is narrowly margined with white.

REDESCRIPTION: Length of males 4.3–5.4 mm. Length of females 3.6–4.3 mm. General body color scarlet. Head and base of rostrum

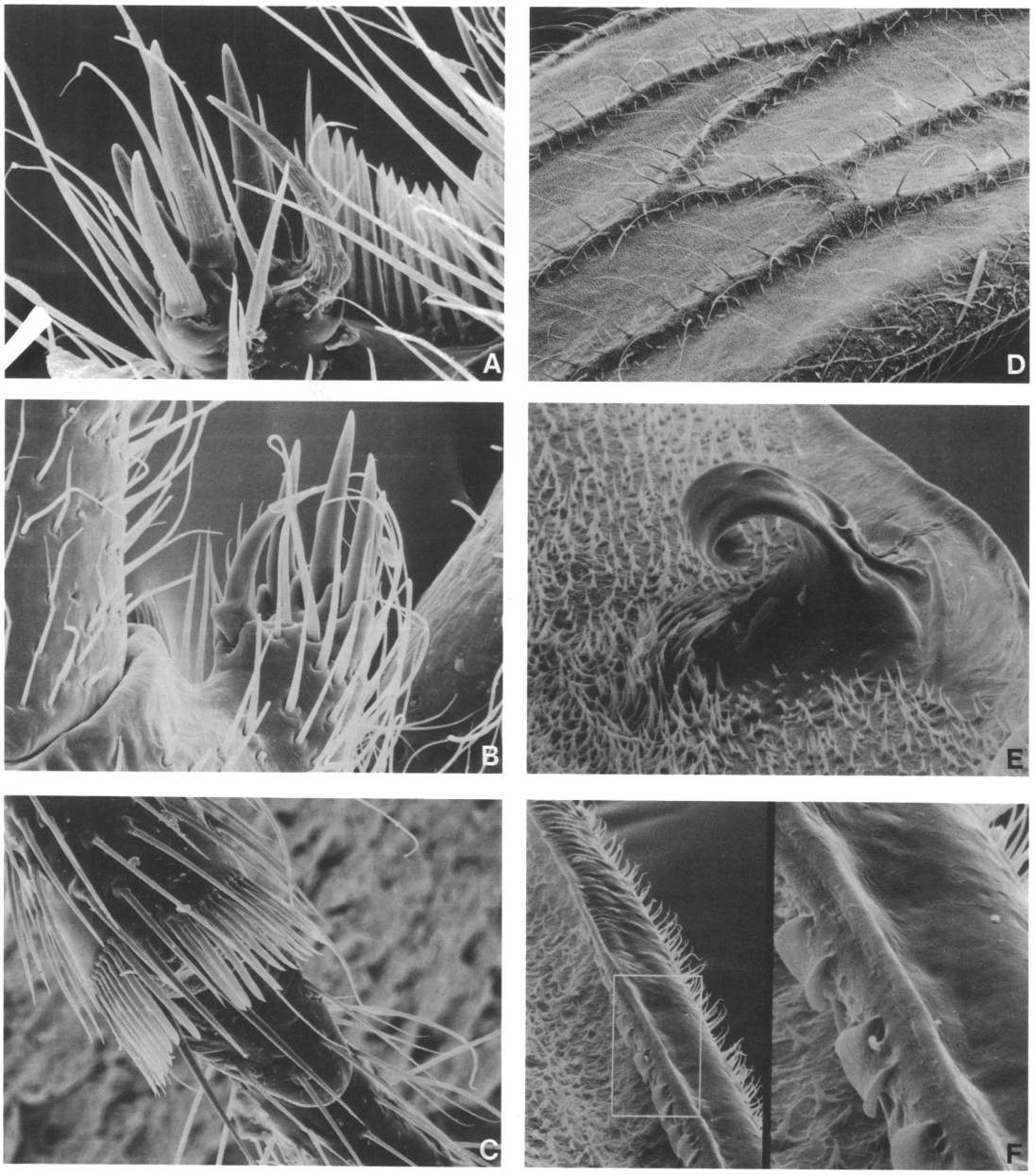


Fig. 73. *Enicocephalus ningulus*. **A**. Foretibial spines, ♂. **B**. Same, showing sub-basal hump on spine VI. **C**. Apex of hind tibia, ♂. **D**. Surface of forewing, ♀. **E**. Wing coupling mechanism on hind edge of forewing, ♂. **F**. Hind wing edge at level of wing coupling mechanism, showing foliaceous structures.

scarlet; apex of rostrum yellowish-brown. First, second, and basal half of third antennal segments light brown; apex of third and entire fourth segment stramineous. Thorax and scutellum entirely scarlet. Membrane of forewing translucent dusky brown. Veins scarlet on basal fifth of forewing, dark brown on remainder; some specimens with mid and hind tibiae and tarsi fading to orange-brown. Abdomen scarlet in both sexes. Females with light brown sclerotized plates regularly arranged on each segment.

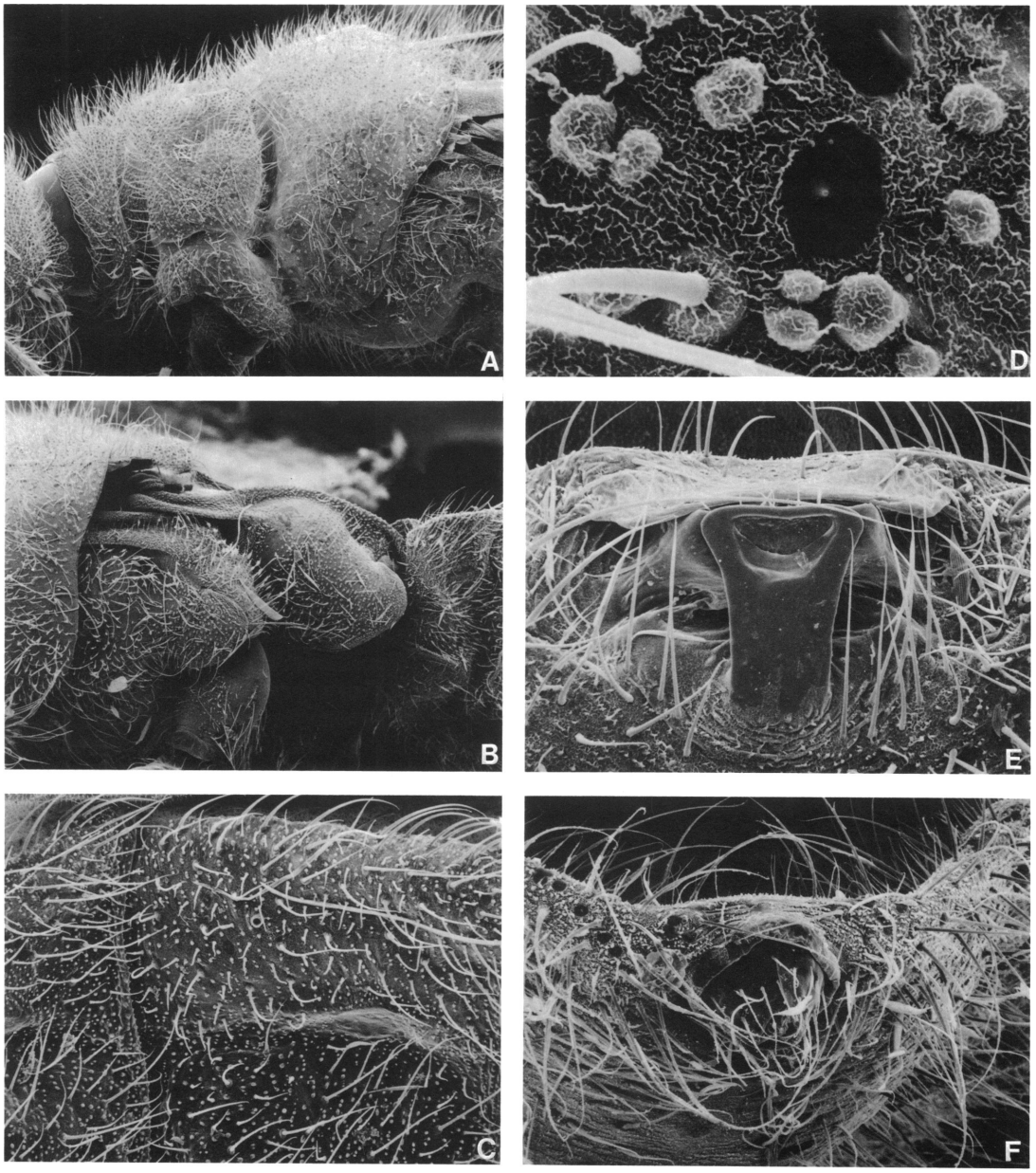


Fig. 74. *Enicocephalus ningulus*. **A**. Pronotum, lateral, ♂. **B**. Meso- and metanotum, lateral, ♀. **C**. Ventral connexival plate IV, ♂. **D**. Detail of surface of midpronotal lobe, ♀. **E**. Genitalia of ♂, posteroventral view. **F**. Genital capsule of ♀, posterolateral view.

Head shorter than pronotum, 1:1.4 in males (fig. 76C), 1: 1.3 in females (fig. 76B). Ratio head length to width across eyes 1:0.7 in both sexes. Ratio length to width of hind lobe of head 1:1.6 in males, 1:1.7 in females. Ratio length of eyes to anteocular portion 1:0.8 in males, 1:1.1 in females. Ratio width of eyes to synthlipsis 1:1.8 in males, 1:2.2 in females. Eyes of males medium size in side view, extending downwards below level of under surface of head, but remote from top (fig. 76D). Eyes of females much smaller, in no case

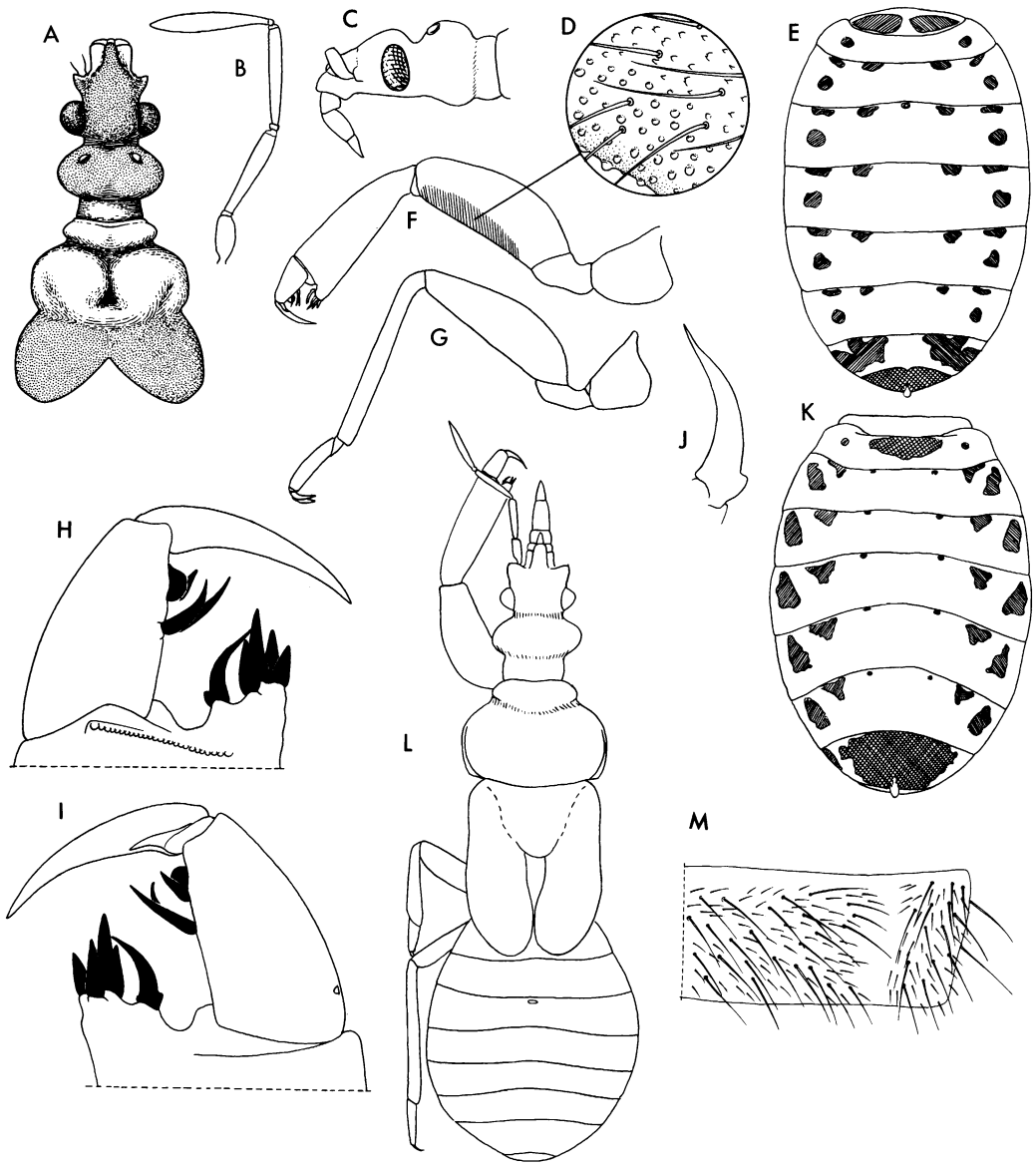


Fig. 75. *Enicocephalus boraceianus*, ♀. **A**. Head and pronotum. **B**. Antenna. **C**. Lateral view of head. **D**. Detail of inner ventral surface of forefemur, showing cuticular granules. **E**, **K**. Abdomen, dorsal and ventral views, respectively. **F**. Foreleg. **G**. Hind leg. **H**, **I**. Apex of foreleg, inner and outer views, respectively. **J**. Foretibial spine VI. **L**. Fifth instar nymph of *Enicocephalus* sp. (not necessarily *boraceianus*). **M**. Same, setation on tergum VI.

reaching level of either surface of head (fig. 76E).

Antennal segments I–IV 1:1.8:2.9:2.5 in males, 1:1.8:2.6:2.3 in females; combined length equal to head plus pronotum in males (1:1) and very slightly shorter in females (1:1.1). Rostrum as shown in figures 76D, E.

Pronotum as shown in figures 76B, C, with deep posterior incision. Proportional width of mid to hind lobes 1:1.5 in males, 1:1.2 in females.

Fore and hind wings fully developed. Forewings often teratological in their venation (figs. 77I–K). Forewings of males approxi-

mately 3 mm long, females 2.3 mm; in some pinned specimens wings extending beyond tip of abdomen, in others not attaining tip of abdomen. Setae on forewings sparse, two-ranked in all veins of disc except marginal ones. Hind wings lacking large setae apically (fig. 76-O).

Forelegs as shown in figures 76F–I. Ratio length to width of forefemur 1:0.23 in males, 1:0.34 in females. Setae on forefemur of uniform length, not interspersed with smaller spines. Granular surface structures limited to narrow band along inner edge of article (fig. 76F). Ratio length to width of hind femur 1: 0.16 in males, 1:0.23 in females. Foretibia as shown in figures 76F, H, I; ratio length to width 1:0.20 in males, 1:0.31 in females. Tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figures 76H, I; tarsal spine III half-moon shaped. Outer claw length, about one-fourth length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Sex in question (see discussion), CUBA: Sierra Maestra, near El Pico del Palma Mocha, 3000–4250 ft (938–1328 m), July 10–20, 1922 (C. H. Ballou and S. C. Bruner; collection of la Estacion Experimental Agronomica, Cuba); not examined. The type was reported by Bruner (1924b) to be in fragments.

MATERIAL EXAMINED: CUBA. – Guantanamo, San Carlos Est., Oct. 4–8, 1913 (AMNH), 1♀ [erroneously called male in original description], paratype; Buenos Aires, Trinidad Mountains, May 8–14, 1936, 2500–3500 ft (769–1400 m) (Darlington; AMNH), 2♀; June, 1939 (C. T. Parsons; AMNH), 3♀; Soledad, Santa Clara Province, June 1–7 (C. T. Parsons; AMNH), 1♀; La Gran Piedra, 25 km W of Santiago, 1250 m, forest (AMNH), 1♀. DOMINICAN REPUBLIC. – Jarabocoa, 1500–4000 ft (600–1600 m), August, 1938 (Darlington; AMNH), 1♀; foothills of Cordillera Central, S of Santiago, June, 1938 (Darlington; AMNH), 1♂. HAITI. – Fond Verrettes de Refuge, May 28, 1950 (H. B. Mills; INHS), 1♀, holotype of *E. marimutti* Kritsky; La Visite, vicinity of Belle Range, September 16–23, 1934 (Darlington; AMNH), 1♂. JAMAICA. – St. Andrew Parish, Harberton, about 1 mi SE of Content, December 29, 1957 (T. H. Farr; INHS), 1♀, holotype of *E. yvonnae* Kritsky; Falmouth, July 1961 (J. Maldonado C.; AMNH), 2♀.

DISCUSSION: Bruner (1924b) erroneously identified the paratype of *E. cubanus* as a male and briefly described it. That specimen is now in the AMNH collection and is definitely a female. Kritsky (1979) published a description of the male, but it is not clear what material he actually examined. Our description of the male of *E. cubanus* is based on two specimens from the island of Hispaniola; one is from Haiti, the other from the Dominican Republic (see Material Examined).

This is the only known species of the genus that occurs on three different islands: Cuba, Jamaica, and Hispanola. We have failed to find among the admittedly few specimens examined any taxonomically useful characters on the specific level that would allow a rational subdivision of this complex into clearly defined species. We have thus found it necessary to synonymize the existing names as follows.

We have examined the slide-mounted holotype of *Enicocephalus marimutti* Kritsky from Haiti. We found no difference between the original description of *E. cubanus* and the type of *E. marimutti*, except size. We have also seen a male specimen from Haiti and one of each sex from the Dominican Republic. There is no chromatic or morphological difference between the specimens that cannot be attributed to individual variation and sexual dimorphism, although their lengths vary from 4.1 to 5.4 mm. [The 5.4 mm male may be hypermacropterous, although it only partially conforms to Štys' list of characters associated with hypermacroptery (Štys, 1969a.] There are also no clear-cut differences between the above specimens from Hispanola and the ones from Cuba and Jamaica, although they vary in length from 3.8 to 4.2 mm. We do not consider size differences alone sufficient to define species of enicocephalids, and therefore synonymize *E. marimutti* with *E. cubanus*.

Enicocephalus yvonneae, described from Jamaica, is based on a poorly preserved female, which we have seen. Two additional females from Jamaica (Falmouth) fully agree with the type of *E. yvonneae*. According to

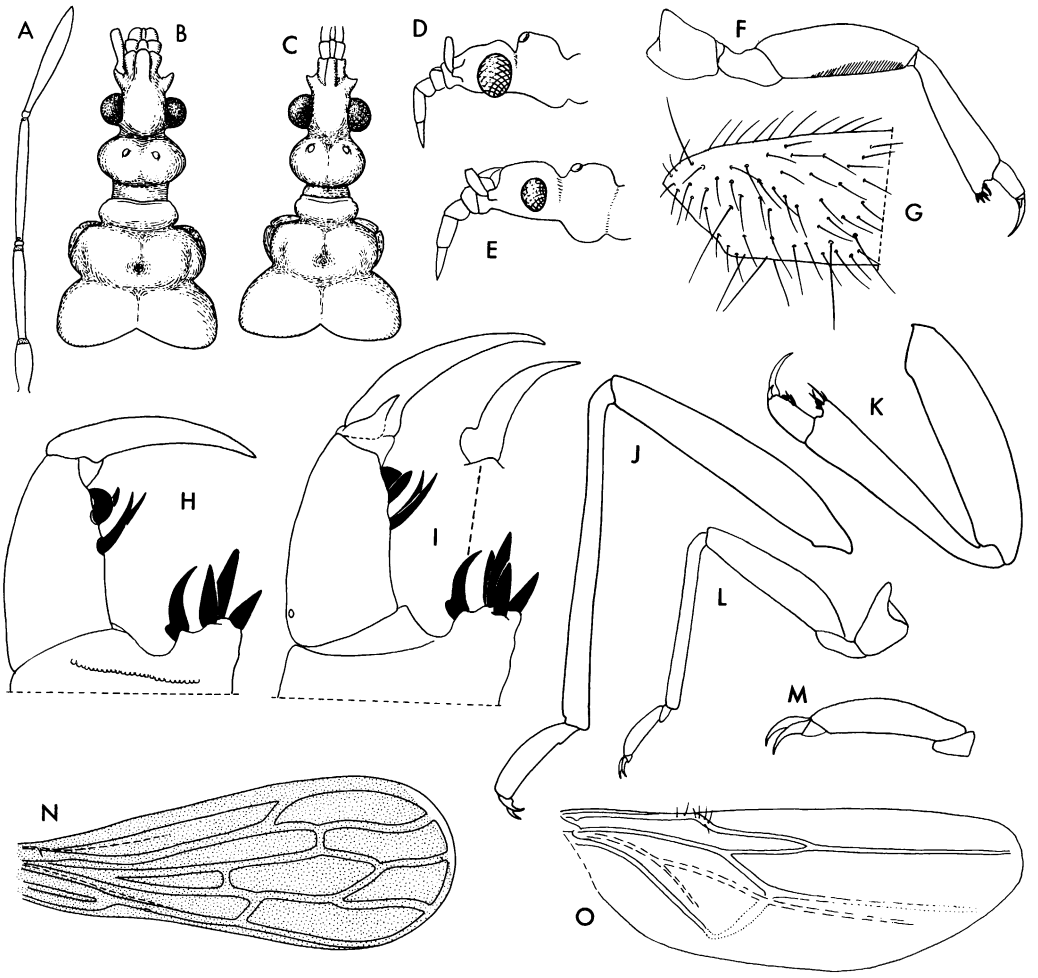


Fig. 76. *Enicocephalus cubanus*. **A**. Antenna, ♀. **B**, **C**. Head and pronotum, ♀ and ♂, respectively. **D**, **E**. Lateral view of head, ♂ and ♀, respectively. **F**. Foreleg, ♀. **G**. Detail of base of forefemur. **H**, **I**. Apex of foreleg of ♀, inner and outer surfaces, respectively. **J**. Hind leg, ♂. **K**. Foreleg, ♂. **L**. Hind leg, ♀. **M**. Hind tarsus, ♀. **N**. Forewing, ♀, showing white tip. **O**. Hind wing, ♀.

Kritsky (1979), *E. yvonneae* (3.75 mm) is distinguishable from *E. marimutti* (5.00 mm) mainly by its size. Therefore, we synonymize also *E. yvonneae* with *E. cubanus*.

We have used *Enicocephalus cubanus* to study and illustrate cases of wing teratology (fig. 77) because it demonstrates a considerable amount of variation in venation. Of 12 specimens studied, eight had both forewings normal, two had one teratological wing, and two others had both wings teratological. Here is another example of the unreliability of the venation of the enicocephalid forewing for taxonomic purposes, supporting the observations of Štys (1970a, 1981a).

Enicocephalus dominicus Bruner
Figures 71, 78

Enicocephalus dominicus Bruner, 1924a: 39. — Usinger, 1945: 335. — Kritsky, 1979: 96.
Henicocephalus dominicus: Jeannel, 1942 (1941): 360.

DISTRIBUTION: Dominica: British West Indies.

DIAGNOSIS: *E. dominicus* differs from all

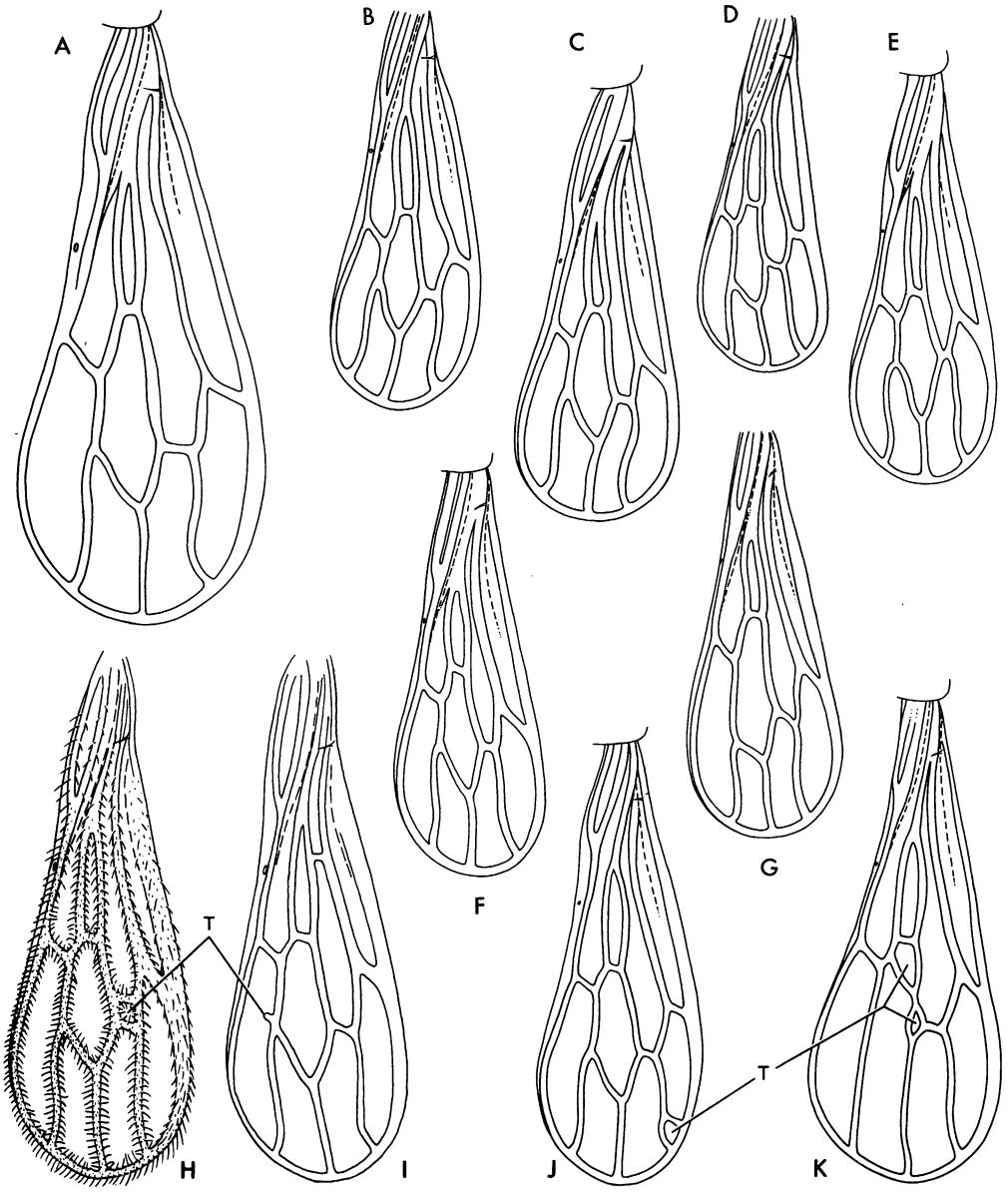


Fig. 77. *Enicocephalus cubanus*. Variation in venation and size of forewings. **A**. ♂ from Haiti (both wings normal). **B**. ♀ from Cuba (both wings normal). **C**. ♀ from Cuba (other wing teratological). **D**. ♀ from Cuba (both wings normal). **E**. ♀ from Jamaica (both wings normal). **F**. ♀ from Jamaica (both wings normal).-20**G**. ♀ from Cuba (both wings normal). **H, I**. Teratological, ♀ (data on localities not available). **J**. ♀ from Dominican Republic (other wing same). **K**. ♂ from Dominican Republic (other wing normal).

other species by the peculiar ratios of the antennal segments as shown in the key and the redescription (fig. 78A).

REDESCRIPTION: Females unknown. Length of male 4.3 mm. General body color scarlet. Head and base of rostrum orange yellow tinged with scarlet; apex of rostrum yellow. First and second antennal segments medium brown; third segment and basal two-thirds of fourth segment light brown fading to yellow-

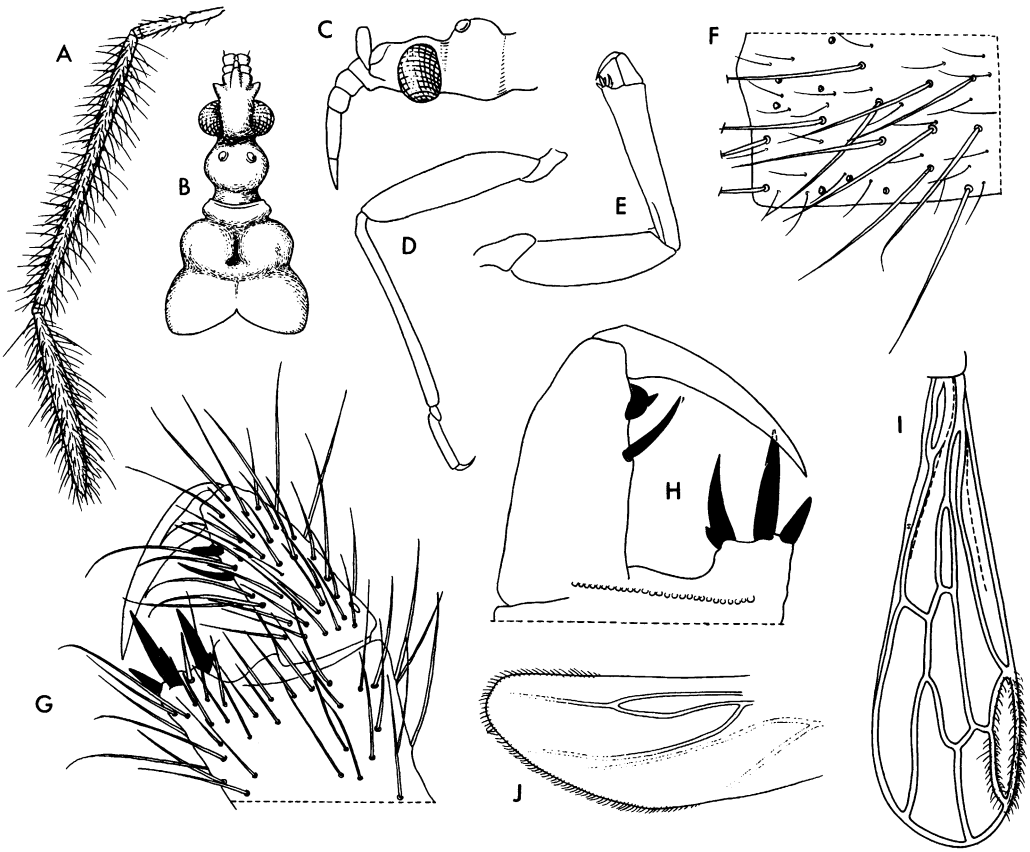


Fig. 78. *Enicocephalus dominicus*, ♂ (holotype). **A**. antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Hind leg. **E**. Foreleg.-20**F**. Anterodorsal angle of forefemur. **G**, **H**. Apex of foreleg, outer and inner surfaces, respectively. **I**. Forewing. **J**. Hind wing.

ish white by apex of fourth. Entire thorax, including scutellum, light scarlet. Membrane of forewings translucent light brown; veins scarlet along costal margin and on basal fifth of wing, opaque yellowish on rest of wing. Legs orange-yellow, tinged with scarlet; distal halves of mid and hind tibiae becoming brownish orange. (Abdomen of holotype missing; the whole specimen looks as if it may have faded.)

Head shorter than pronotum, 1:1.2 (fig. 78B). Ratio head length to width across eyes 1:0.7. Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular distance 1:0.7; ratio width of eyes to synthlipsis 1:1.2. Eyes very large in side view, extending downward some distance beyond level of under surface of head, and upward nearly to level of top of head (fig. 78C).

Antennal segments I–IV 1:1.2:5.9:3.8 (fig. 78A), combined much longer than head plus pronotum (1:0.6). Rostrum as shown in figure 78C.

Pronotum as shown in figure 78B, with a deep posterior incision. Proportional width of mid to hind lobes 1:1.3. Fore and hind wings fully developed (figs. 78I, J); forewings 2.8 mm long. Setae two-ranked on inner veins of forewing, randomly arranged at edges. Large setae of veins interspersed with smaller ones, especially along costal edge of wing. Hind wings setose around edge on entire apical half.

Forelegs as shown in figures 78E–H. Ratio length to width of forefemur 1:0.26. Large setae on forefemur interspersed with smaller ones. Ratio length to width of hind femur 1: 0.23. Ratio length to width of foretibia 1:

0.23. Tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figures 78G, H; tarsal spine III half-moon shaped. Outer claw fairly long, approximately one-third length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BRITISH WEST INDIES: Dominica: Long Ditton, June 20, 1911 (no collector; AMNH).

DISCUSSION: This species is known only from the holotype, which we have examined. Although the abdomen is missing, we have determined that it is a male by the large eyes and the relatively slender foretibiae.

Enicocephalus exophthalmus, new species
Figures 71, 79

DISTRIBUTION: Haiti.

DIAGNOSIS: *Enicocephalus exophthalmus* seems closest to *E. usingeri*; males of both have extremely large eyes, at least as wide as the synthlipsis. They can be distinguished from one another by the color of the thorax, which is brown in *E. exophthalmus* and scarlet in *E. usingeri*.

DESCRIPTION: Females unknown. Length of males 4.3–4.7 mm. General body color brown. Head dark brown tinged with red, especially around ocelli; eyes dark reddish-brown. Rostrum, antennal segments I–III, and basal half of segment IV light brown; apical half of segment IV whitish. Forelobe of pronotum varying from scarlet to brown; mid and hind lobes uniform brown. Scutellum either uniform brown or tinged with scarlet posteriorly. Forewings light dusky brown with slightly darker veins; basal one-fourth of Sc tinged with scarlet. Abdomen whitish brown tinged variably with scarlet. Forelegs dark brown, fading to yellowish at joints and on tarsi. Mid and hind legs light yellowish brown, sometimes with scarlet at distal ends of femora.

Head slightly longer than pronotum (1:0.9; fig. 79B). Ratio head length to width across eyes 1:0.6. Ratio length to width of hind lobe of head 1:1.8. Ratio length of eyes to anteocular portion 1:0.7; ratio eye width to synthlipsis 1:1. Eyes of males large in side view, extending from nearly top of head to below level of under surface of head (fig. 79C). Antennal segments I–IV 1:3.5:3.5:2.4, combined very much longer than head plus pronotum (1:0.6). Rostrum as shown in figure 79C.

Pronotum as shown in figure 79B, with a deep posterior incision. Ratio width of mid to hind pronotal lobes 1:1.4.

Forewings with discal cell remote from wing tip (fig. 79G). Setae on veins of forewing randomly arranged on costa and at wing base; those in center of disc and at apex distinctly two-ranked. Hind wing not setose apically.

Forelegs as shown in figures 79D–F, H, J. Ratio length to width of forefemur 1:0.28. Ventral surface of forefemur with granular structures; setae interspersed with smaller hairlike processes. Hind femur illustrated in figure 79I; ratio length to width 1:0.20. Ratio length to width of foretibia 1:0.23; tibial spine VI with a distinct subbasal hump. Tarsal spine III sickle-shaped. Outer claw of medium length, about one-fifth size of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, HAITI: Desbarriere, Mt. La Hotte, near 4000 ft (1600 m), October 12–14, 1934 (Darlington; AMNH).

Paratype: HAITI: La Visite and vicinity, La Selle Range 5000–7000 ft (2000–2800 m), September 16–23, 1934 (Darlington; AMNH), 1♂, paratype.

ETYMOLOGY: From the Greek *exophthalmos*, meaning "with bulging or protruding eyes."

DISCUSSION: We have three forewings available, two of which are teratological. One case is especially interesting (fig. 79K) because the wing lacks the vein which defines the distal end of the discal cell (cu-1a crossvein). This condition resembles that of *Systelloderes*.

Enicocephalus flavicollis Westwood
Figures 71, 80

Enicocephalus flavicollis Westwood, 1837: 23. — Jeannel, 1942 (1941): 325. — Usinger, 1945: 335. — Kritsky, 1979: 97.

Henicocephalus flavicollis Bergroth, 1889: 319. — Lethierry and Severin, 1896: 67.

DISTRIBUTION: Lesser Antilles: St. Vincent Island.

DIAGNOSIS: *Enicocephalus flavicollis* is the northernmost and only Antillean species with a conspicuously bicolorous pronotum.

REDESCRIPTION: Females unknown. Length of male 4.1 mm. General body color piceous. Upper surface of head, including clypeus, pi-

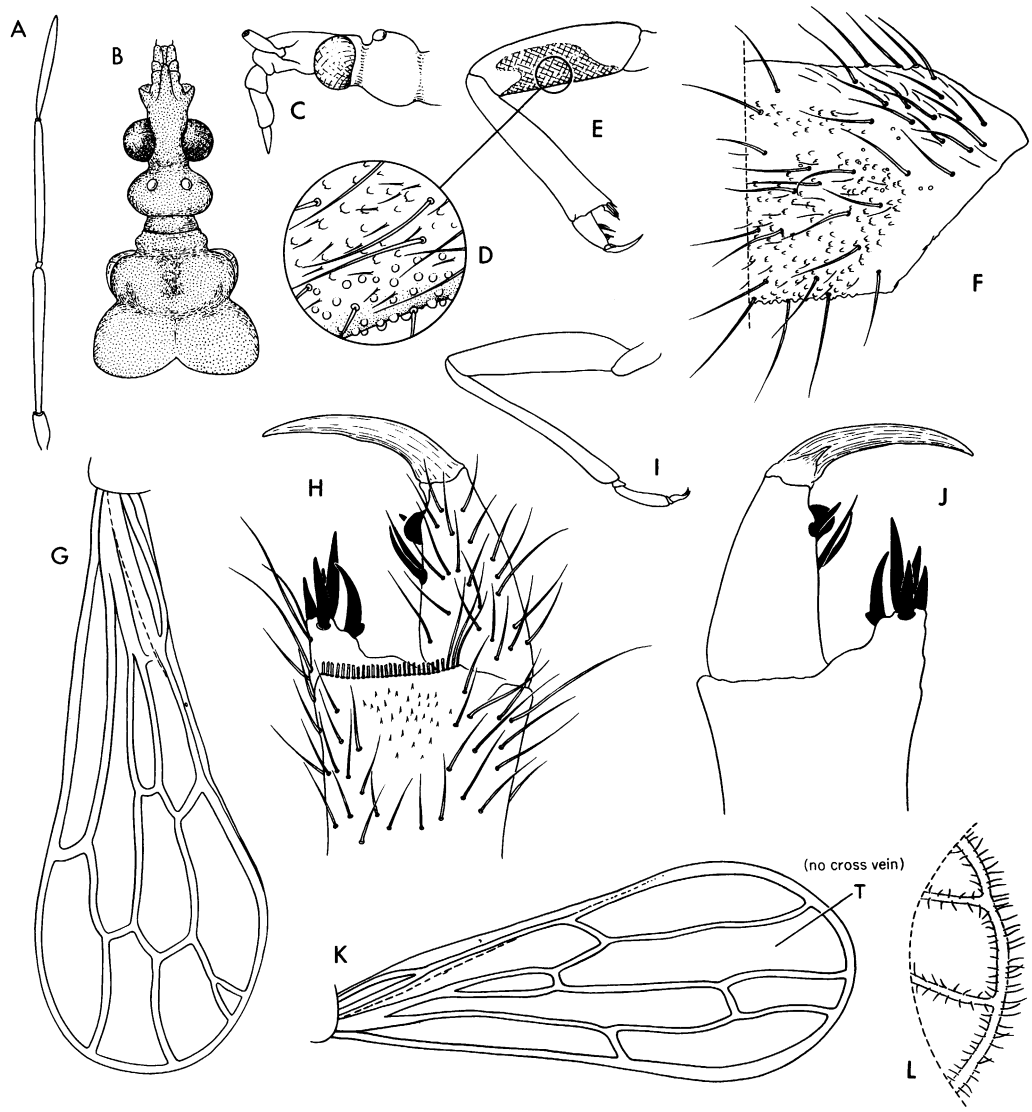


Fig. 79. *Enicocephalus exophthalmus*, ♂. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Detail of inner (ventral) surface of foreleg. **E**. Foreleg. **F**. Detail of inner surface of foreleg, near trocantur. **G**. Forewing with extra cell near apex. **H, J**. Apex of foreleg, inner and outer surface, respectively. **I**. Hind leg. **K**. Forewing, missing crossvein forming discal cell. **L**. Detail of apex of forewing.

ceous. Under surface of head piceous between eyes, and orange-yellow beneath hind lobe. Rostrum and neck orange-yellow. Antennal segments I and II piceous; III and extreme base of IV lighter brown; remainder of IV orange-yellow. Forewings dark. Legs, including coxae, and anterior acetabula orange-yellow; neither femora nor tibiae perceptibly darkened. Abdomen whitish.

Head slightly shorter than pronotum (1:1.2). Ratio head length to width across eyes 1:0.6 (fig. 80A). Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular portion 1:0.7. Ratio width of eyes to synthlipsis 1:1.6. Eyes small, in side view never attaining level of under surface of head and remote from top (fig. 80B). Under surface of head, especially hind lobe, bearded. Antennal segments I–IV 1:2:2.3:2.3, combined, slightly shorter than head plus pronotum (1:1.3). Rostrum as shown in figure 80B.

Pronotum with deep posterior incision

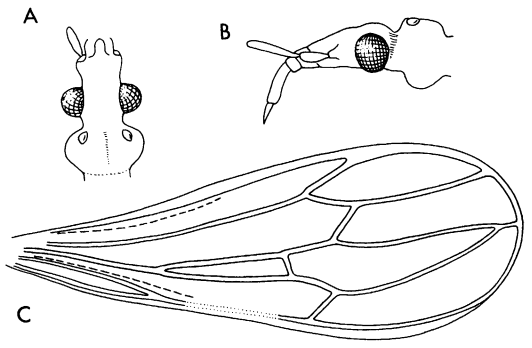


Fig. 80. *Enicocephalus flavicollis*, ♂ (holotype). **A**. Head. **B**. Lateral view of head. **C**. Forewing.

(after Jeannel, 1942 [1941]). Proportional width of mid to hind lobe of pronotum 1:1.5.

Fore and hind wings fully developed. Venation of forewings as shown in figure 80C; apex of discal cell approaching wing tip closely.

Ratio length to width of forefemur 1:0.24. Granules on forefemur occupying a narrow band along under surface of article. Ratio length to width of foretibia 1:0.23.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, LESSER ANTILLES: Saint Vincent Islands, 1837 (Hope Dept. Zoology, Univ. of Oxford), examined.

DISCUSSION: *Enicocephalus flavicollis* is the genotype. We have examined the holotype and have found it to agree quite well with the original description. Several features may merit futher discussion, however.

Neither Westwood (1837) nor Jeannel (1942 [1941]) mentioned the narrow orange stripe along the anterior edge of the hind pronotal lobe. This condition differs from that of the South American species that have bicolorous pronota, in which the change from orange to brown occurs abruptly between the mid and hind pronotal lobes.

Another striking feature of the type is the fact that the apex of the discal cell closely approaches the wing tip. Our illustration of the veins does not agree with either Westwood's or Jeannels's in regard to cell proportions or presence or absence of certain veins. We hesitate to use the closeness of the discal cell to the wing tip as a specific character because of our experience with frequent wing teratologies in other members of the genus.

Enicocephalus guarani,
new species
Figures 71, 81

DISTRIBUTION: Southern Brazil.

DIAGNOSIS: *Enicocephalus guarani* seems closest to *E. boraceianus* but differs from the latter by its darkened acetabulae, uniformly orange-colored foretibiae, presence of small hairlike processes among the larger setae of the forefemora, and other details mentioned in the key.

DESCRIPTION: Males, unknown. Length of female (without wings) 4.5–4.6 mm. General body color piceous. Head piceous above, fading to light brown or orange below. Rostrum and clypeus bright orange-yellow. First antennal segment orange-yellow; second dark brown proximally, fading to light brown or orange apically; third segment medium brown at base, fading to orange or yellow apically; fourth light yellow to stramineous. Fore and midlobes of pronotum bright orange-yellow; hind lobe piceous. Entire pronotum shiny beneath setae. Anterior acetabula darkened. Foretibiae and femora orange-yellow. Mid and hind tibiae and femora stramineous with barely perceptible dusky band around central portion of each article. Abdomen whitish with sclerotized genital area and regularly arranged sclerotized spots; dorsal anterolateral spots short but very wide, nearly twice as wide as submedian spots (fig. 81H).

Head slightly shorter than pronotum (1:1.3; fig. 81B). Ratio head length to width across eyes 1:0.7. Ratio length to width of hind lobe of head 1:1.8. Eyes relatively small, in lateral view, not reaching level of under surface or upper surface of head (fig. 81C). Ratio length of eyes to anteocular portion 1:1.2. Ratio width of eyes to synthlipsis 1:2.4. Antennal segments I–IV 1:2.1:2.8:2.4 (fig. 81A), combined slightly shorter than head plus pronotum (1:1.2). Rostrum as shown in figure 81C.

Pronotum as illustrated in figure 81B, with deep posterior incision. Proportional width of mid to hind lobe 1:1.2.

Wings caducous, not present on specimens examined.

Forelegs as shown in figures 81D, E, G, J. Ratio length to width of forefemur 1:0.31. Setae on forefemur interspersed with minute hairlike processes. Granulose area present on

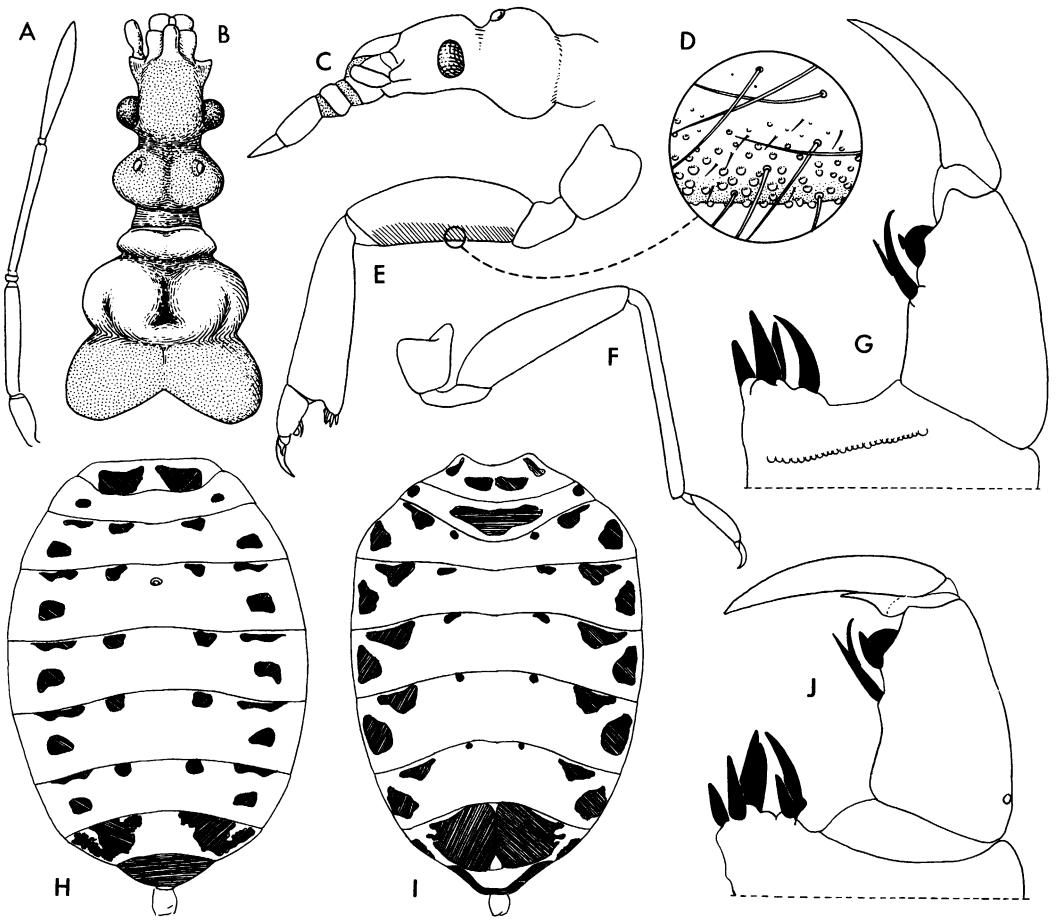


Fig. 81. *Enicocephalus guarani*, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Detail of inner (ventral) surface of forefemur, showing cuticular granules. **E**. Foreleg. **F**. Hind leg.-20**G**, **J**. Apex of foreleg, inner and outer surfaces, respectively. **H**, **I**. Abdomen, dorsal and ventral views, respectively.

inner edge of forefemur, granules fading out toward center of femur and extending less than halfway across article on dorsal and ventral surfaces. Ratio length to width of hind femur 1:0.24. Foretibia as shown in figures 81E, G, J; ratio length to width 1:0.32; tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figures 81G, J; tarsal spine III half-moon shaped. Inner claw small.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BRAZIL: Santa Catarina: Nova Teutonia, July 24, 1969 (F. Plaumann; AMNH).

PARATYPES: BRAZIL: **Santa Catarina**: Nova Teutonia, July 24, 1969 (F. Plaumann; Ashlock collection) 1♀; Ibicare, July 1959 (F. Plaumann; AMNH), 1♀ (on slide).

ETYMOLOGY: Named for one of the great language groups of central South America.

Enicocephalus lenkoi, new species
Figures 71, 82, 83

DISTRIBUTION: Brazil: São Paulo.

DIAGNOSIS: *Enicocephalus lenkoi* seems closest to *E. ningulus* but can be distinguished from it by the uniformly light forefemora and the presence of submedian spots on the ventral surface of the female abdomen.

DESCRIPTION: Length of male 3.8–3.9 mm, of female 3.6–3.8 mm.

General body color piceous. Head piceous; rostrum light yellowish brown. Antennal segments I–III brown; fourth segment brown at

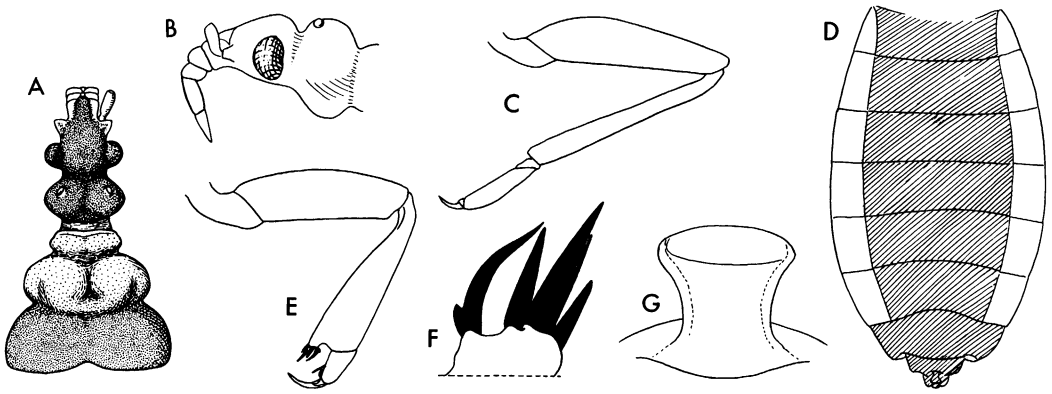


Fig. 82. *Enicocephalus lenkoi*, ♂. **A**. Head and pronotum. **B**. Lateral view of head. **C**. Hind leg. **D**. Abdomen, dorsal view. **E**. Foreleg. **F**. Tibial spines of foreleg. **G**. Guide.

base, light yellowish on distal two-thirds. Forelobe of pronotum light orange-brown; midlobe orange-brown to piceous; hind lobe piceous. Forewings entirely dusky brown with translucent membranes and denser veins. Legs brown to light yellowish brown, variable. Tarsi light yellowish brown. Abdomen of female (fig. 83K, L) whitish with sclerotized genital area and regularly arranged sclerotized spots; anterolateral and posterolateral spots fused dorsally; submedian spots present ventrally. Abdomen of male entirely sclerotized, darker along midline and lightly colored along connexiva. Male genitalia as in figure 82G.

Head slightly shorter than pronotum, 1:1.2 in males (fig. 82A), 1:1.1 in females (fig. 83B). Ratio head length to width across eyes 1:0.6 in both sexes. Ratio length to width of hind lobe of head 1:1.8 in males, 1:1.9 in females. Ratio length of eyes to anteocular portion 1:1.1 in males, 1:1.2 in females. Ratio width of eyes to synthlipsis 1:2.1 in males, 1:2.4 in females. Eyes of both sexes small, not extending to level of either upper or lower surface of head.

Antennal segments I–IV 1:2.2:2.4:2.6 in males, 1:2.1:2.4:2.5 in females. Antenna shorter than head plus pronotum (1:1.3 in both sexes). Rostrum as shown in figure 82B, 83C.

Pronotum as illustrated in figures 82A, 83B, with shallowly incised posterior margin. Proportional width of mid to hind lobes 1:1.3 in males, 1:1.2 in females. Fore and hind wings fully developed. Forewings of males 2.3 mm in length, those of females 2.1–2.2 mm, extending 0.1–0.4 mm beyond tip of abdomen in pinned specimens. Venation as shown in figure 83I; discal cell remote from apex of wing. Setae on wing veins interspersed with smaller hairlike processes. Setae randomly arranged on veins at base of wing and along edge of apex; setae on central veins two-ranked.

Forelegs as shown in figures 82E, 83E. Ratio length to width of forefemur 1:0.28 in males, 1:0.29 in females. Setae on forefemur of uniform length, not interspersed with shorter hairlike processes (fig. 83F). Surface of forefemur smooth with no granular area present (fig. 83F). Ratio length to width of hind femur 1:0.26 in both sexes. Foretibia as shown in figures 82E, F, 83E, G, H; ratio length to width 1:0.31 in males, 1:0.33 in females. Tibial spine VI with distinct subbasal hump. Foretarsi as in figures 83G, H; tarsal spine III half-moon shaped. Outer claw long, approximately one-half length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BRAZIL: São Paulo: Barueri, March 19, 1967 (Lenko; Museo de Zoologia, São Paulo).

PARATYPES AND NYMPHS: BRAZIL: **São Paulo**: Barueri, March 19, 1967 (Lenko; AMNH, MZSP) 1♂, 3♀ (one on slide), 2 nymphs.

ETYMOLOGY: Named for its collector, Mr. Karol Lenko.

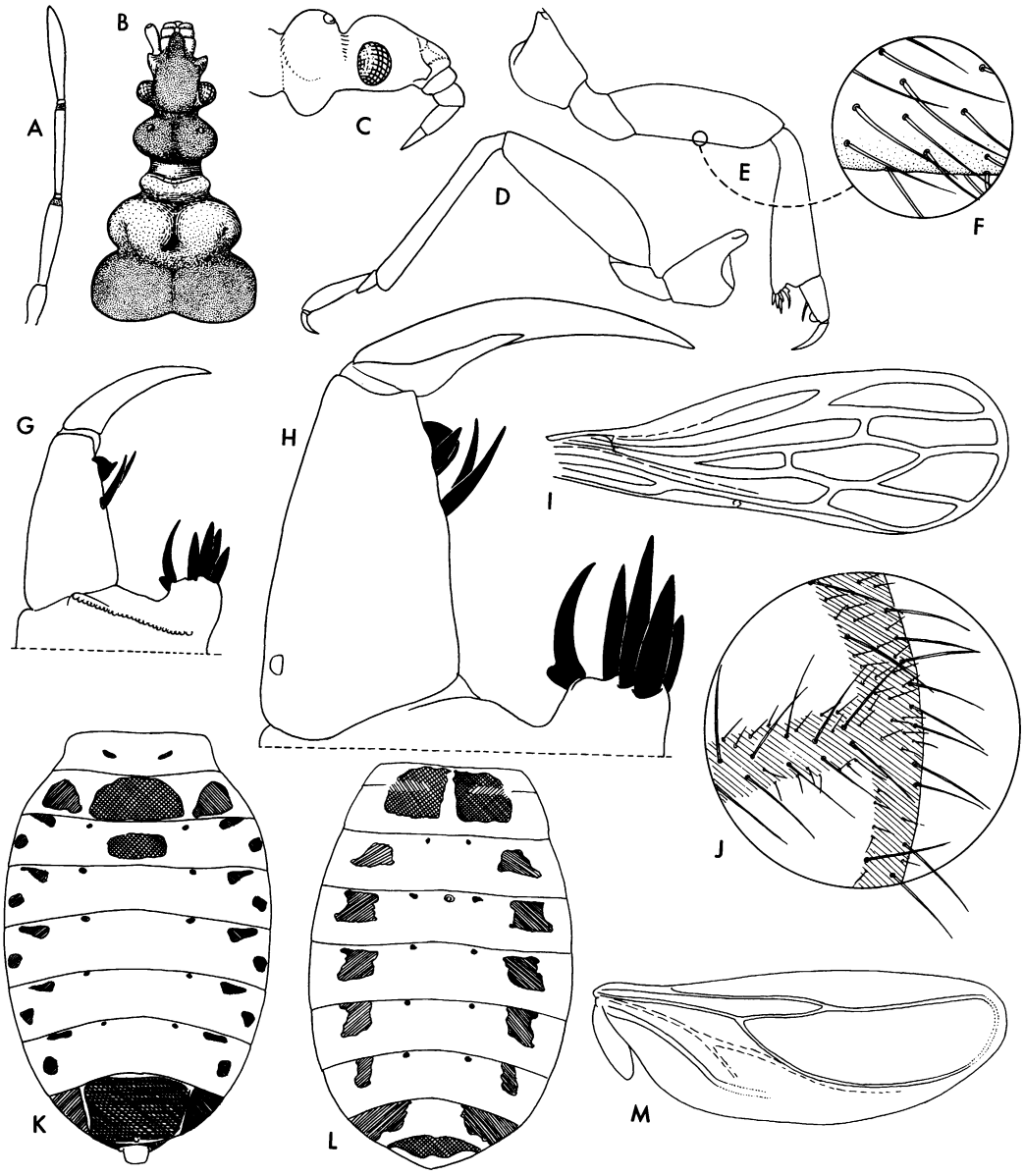


Fig. 83. *Enicocephalus lenkoi*, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Hind leg. **E**. Foreleg. **F**. Detail of inner (ventral) surface of forefemur. **G**, **H**. Apex of foreleg, inner and outer surfaces, respectively. **I**. Forewing venation. **J**. Apex of forewing. **K**, **L**. Abdomen, ventral and dorsal views, respectively. **M**. Hind wing.

Enicocephalus neblinensis, new species
Figures 71, 84

DISTRIBUTION: Know only from Cerro de la Neblina, Venezuela.

DIAGNOSIS: *Enicocephalus neblinensis* can be distinguished by its brown color, small size, thin third antennal segment, and slender guide, which is spoon-shaped at its apex.

DESCRIPTION: Females unknown. Length of male 3.2 mm.

General body color brown. Eyes piceous, head very dark brown. Pronotum, scutellum, and abdomen medium brown; rostrum,

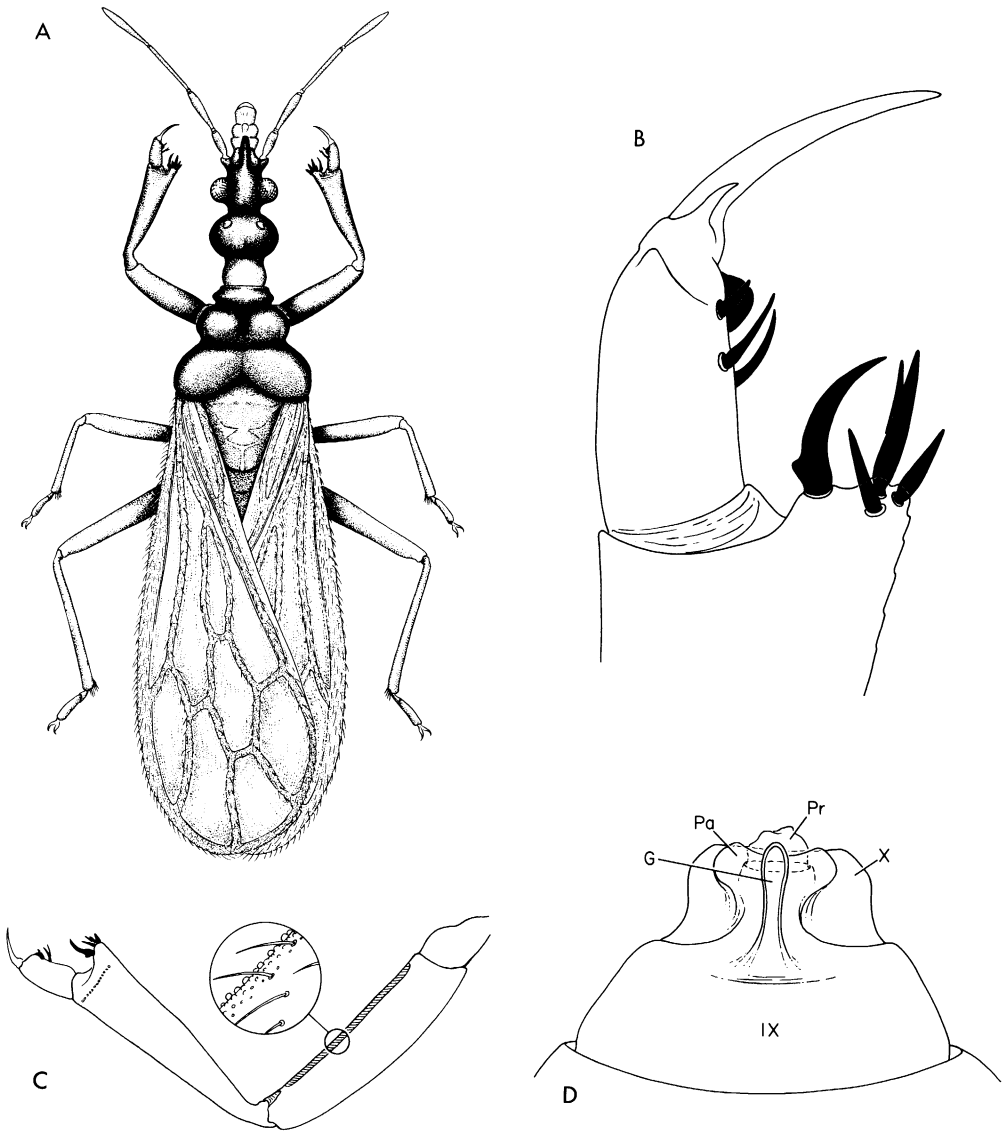


Fig. 84. *Enicocephalus neblinensis*, ♂. **A**. Dorsal view. **B**. Apex of foreleg, outer view. **C**. Foreleg, inner view, showing band of cuticular granules. **D**. Genitalia, ventral view.

neck, legs, and wings somewhat lighter. Dark brown tylus contrasting with light color of underlying rostrum, head with lighter colored neck. Mid and hind legs light brown; forelegs slightly darker. Antennal segments I and II darker than III and IV.

Head slightly shorter than pronotum (1: 1.2) (fig. 84A). Ratio head length to width across eyes 1:0.7. Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular portion 1:0.6. Ratio width of eyes to synthlipsis 1:2.0.

Antennal segments I–IV 1:1.6:1.9:1.9, combined length slightly shorter than head plus pronotum (1:1.3). Segments I and II twice as thick as segment III (fig. 84A).

Pronotum as illustrated in figure 84A, with a deep posterior incision. Proportional width of mid to hind lobes 1:1.5.

Wings present, longer than abdomen, with normal venation (fig. 84A).

Forelegs as shown in figures 84B, C. Ratio length to width of forefemur 1:0.24. Setae on forefemur subequal in length, not inter-

spersed with shorter hairlike processes (fig. 84C). Cuticular granules present, but limited to a narrow band on inner (ventral) surface (fig. 84C). Ratio length to width of hind femur 1:0.17. Foretibia as shown in figure 84B, C; ratio length to width 1:0.24. Tibial spine VI with a distinct subbasal hump. Foretarsus with spine III half-moon shaped. Outer claw ¼–⅓ length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, VENEZUELA: T. F. Amazonas: Cerro de la Neblina, Basecamp, 140 m, 0°50'N, 66°10'W, flight intercept trap in rain forest, January 26–31, 1985 (P. J. and P. M. Spangler, R. A. Faitoute, and W. E. Steiner; USNM).

PARATYPE: Same data as for holotype, but February 21–28, 1985 (Spangler et al.; AMNH), 1♂.

ETYMOLOGY: The name of this species is taken from its collection locality in southern Venezuela.

Enicocephalus ningulus, new species

Figures 71–74, 85, 86

DISTRIBUTION: Eastern coastal region of Brazil; known from Pernambuco and Rio de Janeiro.

DIAGNOSIS: *Enicocephalus ningulus* seems closest to *E. lenkoi* but can be distinguished from it by the darkened central portions of the forefemora and the absence of submedian sclerotized spots on the ventral surface of the female abdomen (fig. 86K).

DESCRIPTION: Length of male 3.8–4.2 mm, of female 3.0–4.0 mm. General body color dark brown to piceous. Head piceous; rostrum yellow to light yellowish brown. Antenna medium to light brown, the fourth segment slightly lighter than the first three. Forelobe of pronotum light orange-brown to piceous; middle and hind lobes brown to piceous. Forewings entirely dusky brown with translucent membranes and denser veins. Legs brown to light yellowish brown; forelegs, especially, darker at centers of articles and lighter at joints. Forecoxae light orange-brown to brown. Tarsi light yellowish brown. Abdomen of female (fig. 86J, K) whitish with sclerotized genital area and regularly arranged sclerotized spots; anterolateral and posterolateral spots fused dorsally; submedian spots missing (or fused) ventrally. Abdomen of male (fig. 85H) entirely sclerotized, with terga, sterna, and genital area heavily so; connexiva lightly sclerotized. Male genitalia as in figures 74E, 85K.

Head shorter than pronotum, varying from 1:1.1 to 1:1.4 in males (fig. 72C) and 1:1.3 in females (fig. 72A). Ratio head length to width across eyes 1:0.7 in both sexes. Ratio length to width of hind lobe of head 1:1.6 in males, 1:1.7 in females. Ratio length of eyes to anteocular distance 1:0.8 in males, 1:1.2 in females. Ratio width of eyes to synthlipsis 1:2 in males, 1:2.4 in females. Eyes of males medium in side view, extending downward farther than level of under surface of head, but remote from upper surface (fig. 85E); eyes of females smaller, not quite reaching level of under surface of head (fig. 72D). Antennal segments I–IV 1:2.1:2.2:2.4 (fig. 72B), combined slightly shorter than head plus pronotum (1:1.2). Rostrum as shown in figure 72D.

Pronotum as shown in figures 72A, C, posterior margin shallowly to moderately incised. Proportional width of mid to hind lobes in male 1:1.5, in female 1:1.2.

Fore and hind wings fully developed, but frequently teratological in their venation (figs. 86L, N, the latter lacking veins altogether). Forewings of males 2.4–2.7 mm in length, of females 2.2–2.4 mm, extending 0.3–0.5 mm beyond tip of abdomen in pinned specimens. Venation as shown in figure 85A; discal cell remote from apex of wing. Setae on veins of base of wing and on Sc randomly arranged; those on main disc of wing distinctly two-ranked. Hind wing not setose apically (figs. 86M, O).

Forelegs as shown in figures 85C, D, G, J, 86D, F, G. Ratio length to width of forefemur 1:0.22 in males (1:0.25 in the two specimens from Pernambuco), 1:0.29 in females. Setae on forefemur of uniform length, not interspersed with shorter hairlike processes (fig. 85J). Surface of forefemur smooth with no granular area present, but with a patch of several-toothed microtrichiae (figs. 85G, J). Ratio length to width of hind femur 1:0.18 in males (1:0.20 in Pernambuco males), 1:0.25 in females. Ratio length of foretibia to width 1:0.23 in males, 1:0.29 in females. Tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figures 72G; tarsal spine III sickle-shaped. Outer claw long, approximately two-fifths length of inner claw.

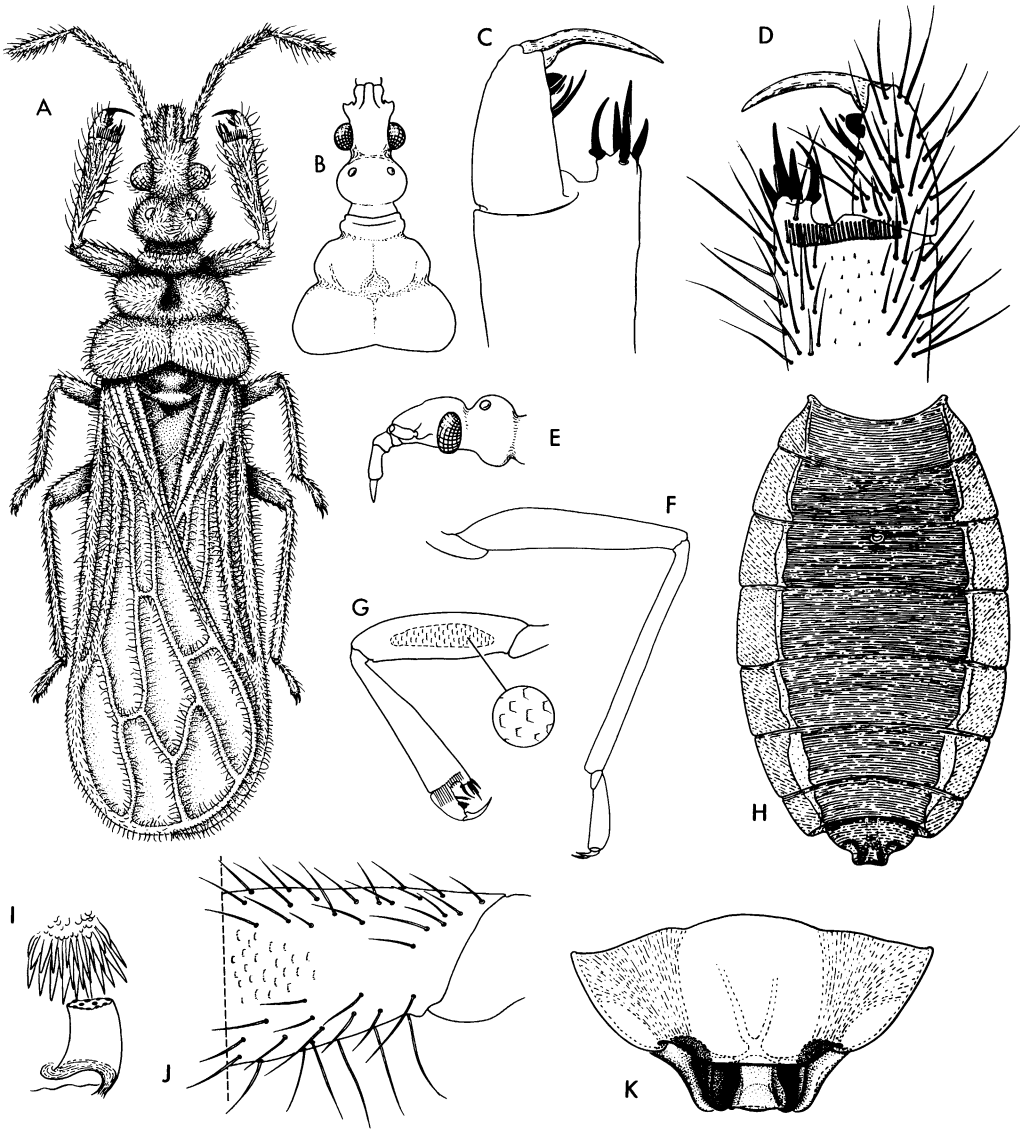


Fig. 85. *Enicocephalus ningulus*, ♂. **A**. Dorsal view. **B**. Head and pronotum. **C**, **D**. Apex of foreleg, outer and inner views, respectively. **E**. Lateral view of head. **F**. Hind leg. **G**. Foreleg, showing toothed cuticular structures. **H**. Dorsal view of abdomen. **I**. Wing coupling mechanism on hind edge of forewing. **J**. Detail of inner surface of foreleg. **K**. Ventral view of genital region.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRAZIL: Rio de Janeiro: Corcovado, August 12, 1945 (P. Wygodzinsky; AMNH).

PARATYPES: BRAZIL: **Rio de Janeiro**: Guanabara, Represa Rio Grande, January, 1972 (M. Alvarenga; AMNH), 1♂; Corcovado, Represa do Cabeca, January 12, 1947 (Wygodzinsky; AMNH), 1♀; Mangaratiba, Parada Ribiera, February 2–December 19, 1959 (Alceu and Arnaldo; MNR), 1♀; Guanabara, Represa Rio Grande, January–February, 1972 (M. Alvarenga; AMNH), 1♂ and 2♀ (one used for SEM).

OTHER SPECIMENS EXAMINED: BRAZIL: **Pernambuco**: Caruaru, 900 m, May–June, 1972 (J. Lima; AMNH) 6♂ (one used for SEM).

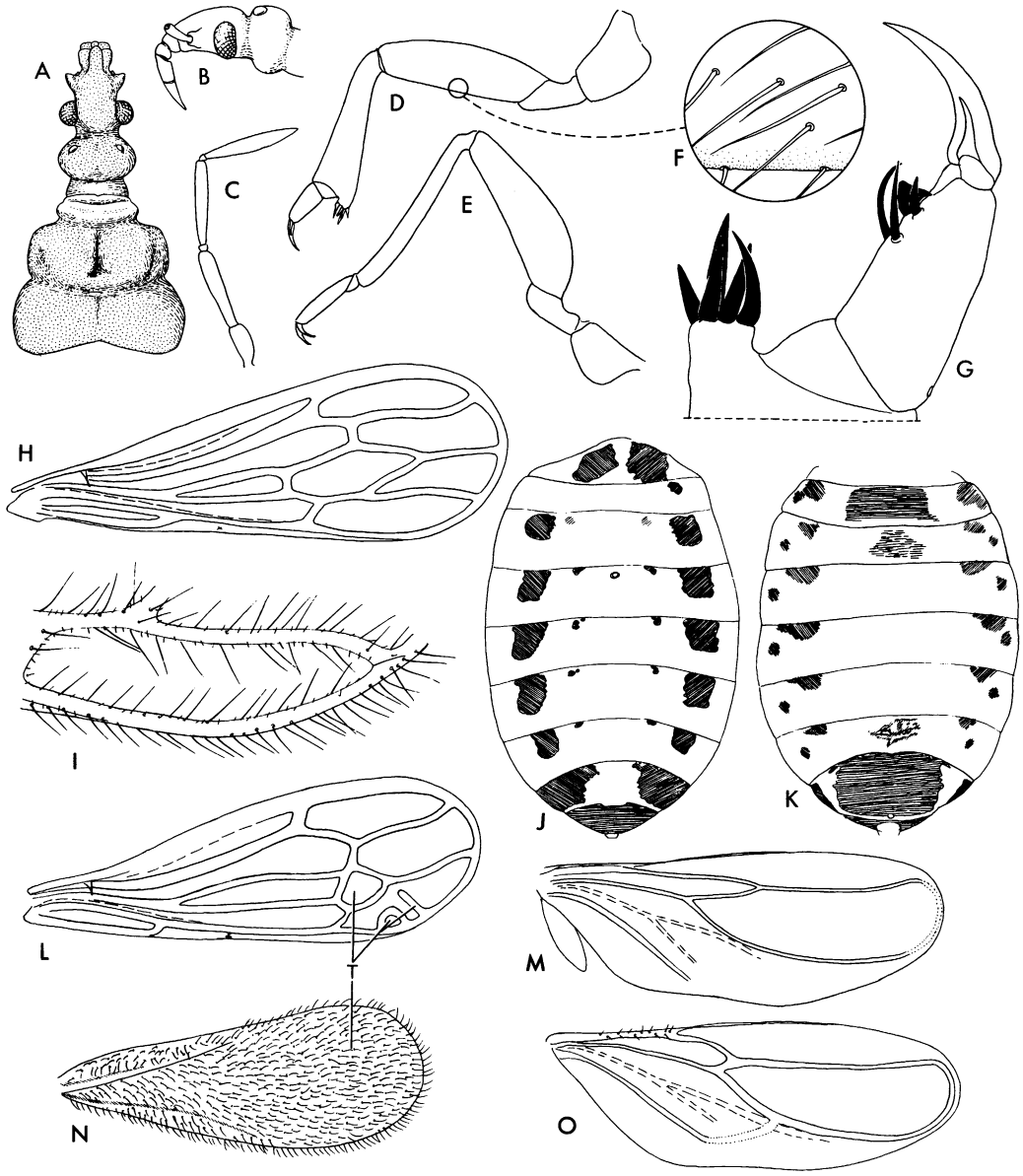


Fig. 86. *Enicocephalus ningulus*. **A**. Head and pronotum, ♀. **B**. Lateral view of head, ♂. **C**. Antenna, ♀. **D**. Foreleg, ♀. **E**. Hind leg, ♀. **F**. Detail of inner (ventral) surface of forefemur. **G**. Apex of foreleg, outer surface. **H**. "Normal" forewing. **I**. Detail of forewing setation. **J**, **K**. Abdomen, dorsal and ventral views, respectively. **L**, **N**. Teratological forewings. **M**, **O**. Hind wings.

ETYMOLOGY: From the Latin *ningulus* meaning "nobody," in reference to its lack of distinguishing characters.

DISCUSSION: Since Pernambuco is so widely separated geographically from Rio de Janeiro, there is some question as to whether our specimens from these two areas are conspecific. The general body color matches perfectly and the proportions are the same with the exception of slightly shorter fore and hind femora in the Perambuco specimens. Both have microscopic toothed structures on their forefemora, lack cuticular granules and smaller interspersed hairs on this article, and have long outer tarsal claws. In short, we can find no consistent distinguishing features.

This species is sympatric with *E. tupi* but is not closely related to it.

Teratology of the forewings is frequent in the Enicocephalidae, but one of the modifications shown here for *ningulus* (fig. 86N) is amazing indeed. In most cases, a given modifications will be found only on one of the forewings, the other one being either normal, or showing a different modification. The practically veinless forewing illustrated here is identical with the other forewing; we have not observed this teratological condition in any other group of enicocephlids. It most closely, if superficially, resembles the normal condition in *Alienates* males.

Enicocephalus pilosus (Champion)
Figures 71, 87–89

Henicocephalus pilosus Champion, 1898: 160. — Jeannel, 1942 (1941): 325.
Henicocephalus emarginatus Champion, 1898: 161. — Jeannel, 1942 (1941): 325. NEW SYNONYMY.
Chinella emarginatus Usinger, 1945: 337.
Chinella pilosus Usinger, 1945: 337.
Enicocephalus pilosus Kritsky, 1979: 98.
Enicocephlaus emarginatus: Kritsky, 1979: 97.

DISTRIBUTION: Guatemala; Panama.

DIAGNOSIS: This is the only small uniformly brown species of *Enicocephalus* known from Central America. It has an extremely deep incision in the hind margin of the pronotum.

REDESCRIPTION: Length of males 3.8–4.0 mm. Length of female 4.5 mm. General body color brown. Head, pronotum, underside of thorax, antennal segments I–III, and base of segment IV varying from medium to dark brown. Apex of antennal segment IV and rostrum whitish yellow. Forewings translucent brown with slightly darker veins. Forefemora and mid and hind legs light yellowish; foretibiae and tarsi brown. Abdomen whitish with brown sclerotized genital area.

Head as shown in figures 87B, 88D, 89D. Head length subequal to pronotum length, 1:1.1 in males, 1:1.0 in female. Ratio head length to width across eyes 1:0.6 in both sexes. Ratio length to width of hind lobe of head 1:1.6 in males, 1:2.1 in female. Ratio length of eyes to anteocular portion 1:0.7 in males, 1:1.5 in female. Ratio width of eyes to synthlipsis 1:1.6 in males, 1:2.8 in female. Eyes of males of medium size in side view, just reaching level of under surface of head but remote from top (fig. 88A). Antennal segments I–IV 1:2.1:2.5:2.8 in males, 1:2:2.4:2.4 in female, shorter than head plus pronotum (1:1.4 in males, 1:1.1 in female). Rostrum as shown in figures 87C, 88A, 89A.

Pronotum as shown in figures 87B, 88D, 89D, with a very deeply incised posterior margin. Proportional width of mid to hind lobes 1:1.5 in males, 1:1.2 in female.

Fore and hind wings fully developed. Venation of normal forewing with discal cell remote from wingtip (fig. 88J); teratological forewings as shown in figures 87B, 88H, I, 89F. Setae on veins of forewings randomly arranged at wing base and on Sc, sparsely two-ranked on main disc of wing. Hind wings setose apically (fig. 88L).

Forelegs as shown in figures 87D, E, 88B, G, 89E. Ratio length to width of forefemur 1:0.20 in males, 1:0.27 in female. Setae on forefemur interspersed with smaller hairlike processes (fig. 88G). Granular structures present on ventral surface of forefemur (fig. 88G). Hind femur as shown in figure 88F; ratio length to width 1:0.24 in males, 1:0.26 in female. Foretibia as shown in figures 87F, G, 88C, K, 89B, C; ratio length to width 1:0.22 in males, 1:0.26 in female. Tibial spine VI with distinct subbasal hump. Foretarsal spine III sickle-shaped. Outer claw long, nearly half the length of inner claw.

Genitalia as in figure 88M, N.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, GUATEMALA: Cerro Zunil (no collector; BM); examined.

MATERIAL EXAMINED: GUATEMALA. – El Reposo (no collector; BM), 1♂ (holotype of *Henicocephalus emarginatus* Champion): PANAMA. – El Valle, January 1947 (N. L. H. Krauss, USNM), 2♂; Canal Zone, Summit, January 1947 (N. L. H. Krauss, USNM), 1♂.

DISCUSSION: We here synonymize *Henicocephalus emarginatus* Champion with *H. pilosus* Champion. The type and only specimen of *H. pilosus* is a female; the type and other three specimens of H. *emarginatus* are males, thus giving rise to the difference in proportions between the two supposed species. The greatest differences in proportion between the above occur in those characters where sexual dimorphism is most pro-

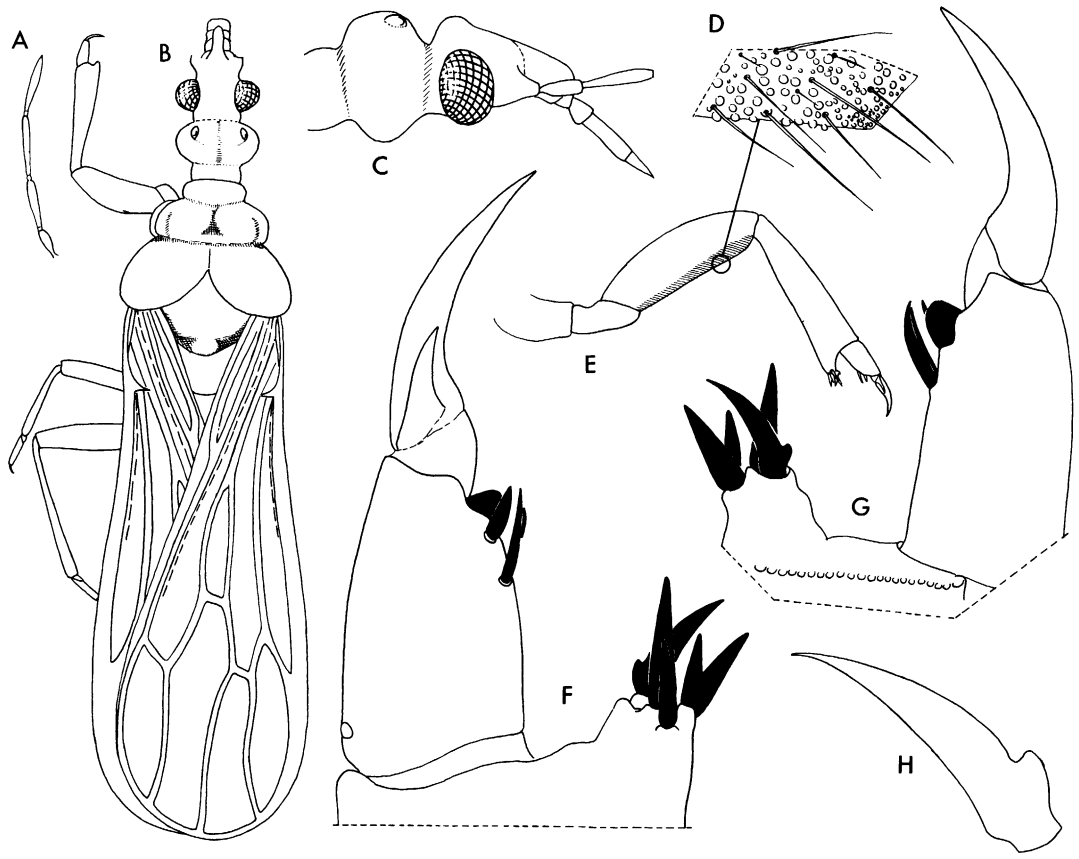


Fig. 87. *Enicocephalus pilosus*, ♂ (drawn from former holotype of *emarginatus*). **A**. Antenna. **B**. Dorsal view. **C**. Lateral view of head. **D**. Detail of inner (ventral) surface of forefemur, showing cuticular granules. **E**. Foreleg. **F**, **G**. Apex of foreleg, outer and inner surfaces, respectively. **H**. Foretibial spine VI, showing sub-basal hump.

nounced in the rest of the genus, i.e., eye length to anteocular distance and eye width to synthlipsis. In appearance these two Central American species look strikingly similar.

Wing teratologies are common in the genus *Enicocephalus* and our material of *E. pilosus* is no exception. The following is a summary of wing teratologies in the five specimens that we examined:

Female holotype of *Enicocephalus pilosus*: both wings teratological, missing cu-1a crossveins (fig. 89F).

Male of *E. emarginatus*: one wing as above, other not known (fig. 87B).

Male from Panama, Canal Zone: one wing normal, the other extremely atypical with many small cells (fig. 88I).

Male from Panama, El Valle: one wing normal, the other with a small additional cell at the cu-1a crossvein (fig. 88H).

Male from Panama, El Valle (slide): both wings normal. (fig. 88J).

We consider lack of a cu-1a crossvein in type specimens of *pilosus* and *emarginatus* to be teratological. Since these and the other three specimens examined by us are strikingly similar in all other respects, and since wing venation proves so inconsistent in this group (see discussion under *E. cubanus*), we are treating all five specimens as *E. pilosus*.

Enicocephalus schuhi, new species

Figures 71, 90, 91

DISTRIBUTION: Southern Brazil.

DIAGNOSIS: This is the largest species pos-

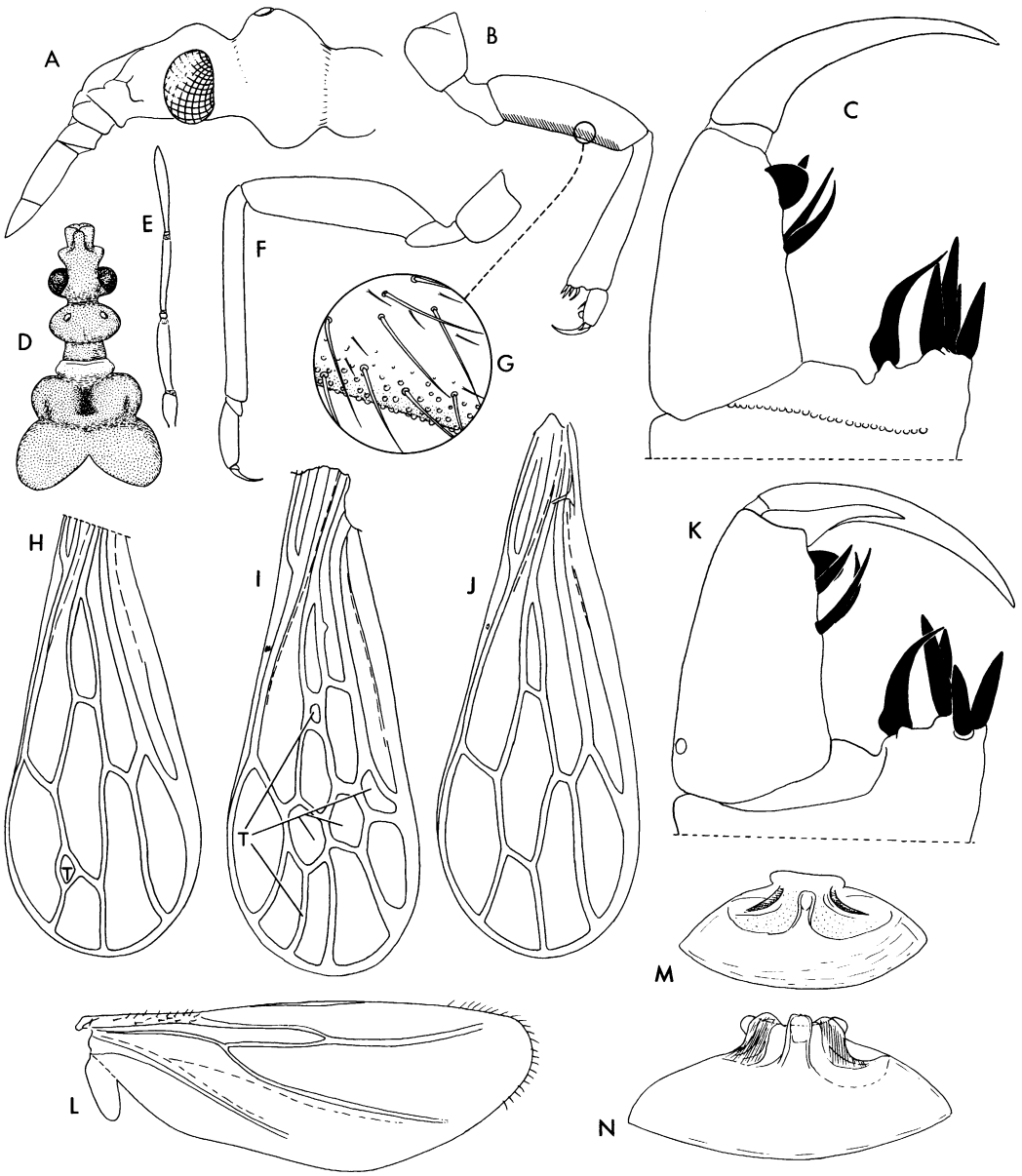


Fig. 88. *Enicocephalus pilosus*, ♂. **A**. Lateral view of head. **B**. Foreleg. **C**. Apex of foreleg, inner surface. **D**. Head and pronotum. **E**. Antenna. **F**. Hind leg. **G**. Detail of innner (ventral) surface of forefemur, showing cuticular granules. **H, I**. Teratological forewings. **J**. Forewing. **K**. Apex of foreleg, outer surface. **L**. Hind wing. **M**. Genital capsule, posterior view. **N**. Genital capsule, ventral view.

sessing a conspicuously bicolorous pronotum.

DESCRIPTION: Males, unknown. Length of female 6.5 mm (wingless)–6.7 mm (winged). General body color piceous. First antennal segment yellow; second, third, and basal two-thirds of fourth segment brown; joints of articles and apical third of fourth segment yellow. Head piceous; rostrum yellow. Fore and midlobe of pronotum light orange-yellow, sharply contrasting with piceous hind lobe (fig. 90B). Forewings and veins uniformly piceous. Legs light orange-yellow, occasionally with faint dusky bands around bases of femora and central third of tibiae; foretibiae with more distinct brown bands around their cen-

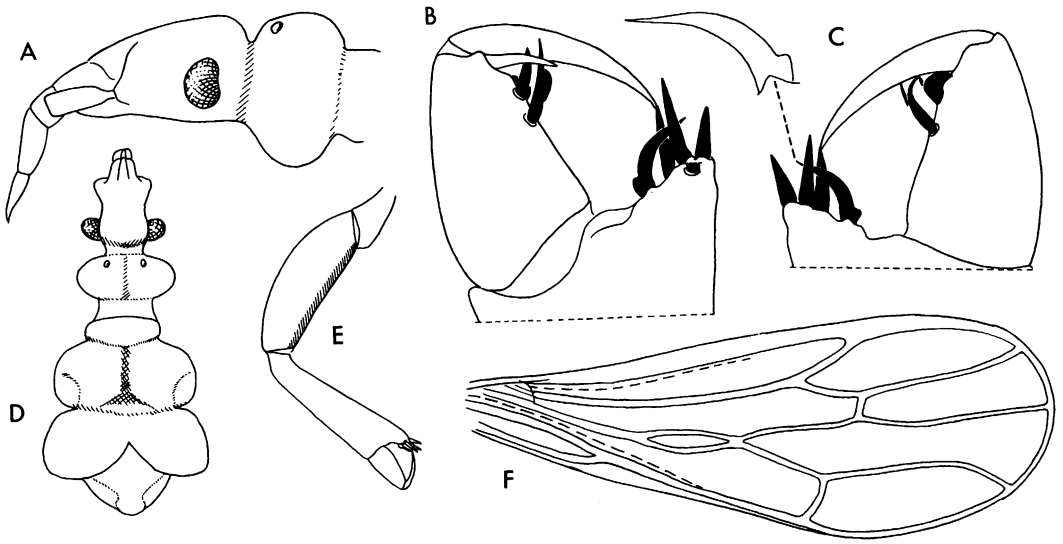


Fig. 89. *Enicocephalus pilosus*, ♀ (drawn from holotype). **A**. Lateral view of head. **B**, **C**. Apex of foreleg, outer and inner surfaces, respectively. **D**. Head and pronotum, dorsal view. **E**. Foreleg. **F**. Forewing.

tral thirds. Abdomen whitish with sclerotized genital area and regularly arranged sclerotized spots. Submedian, anterolateral, and posterolateral spots never fused, either dorsally or ventrally (figs. 90E, F).

Head shorter than pronotum (1:1.4). Ratio head length to width across eyes 1:0.7. Ratio length to width of hind lobe of head 1:1.6. Ratio length of eyes to anteocular portion 1:1.2; ratio width of eyes to synthlipsis 1:2.5. Eyes medium size in side view, nearly attaining level of under surface of head, but remote from top. Under surface of head, especially hind lobe, heavily bearded (fig. 90C). Antennal segments I–IV 1:2.3:2.8:2.4, combined somewhat shorter than head and pronotum together (1:1.2). Rostrum as shown in figure 90C.

Pronotum as illustrated in figure 90B, with deep posterior incision; proportional width of mid to hind lobe 1:1.3. Fore and hind wings fully developed, but frequently caducous, extending 0.9 mm beyond apex of abdomen in pinned specimens. Forewings 4.2 mm long. Venation of forewing as shown in figure 90G; discal cell remote from apex of wing. R+M and all veins along sides of wing with setae arranged randomly; central veins of wing with setae in two ranks. Hind wings setose apically (fig. 90H).

Forelegs as shown in figures 91A, B. Ratio length to width of forefemur 1:0.37. Forefemur with minute hairlike processes interspersed among larger setae; also with a granulose area on inner edge extending approximately halfway across width of femur on both dorsal and ventral surfaces, tapering to narrow area both proximally and distally (figs. 91A, B). Ratio length to width of hind femur 1:0.28. Foretibia as shown in figures 91A, D, E; ratio length to width 1:0.33. Tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figures 91D, E; tarsal spine III half-moon shaped. Outer claw normal size for genus, about one-third length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRAZIL: São Paulo: Campos do Jordao, 1600 m, March, 1945 (Wygodzinsky; AMNH).

PARATYPES AND NYMPHS: BRAZIL: Same data as holotype (AMNH), 1♀. BRAZIL: **Rio de Janeiro**: Teresopolis, March 29, 1957 (R. L. Usinger; AMNH), 2♀, 1 nymph.

ETYMOLOGY: Named for Dr. Randall T. Schuh, in appreciation of his invaluable help in the preparation of this monograph.

DISCUSSION: The above description fits our two specimens from São Paulo, Brazil (holotype and paratype). Two other adult specimens and one nymph from a similar habitat in Rio de Janeiro appear to be *E. schuhi* but differ slightly in the following respects:

Size smaller; length 5.2–5.3 mm (wingless

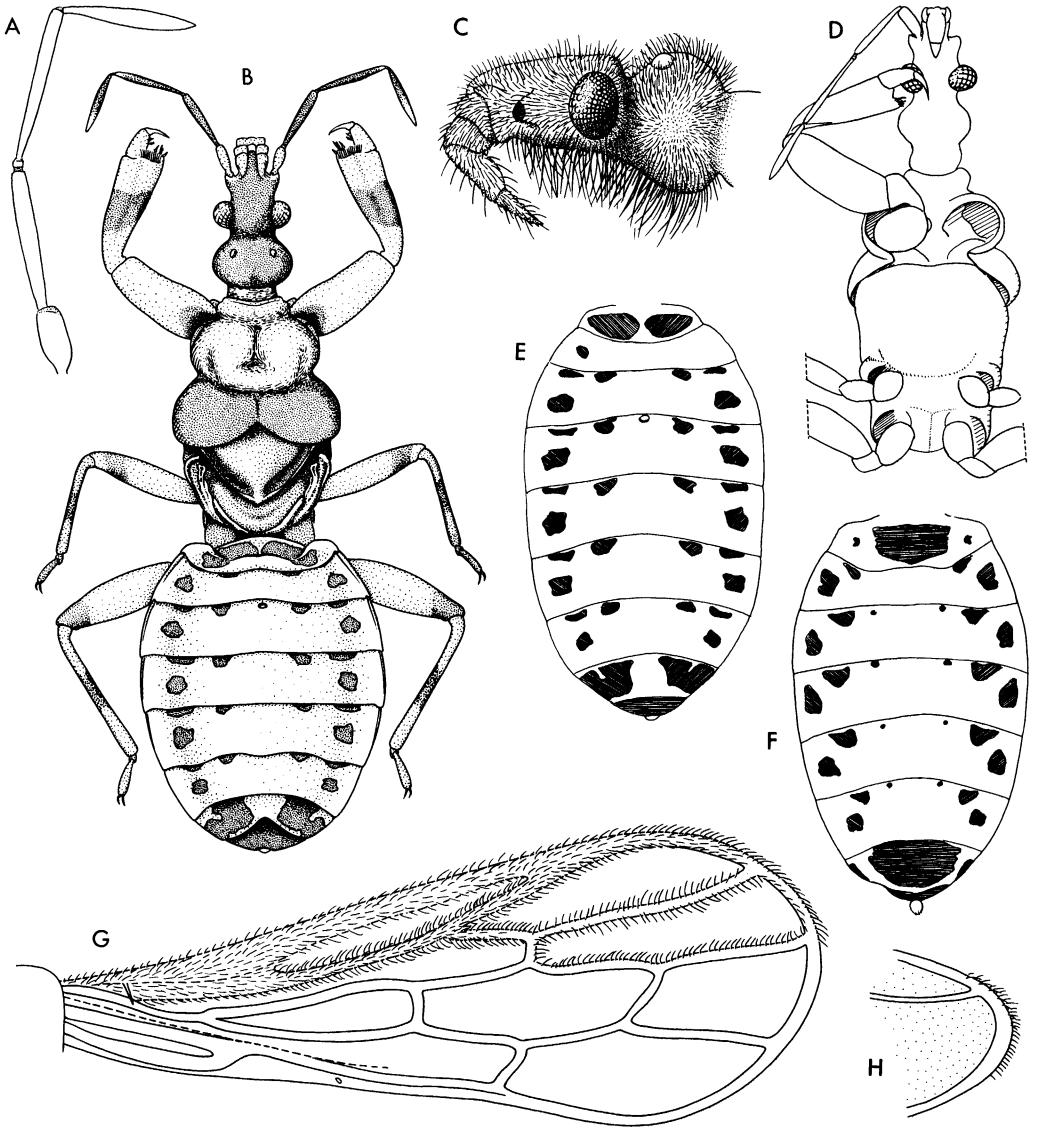


Fig. 90. *Enicocephalus schuhi*, ♀. **A**. Antenna. **B**. Dorsal view. **C**. Lateral view of head. **D**. Ventral view. **E**, **F**. Abdomen, dorsal and ventral views, respectively. **G**. Forewing. **H**. Apex of hind wing.

females). Eyes slightly smaller, not quite attaining level of under surface of head. One specimen has dusky bands around apices of mid and hind femora.

Enicocephalus semirufus Barber
Figures 71, 92

Enicocephalus semirufus Barber, 1939: 382. — Usinger, 1945: 335. — Wolcott, 1948: 210. — Kritsky, 1979: 96.

DISTRIBUTION: Puerto Rico.

DIAGNOSIS: This species, together with *E. usingeri* Maldonado, is characterized by an extreme reduction in size of the outer claw of the forelegs. It can be distinguished from *E. usingeri* by the smaller size of its eyes which are narrower than the synthlipsis, and in side view remote from level of upper surface of head.

REDESCRIPTION: (We measured two ma-

cropterous males, including the holotype (m-males), one macropterous female (m-females), and three brachypterous females (b-females). All measurements stated below represent averages where applicable.)

Length of macropterous males 3.4–3.6 mm; of macropterous females 4.1 mm; of brachyterous females 3.5–3.9 mm. General body color scarlet. Hind lobe of head and neck scarlet above, turning brownish below. Forelobe of head dark brown with scarlet tinge on dorsal interocular region. Both rostrum and antennae medium to dark brown on all segments but the terminal ones, varying from light brown to yellowish white. Anterior lobe of pronotum scarlet; midlobe varying from scarlet to dark brown tinged with scarlet; hind lobe yellow to scarlet. Scutellum and underside of thorax scarlet; acetabula tinged with dark brown.

Membrane of forewing translucent dusky brown; veins red basally to level of end of scutellum, and whitish brown to darker brown beyond, on both long and short winged forms. Abdomen scarlet and entirely membranous. Forelegs of males entirely dark brown. Forelegs of females varying from chestnut brown to yellowish brown; some specimens with distinct dark brown band surrounding central third of tibiae.

Head shorter than pronotum, 1:1.2 in m-females, 1:1.3 in m-males, and 1:1.1 in b-females (same order will be used throughout) (figs. 92B–D). Ratio head length to width across eyes 1:0.8, 1:0.7, 1:0.6. Ratio length to width of hind lobe of head 1:1.5, 1:1.4, 1:1.6. Ratio width of eyes to anteocular portion 1:1.3, 1:0.6, 1:1.6. Ratio length of eyes to synthlipsis 1:2.4, 1:1.4, 1:1.6. Eyes of males large in side view, extending downward farther than level of under surface of head, and nearly reaching level of top of head (fig. 92G). Eyes of females small, never reaching level of under surface of head (fig. 92F). Antennal segments I–IV 1:1.9:2.4:2, 1:1.6:2.4:2, 1:2:2.7:2.4, combined slightly shorter than head plus pronotum (1:1.2 in macropterous specimens, 1:1 in b-females). Rostrum as shown in figures 92F, G.

Pronotum as illustrated in figures 92B–D, with shallow posterior incision. Ratio width of mid to hind pronotal lobes 1:1.2, 1:1.5, 1:0.9. Length of hind pronotal lobe less than that of mid pronotal lobe in brachypterous forms, equal to or greater in macropterous forms.

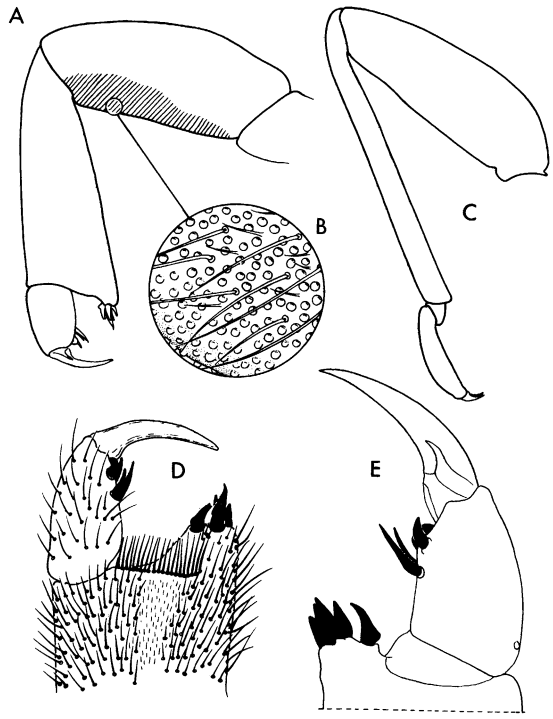


Fig. 91. *Enicocephalus schuhi*, ♀. **A**. Foreleg. **B**. Detail of inner (ventral) surface, showing cuticular granules. **C**. Hind leg. **D**, **E**. Apex of foreleg, inner and outer surfaces, respectively.

Fore and hind wings of females either macropterous or brachypterous. Forewing length of m-females 2.4 mm, of b-females approximately 0.9 mm. Forewing length of m-males approximately 2.2 mm. In all pinned macropterous specimens, wings extending beyond tip of abdomen. Setae on forewings two-ranked on all interior veins and interspersed with minute spines (fig. 92N). Hind wing lacking setae apically (fig. 92-O).

Forelegs as shown in figures 92E, H–K. Ratio length to width of forefemur 1:0.33, 1:0.27, 1:0.37. Setae on forefemur of uniform length, not interspersed with smaller spines; granular surface structures limited to narrow band along inner edge of article (figs. 92E, H). Ratio length to width of hind femur 1:0.25, 1:0.18, 1:0.29. Foretibia as shown in figures 92H, I; ratio length to width 1:0.30, 1:0.26, 1:0.33. Tibial spine VI with distinct subbasal

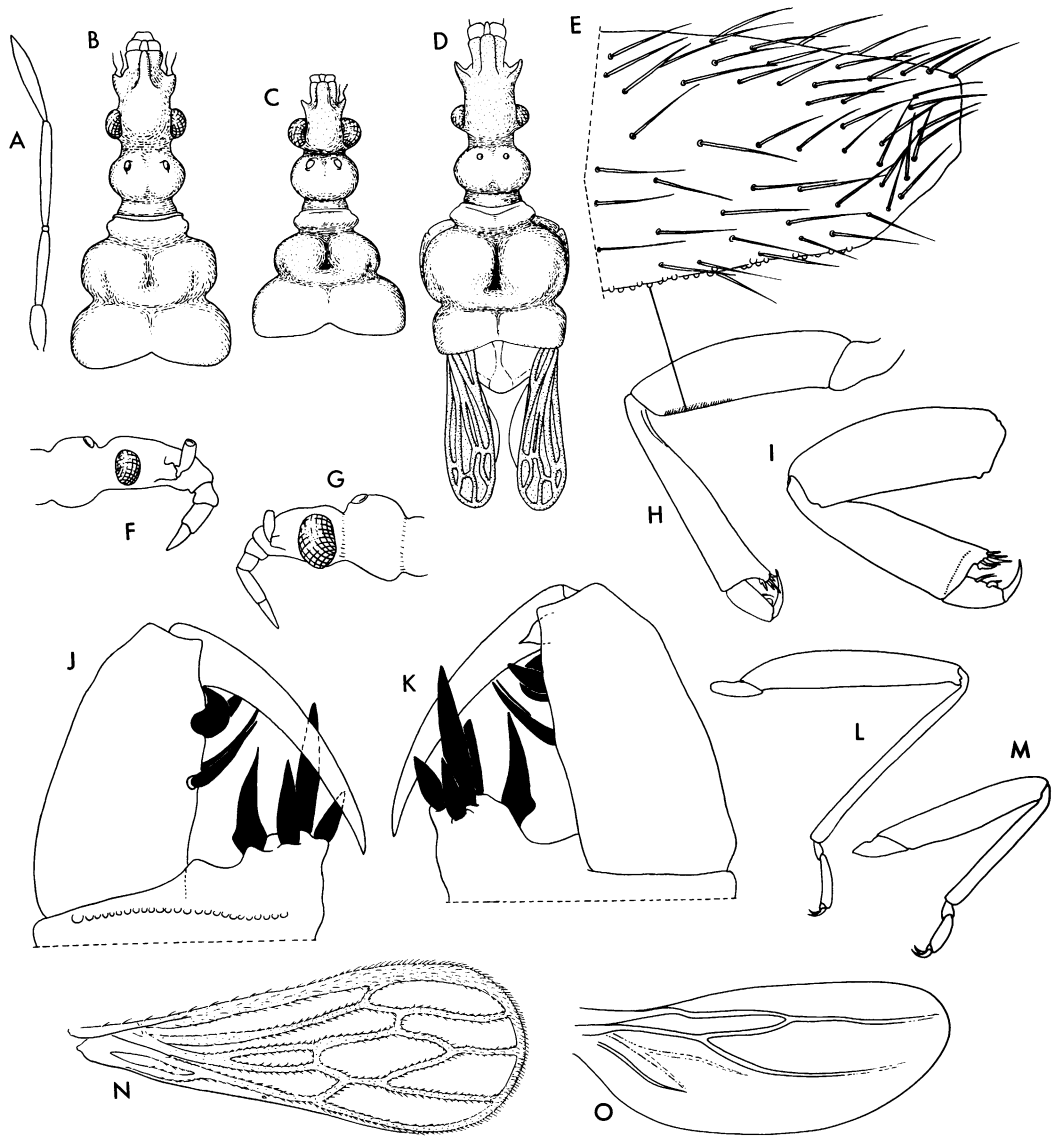


Fig. 92. *Enicocephalus semirufus* (♂ drawn from holotype). **A**. Antenna of ♂. **B**. Head and pronotum, macropterous, ♀. **C**. Head and pronotum, macropterous, ♂. **D**. Brachypterous ♀. **E**. Inner surface of forefemur, showing cuticular granules. **F**. Lateral view of head, macropterous ♀. **G**. Lateral view of head, macropterous ♂. **H**. Foreleg, ♂. **I**. Foreleg, ♀. **J**, **K**. Apex of foreleg, inner and outer surface, respectively. **L**. Hind leg, ♂. **M**. Hind leg, ♀. **N**. Forewing. **O**. Hind wing.

hump (figs. 92J, K). Foretarsi illustrated in figures 92J, K; tarsal spine III half-moon shaped. Outer claw extremely small, approximately one-eighth length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, PUERTO RICO: Adjuntas, June 8–13, 1915 (Lutz and Mutchler; AMNH); examined.

MATERIAL EXAMINED: PUERTO RICO. – Maricao, insular forest, November 3, 1945 (J. A. Ramos; USNM), 1♂, 1♀; El Yunque, about 3000 ft (1333 m), May, 1938 (Darlington; AMNH), 2♀; El Yunque, 3000–3300 ft (1333–1467 m), February 15–24, 1969 (T. and B. Hlavac, L. Herman; AMNH), 1♀; Adjuntas, June 8–13, 1915 (Lutz and Mutchler;

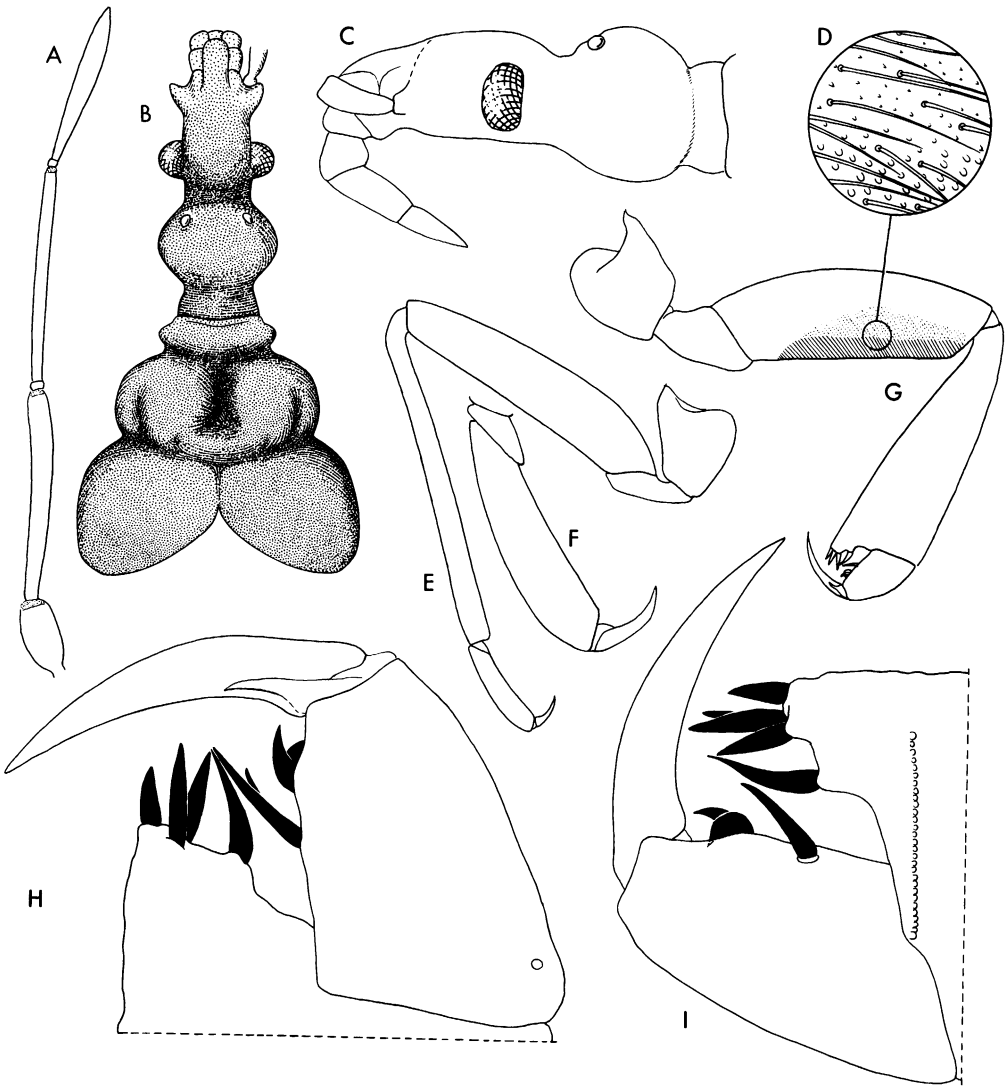


Fig. 93. *Enicocephalus sturmi*, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Detail of inner (ventral) surface of forefemur. **E**. Hind leg. **F**. Hind tarsus. **G**. Foreleg. **H**, **I**. Apex of foreleg, outer and inner view, respectively.

AMNH), 6 nymphs; El Yunque Peak, February 22, 1969 (L. Herman; AMNH), 1♀.

A female paratype, which we have not seen, has the following information: PUERTO RICO, Yauco, December 19, 1935 (Dozier; USNM, cat. no. 51592).

Enicocephalus sturmi, new species
Figures 71, 93, 94

DISTRIBUTION: Colombian Andes.

DIAGNOSIS: This is the largest species of the genus, and the only one in which tibial spine VI lacks a distinct subbasal hump.

DESCRIPTION: Males unknown. Length of female 7.3 mm (wingless)–8.6 mm (winged). General body color piceous. Head nearly black; rostrum orange-yellow. First, second, third, and proximal half of fourth antennal segments dark brown; joints of articles and apical half of fourth segment yellowish white. Pronotum entirely piceous, slightly lighter than head. Forewings dusky brown with reddish brown veins. Forefemur medium brown

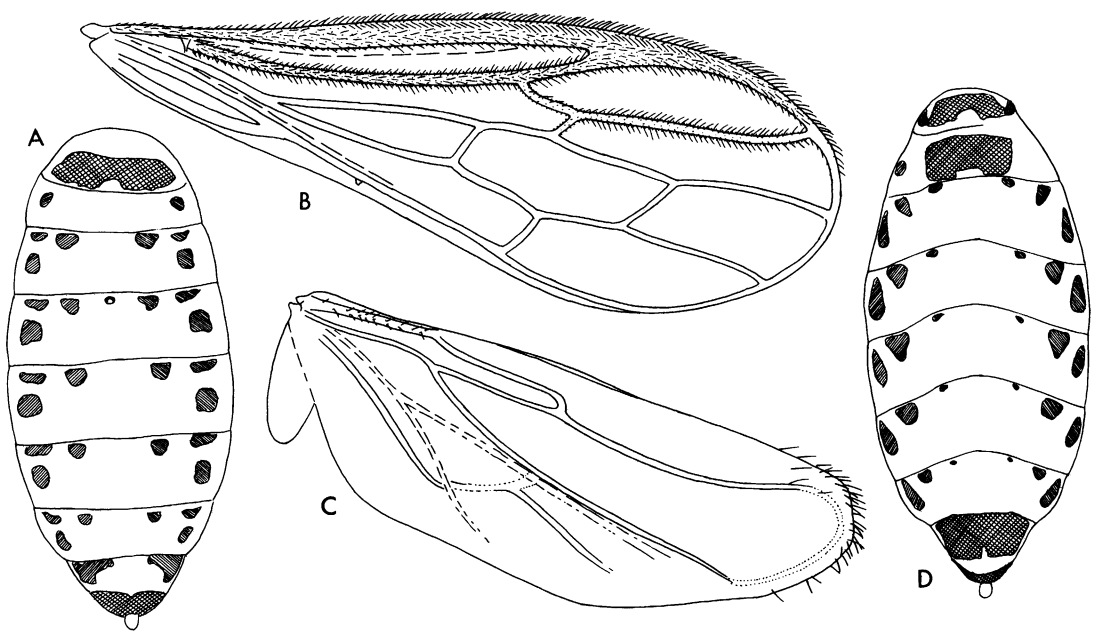


Fig. 94. *Enicocephalus sturmi*, ♀. **A**. Dorsal view of abdomen. **B**. Forewing. **C**. Hindwing. **D**. Ventral view of abdomen.

with narrow yellow apical band. Foretibia varying from yellowish on its proximal half and medium brown apically to mostly yellow with small apicolateral brown bar. Foretarsus brown proximally and yellow distally. Middle and hind legs dusky yellow to light brown, fading to light yellow on either side of femoro-tibial joints. Abdomen whitish with sclerotized genital area and regularly arranged sclerotized spots; submedian, anterolateral, and posterolateral spots never fused either dorsally or ventrally (figs. 94A, D).

Head slightly shorter than pronotum (1:1.3). Ratio head length to width across eyes 1:0.6. Ratio length to width of hind lobe of head 1:1.4. Ratio length of eyes to anteocular portion 1:1.4. Ratio width of eyes to synthlipsis 1:2.6. Eyes small, in side view, never attaining level of under surface of head and remote from upper surface (fig. 93C). Under surface of head, especially hind lobe, bearded. Antennal segments I–IV 1:2.8:2.9:2.3 (fig. 93A), combined slightly shorter than head plus pronotum (1:1.1). Rostrum as shown in figure 93C.

Pronotum as shown in figure 93B, with deep posterior incision. Proportional width of mid to hind lobe 1:1.5.

Fore and hind wings fully developed in macropterous specimens, but potentially caducous, extending 1.2 mm beyond apex of abdomen (in pinned specimens); micropterous specimens known. Forewings 5.8 mm long; venation as shown in figure 94B. Discal cell remote from apex of wing. Setae on veins interspersed with short hairlike processes. R+M and veins near wing base with setae arranged randomly; setae on veins of apical half of wing two-ranked. Hind wings setose apically (fig. 94C).

Forelegs as shown in figures 93D, G. Ratio length to width of forefemur 1:0.26. Setae on forefemur of uniform length, not interspersed with shorter hairlike processes (fig. 93D). Granulose area present on inner edge of forefemur, granules gradually changing into minute spines toward center of femur and extending approximately halfway across width of article on both dorsal and ventral surfaces (figs. 93D, G). Ratio length to width of hind femur 1:0.18 (figs. 93E, F). Foretibia as shown in figures 93G–I; ratio length to width 1:0.27;

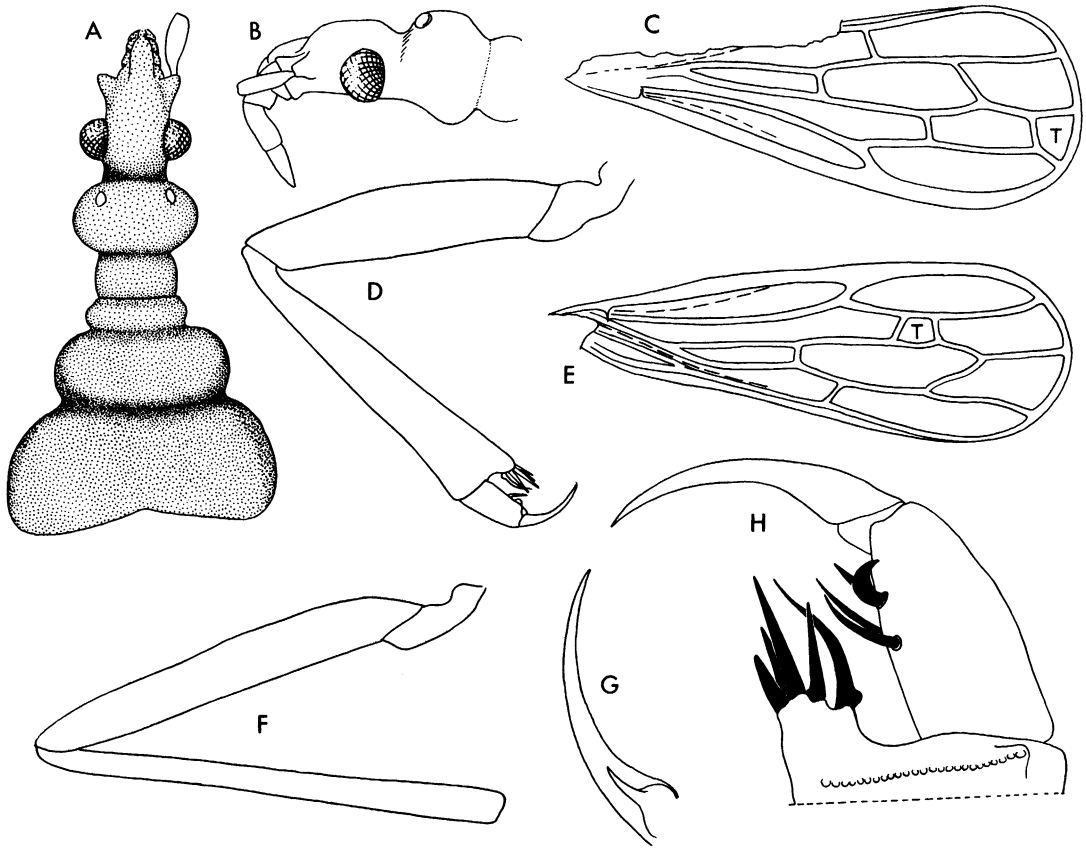


Fig. 95. *Enicocephalus taeuberi*, ♂, (holotype). **A**. Head and pronotum. **B**. Lateral view of head. **C**, **E**. Forewings of holotype, showing extra cells. **D**. Foreleg. **F**. Hindleg. **G**. Foreleg claws, outer view. **H**. Apex of foreleg, inner view.

tibial spine VI distinctly lacking subbasal hump. Foretarsi illustrated in figures 93H, I; tarsal spine III half-moon shaped. Outer claw normal size, approximately one-third length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, COLOMBIA: **Cundinamarca**: Bogota, above military hospital, ca. 2700 m, under rock, October 1, 1956 (Sturm; AMNH).

PARATYPES AND NYMPHS: COLOMBIA: **Cundinamarca**: Tibabita, 6 km N Usaquen near Bogota, 2600–2800 m, July 7 and 19, 1967 (Sturm; AMNH), 2♀; Bogota, 3125 m, May 3, 1946 (E. A. Chapin; USNM), 1♀; stream valley above 70–72 streets, 2700–2800 m, under rock, February 14, 1969 (Sturm; AMNH), 1♀; 2700–2900 m, August 12, 1967 (Sturm; AMNH), 1♀, 1 nymph.

ETYMOLOGY: Named for its collector, Dr. H. Sturm.

Enicocephalus taeuberi Jeannel
Figures 71, 95

Enicocephalus taeuberi Jeannel, 1944 (1943): 127. — Kritsky, 1979: 99.

DISTRIBUTION: Bolivia.

DIAGNOSIS: This species seems to be closest to the Brazilian *E. ningulus* and *E. lenkoi*, with which it agrees in the very shallow emargination of the hind border of the pronotum and the lack of cuticular structures on the legs; it differs by its very slender forelegs.

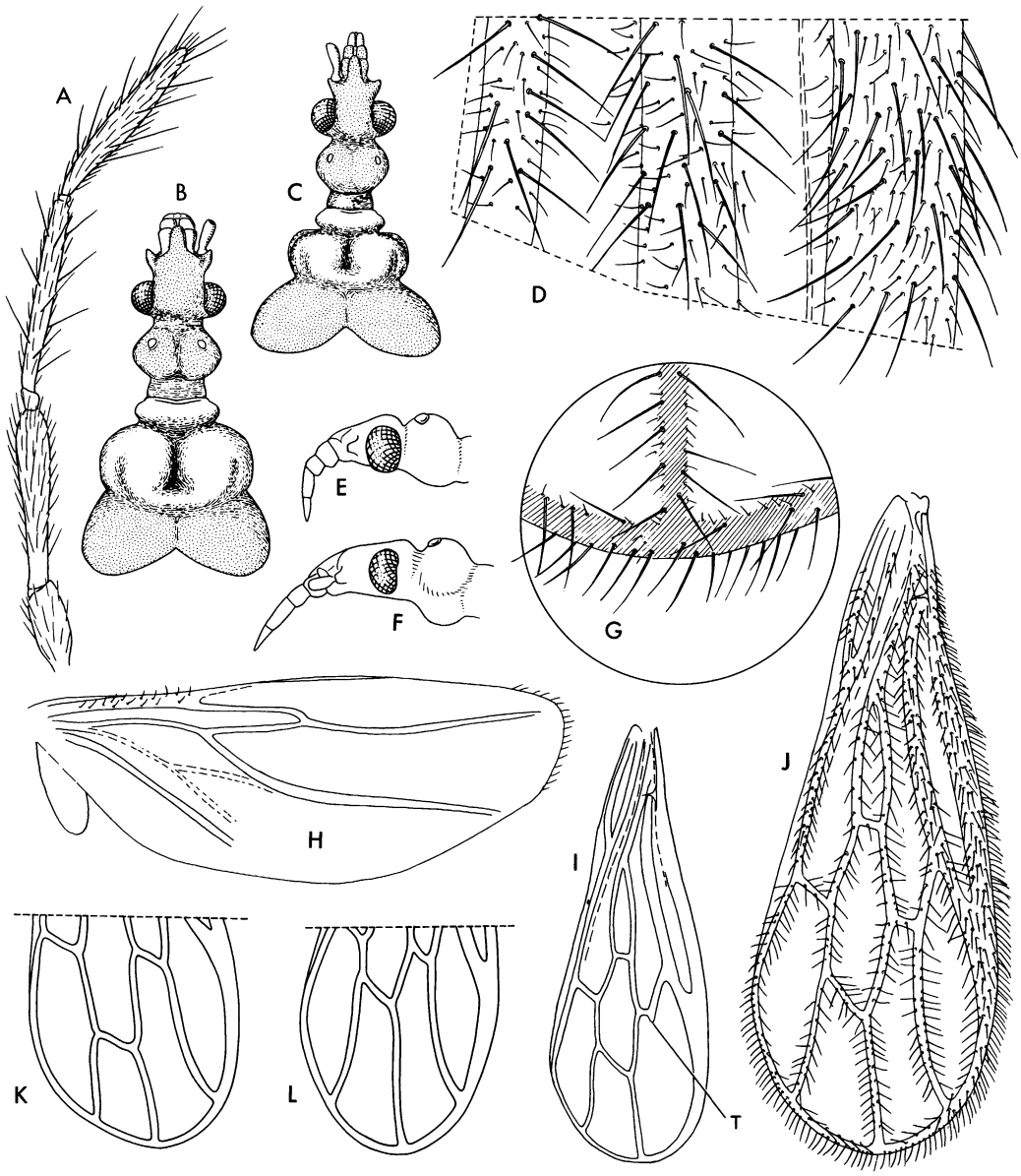


Fig. 96. *Enicocephalus tupi*. **A**. Antenna of ♂. **B**. ♀ head and pronotum. **C**. ♂ head and pronotum. **D**. Detail of forewing setation at level of basal cell. **E**. ♂ head, lateral view. **F**. ♀ head, lateral view. **G**. Detail of forewing apex. **H**. Hind wing. **I**. Teratological forewing. **J**. Forewing. **K**, **L**. Variation in venation and cell size in forewings.

REDESCRIPTION: Females unknown. Length of male 3.7 mm. General body color uniform light brown. Head, antennal segments I–III, and base of segment IV, brown; apical two-thirds of segment IV whitish. Forewings dusky brown with brown veins.

Head equal in length to pronotum (fig. 95A). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.6. Ratio width of eyes to anteocular portion 1:1.0. Ratio length of eyes to synthlipsis 1:2.6. Eyes medium size in side view, attaining level of under surface of head but remote from upper surface (fig. 95B). Anten-

nal segments I–IV 1:1.8:2.3:2.5, combined slightly shorter than head plus pronotum (1:1.1). Rostrum as shown in figure 95B.

Pronotum as illustrated in figure 95A, with very shallow posterior incision. Proportional width of mid to hind lobes 1:1.6.

Fore and hind wings fully developed. Both forewings of the type specimen teratological in their venation (fig. 95C, E and see Discussion). Discal cell remote from apex of wing. Setae on R+M randomly arranged. Hind wing setose apically.

Forelegs as shown in figure 95D. Ratio length to width of forefemur 1:0.25. Cuticular granules not present on forefemur, nor smaller hairlike processes interspersed among the larger setae. Ratio length to width of hind femur 1:0.15 (fig. 95F). Foretibia as shown in figures 95D, H; ratio length to width 1:0.19. Tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figure 95H; tarsal spine III half-moon shaped. Outer claw short, about one-fourth as long as inner claw (fig. 95G).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BOLIVIA: Coroico, mountains E of Lake Titicaca, (collection H. Taeuber and Mus. Paris); examined. (Jeannel mentions another male from the same locality, which we did not see.)

DISCUSSION: Based on our experience with other members of this genus, we judge that both forewings are teratological, each containing a small extra cell. The extra cells do not correspond in both wings (fig. 95C, E).

Enicocephalus tupi, new species

Figures 71, 96, 97

DISTRIBUTION: Southern Brazil.

DIAGNOSIS: This species differs from others (with a conspicously bicolored pronotum) by the absence of most or all of the distinctly sclerotized spots on the abdomen of the female.

DESCRIPTION: Length of male 4.0–4.2 mm, of female 4.5–5.0 mm.

General body color brown to piceous. Head brown to piceous; rostrum light yellowish. Antennae light brown; joints of articles and apical half of terminal segment frequently yellowish white. Fore and midlobe of pronotum light orange-yellow, sharply contrasting with dark hind lobe (figs. 96B, C). Membrane of forewings dark brown, all veins yellowish white. Legs light orange-yellow. Forefemora and tibiae somewhat darkened on basal half. Mid and hind femora brownish except for basal and apical yellowish white annulus. Abdomen whitish with dark sclerotized spots regularly arranged on segments. Submedian, anterolateral, and posterolateral spots not fused dorsally; undeterminable ventrally. Male genitalia as shown in figure 97J.

Head in both sexes (figs. 96B, C) slightly shorter than pronotum (1:1.2). Ratio head length to width across eyes 1:0.6 in males, 1:0.7 in females. Ratio length of eyes to anteocular portion 1:0.7 in males, 1:0.8 in females. Ratio width of eyes to synthlipsis 1:1.3 in males, 1:2.1 in females. Ratio length to width of hind lobe of head 1:1.6 in males, 1:1.7 in females. Eyes of male medium size in lateral view, attaining level of under surface of head but remote from upper surface (fig. 96E). Eyes of female smaller, not attaining level of under surface of head (fig. 96F). Antennal segments I–IV 1:2.0:2.8:2.6 (fig. 96A), combined much shorter than head plus pronotum. Rostrum as shown in figures 96E, F.

Pronotum as illustrated in figures 96B, C, with deep posterior incision. Proportional width of mid to hind lobe in male 1:1.6, in female 1:1.4.

Fore and hind wings fully developed but caducous, extending by 0.1 mm beyond apex of abdomen (in pinned specimens). Forewings 3 mm long. Venation of forewings as shown in figures 96I–L; discal cell remote from apex of wing. Setae on forewing veins interspersed with smaller hairlike processes (fig. 96D). R+M and all veins near wing base with setae arranged randomly; setae on veins on apical half of wing two-ranked. Hind wing setose apically (fig. 96H).

Forelegs as shown in figures 97A–F. Ratio length to width of forefemur of male 1:0.33, of female 1:0.37. Forefemur with minute hairs interspersed among larger setae, and with miniscule tubercles forming narrow field along under surface of article; granulose area at center of femur not quite half as wide a femur (fig. 97F). Ratio length to width of hind femur of male 1:0.24, of female 1:0.36. Foretibia as shown in figures 97A–E; tibial spine VI with

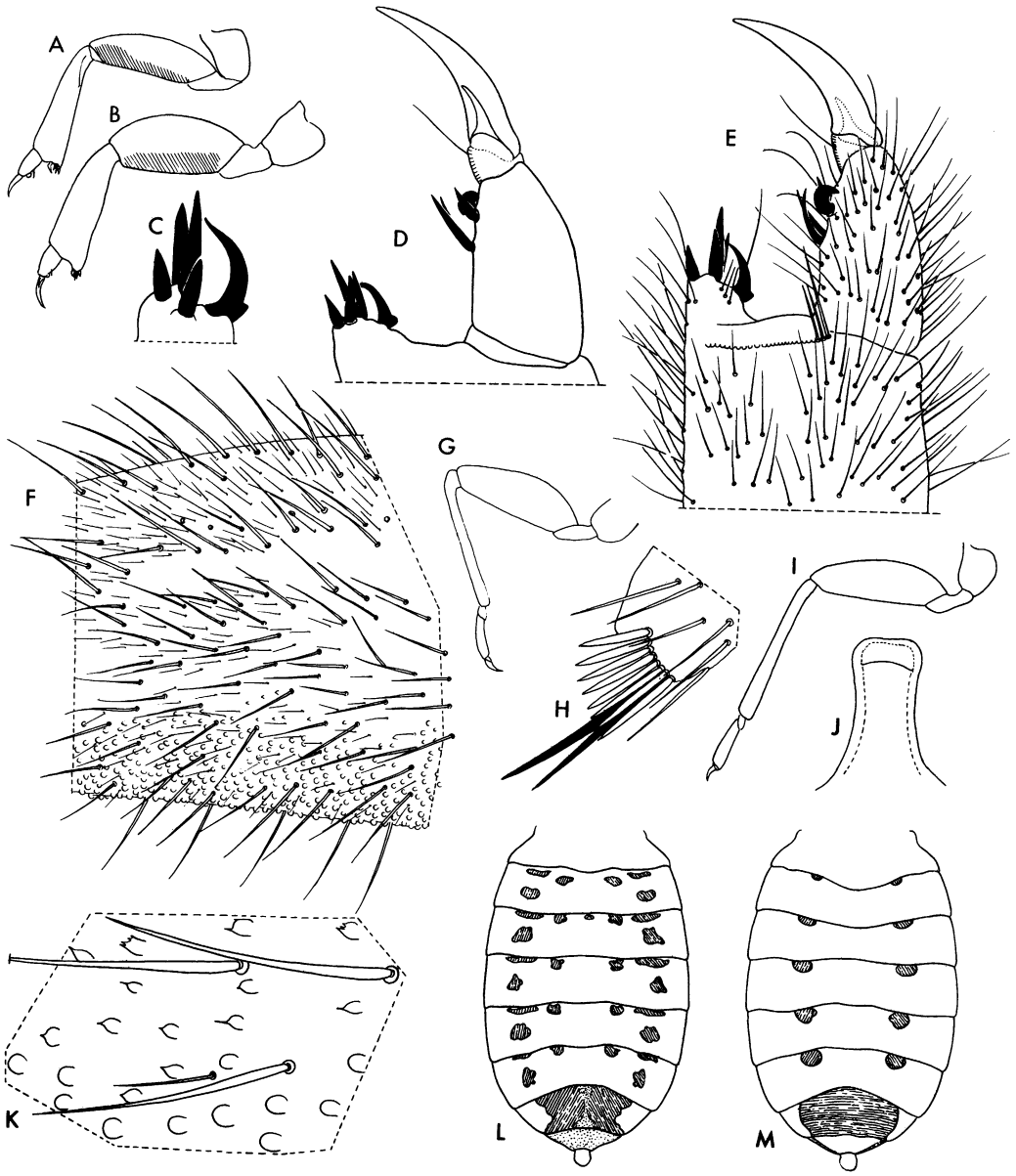


Fig. 97. *Enicocephalus tupi*. **A**. Foreleg of ♂. **B**. Foreleg of ♀. **C**. Tibial spines of ♂. **D**. Outer surface of ♀ foreleg apex. **E**. Inner surface of ♀ foreleg, showing setae except for bristle comb. **F**. Detail of ♀ forefemur. **G**. Hind leg of ♀. **H**. Apex of ♀ hind leg, showing bristle comb. **I**. Hind leg of ♂. **J**. Guide of ♂. **K**. Detail of ♀ forefemur, showing change in shape of cuticular granules dorsad. **L**. Dorsal surface of ♀ abdomen. **M**. Ventral surface of ♀ abdomen.

distinct subbasal hump. Ratio length to width of foretibia of male 1:0.26, of female 1:0.36. Foretarsi illustrated in figures 97D, E; tarsal spine III half-moon shaped. Outer claw of normal size, about one-third length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BRAZIL: Rio de Janeiro: Corcovado, May, 1944 (Wygodzinsky; AMNH).

PARATYPES AND NYMPHS: BRAZIL: **Rio de Janeiro**: Corcovado, May, 1944 (Wygodzin-

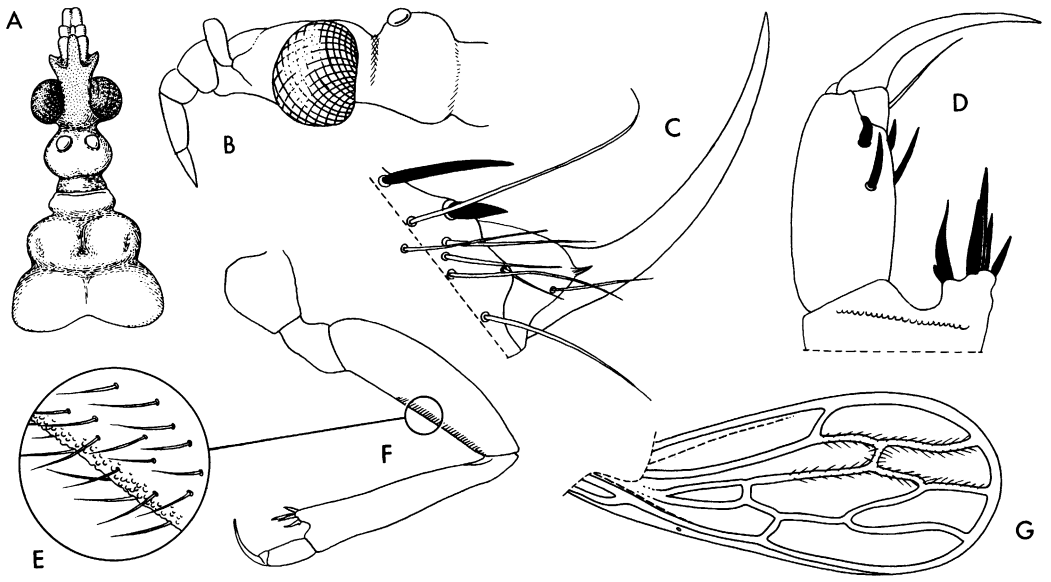


Fig. 98. *Enicocephalus usingeri*, ♂ (paratype). **A**. Head and pronotum, dorsal. **B**. Lateral view of head. **C**. Outer view of foreleg claws. **D**. Apex of foreleg, showing tibial and tarsal spines and bristle comb, inner view. **E**. Detail of forefemur, showing cuticular granules. **F**. Foreleg. **G**. Forewing.

sky; AMNH), 1♂, 2♀; October, 1945 (Wygodzinsky; AMNH), 1♀; February 24, 1946 (Wygodzinsky; AMNH), 1♂; August 25, 1948 (Wygodzinsky; AMNH), 1♂; Grajau, February 26, 1949 (H. S. Lopes; AMNH), 1♀; Tijuca, July, 1960 (H. Schubart; MNR), 1♀; September, 1945 (Wygodzinsky; AMNH), 1 nymph; Gavea, April 4, 1943 (Wygodzinsky; AMNH), 1♀.

ETYMOLOGY: Species name taken from one of the language groups of the Brazilian Indians.

DISCUSSION: We also examined a specimen from Itataia National Park in the state of Rio de Janeiro with a similar abdomen (lacking ventral sclerotized spots). The specimen is quite a bit larger than any of the other *E. tupi* specimens and has plain orange foretibiae with no banding. An undescribed species with a similar abdomen also occurs in Beni, Bolivia.

Enicocephalus usingeri Maldonado
Figures 71, 98

Enicocephalus usingeri Maldonado, 1948: 159. — Wolcott, 1948: 210. — Kritsky, 1979: 96.

DISTRIBUTION: Puerto Rico.

DIAGNOSIS: *Enicocephalus usingeri* seems closest to *E. exophthalmus*; males of both have extremely large eyes, at least as wide as the synthlipsis. They can be distinguished from one another by the color of the thorax, which is scarlet in *E. usingeri*, and brown in *E. exophthalmus*.

REDESCRIPTION: We add the following to Maldonado's (1948) description. We include our own proportions in order to be consistent. Females unknown. Length of male 4.1 mm. Ratio head length to pronotum length 1:1.2. Ratio head length to width across eyes 1:0.8. Ratio length of eyes to anteocular distance 1:0.5; ratio width of eyes to synthlipsis 1:0.7. Ratio hind lobe of head length to width 1:1.6. Antenna slightly shorter than head plus pronotum (1:1.1); ratio segments I–IV 1:2.1:2.8:2.3. Ratio width of mid to hind pronotal lobes 1:1.3. Ratio length to width of forefemur 1:0.28; of foretibia 1:0.22; of hind femur 1:0.22. Eyes of male large in side view extending from level of upper surface of head to below level of under surface. Setae on forefemora not interspersed with smaller hair-like processes. Cuticular granules present in narrow band on inner surface of forefemur (fig. 98E, F). Tarsal spine III only slightly curved, not half-mooned shaped (fig. 98D). Outer claw of foreleg extremely small, only one-tenth of inner claw (fig. 98C).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, PUERTO RICO: El Yunque National Forest, 625 m, at light, November 27, 1943 (J. Maldonado Capriles; USNM type no. 58661); not examined.

MATERIAL EXAMINED: Same data as holotype (CIS), 1♂ paratype.

DISCUSSION: The redescription has been drawn up from a paratype in the CIS collection.

Enicocephalus wygodzinskyi Villiers
Figures 71, 99, 100, frontispiece

Enicocephalus wygodzinskyi Villiers, 1978: 728.

DISTRIBUTION: Guadeloupe.

DIAGNOSIS: The very large genitalia of the male distinguish this species from all other *Enicocephalus*.

REDESCRIPTION: (Measurements from the holotype of *E. wygodzinskyi* appear in parentheses after average measurements of three other specimens.)

Females unknown. Length of male 4.1–4.6 mm. General body color scarlet. Head and basal two-thirds of rostrum scarlet; apex of rostrum yellowish brown. First antennal segment scarlet at base and dark brown at apex; second and third segments dark brown; fourth segment lighter brown. Thorax, including scutellum, entirely scarlet. Membrane of forewing translucent dusky brown; all veins scarlet, contrasting sharply with background. Legs scarlet; tarsi brown. Abdomen scarlet.

Head shorter than pronotum, 1:1.3 (1:1.3; fig. 99B). Ratio head length to width across eyes 1:0.7 (1:0.7). Ratio length to width of hind lobe of head 1:1.6 (1:1.7). Ratio width of eyes to anteocular portion 1:1.2 (1:1). Ratio length of eyes to synthlipsis 1:2.3 (1:2.5). Eyes relatively small, in side view, not extending downward far enough to reach level of under surface of head and remote from upper surface. Antennal segments I–IV 1:2.2: 3.8:2.6 (1:1.8:4.2:2.7), combined slightly longer than head plus pronotum (1:0.8, both groups; fig. 99A). Rostrum as shown in figure 99C.

Pronotum as illustrated in figure 99B, with a deep posterior incision. Pronotum approximately as long as wide 1:1.1 (1:1.0); anterior lobe 3 (2.6) times as wide as long; midlobe 2.2 (1.9) times as wide as long; hind lobe 2.4 (2.2) times as wide as long. Proportional width of mid to hind lobes 1:1.2 (1:1.3).

Fore and hind wings fully developed (fig. 99K); forewings approximately 3 mm long and in some cases teratological in their venation (fig. 99L). Wings extend approximately 0.1 mm beyond abdomen in pinned specimens. Setae on forewings sparse, two-ranked on all interior veins and interspersed with short spines basally (fig. 99I). Hind wing setose apically and on costal margin (fig. 99J).

Forelegs as shown in figure 99D, E. Ratio length to width of forefemur 1:0.26 (1:0.26). Setae on forefemur of uniform length, not interspersed with shorter spines; granular surface structures absent (fig. 99D). Ratio length to width of hind femur 1:0.19 (1:0.19). Foretibia as shown in figure 99E, G, H; ratio length to width 1:0.24 (1:0.25). Tibial spine VI with distinct subbasal hump. Foretarsi illustrated in figure 99G, H; tarsal spine III half-moon shaped. Outer claw about one-fourth length of inner claw.

Abdomen as shown in figure 100A, with distinct patches of setae on each segment. Male genitalia atypically well developed with the guide flattened anteroposteriorly and affixed to the pygophore ventrally, as in other members of this genus, but characteristically expanded laterally and dorsally to form a leaf-like cover which enfolds the rest of the genitalia (fig. 100B, C, E–G).

Parameres evident (figs. 100B, E, G). The membranous posterior surface of the pygophore bearing numerous spicules and its dorsal and lateral surfaces are provide with specialized setae (fig. 100B; see also introductory section: Genitalia, Homologies, and the Phylogeny of the New World Taxa).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, GUADELOUPE: Pointe-Noire, Mamelle de Pigeon, in rachis of dried leaf of *Euterpe globosa*, November 10, 1965 (J. Bonfils; Mus. Par.).

MATERIAL EXAMINED: GUADELOUPE. – (no collector; Mus. Nat. Hung.), 1♂; same (no collector; AMNH), 2♂ (one on slide).

DISCUSSION: We have examined Villier's holotype and find it to agree in general appearance with the AMNH specimens. How-

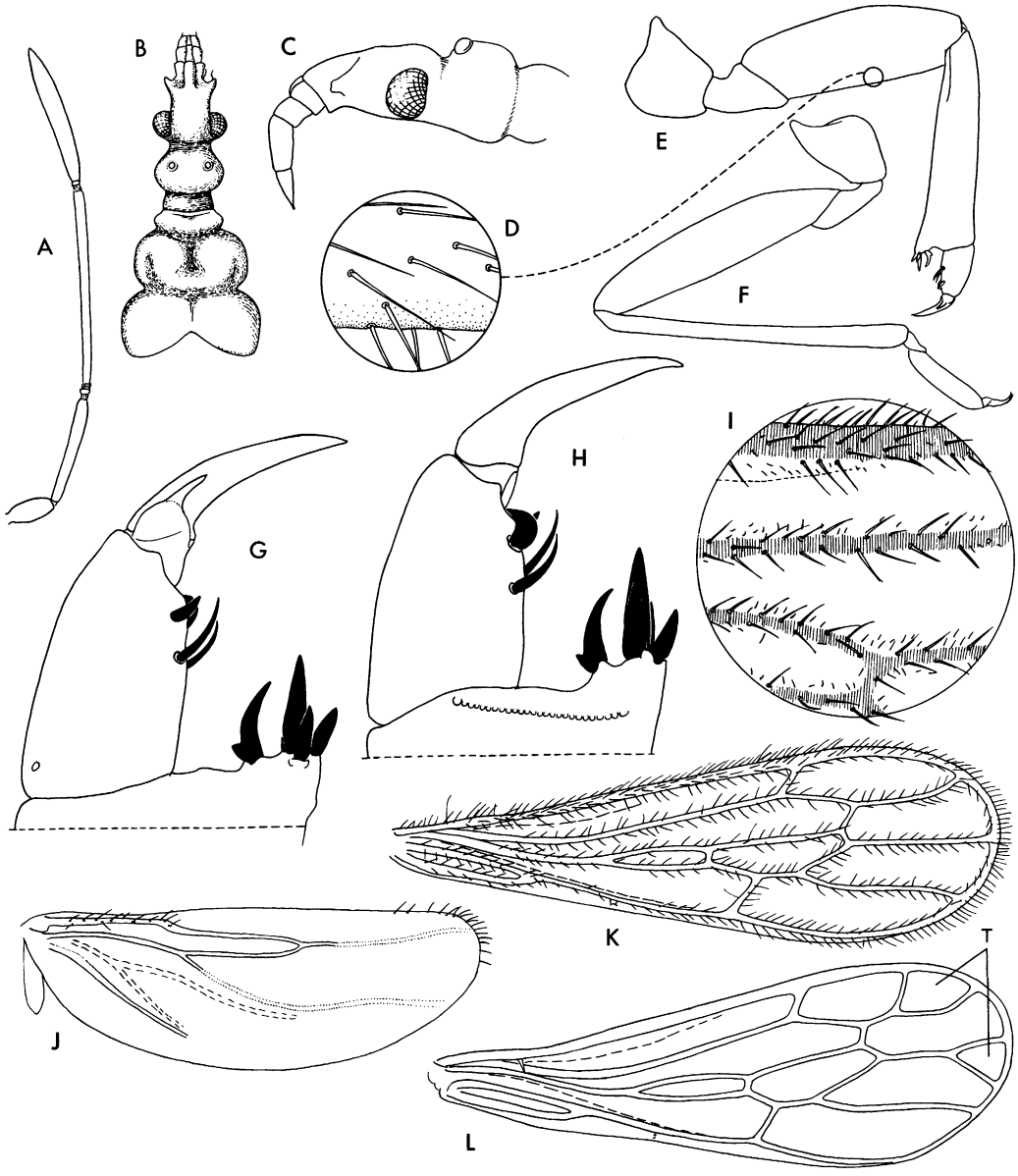


Fig. 99. *Enicocephalus wygodzinskyi*, ♂. **A**. Antenna. **B**. Head and pronotum, dorsal. **C**. Lateral view of head. **D**. Detail of inner surface of forefemur. **E**. Foreleg. **F**. Hind leg. **G**. Apex of foreleg, outer surface. **H**. Apex of foreleg, inner surface, showing bases of bristle comb. **I**. Detail of wing setation at level of basal cell. **J**. Hind wing. **K**. Forewing. **L**. Teratological forewing.

ever, our proportions differ somewhat from his, especially eye width/synthlipsis and length of antennal segments. Also, Villier's description does not mention the highly autapomorphic structure of the male genital region, which was strikingly evident in the holotype. We thus conclude that our specimens and Villier's are conspecific.

This is obviously a highly apomorphic species, but still within the framework of *Eni-*

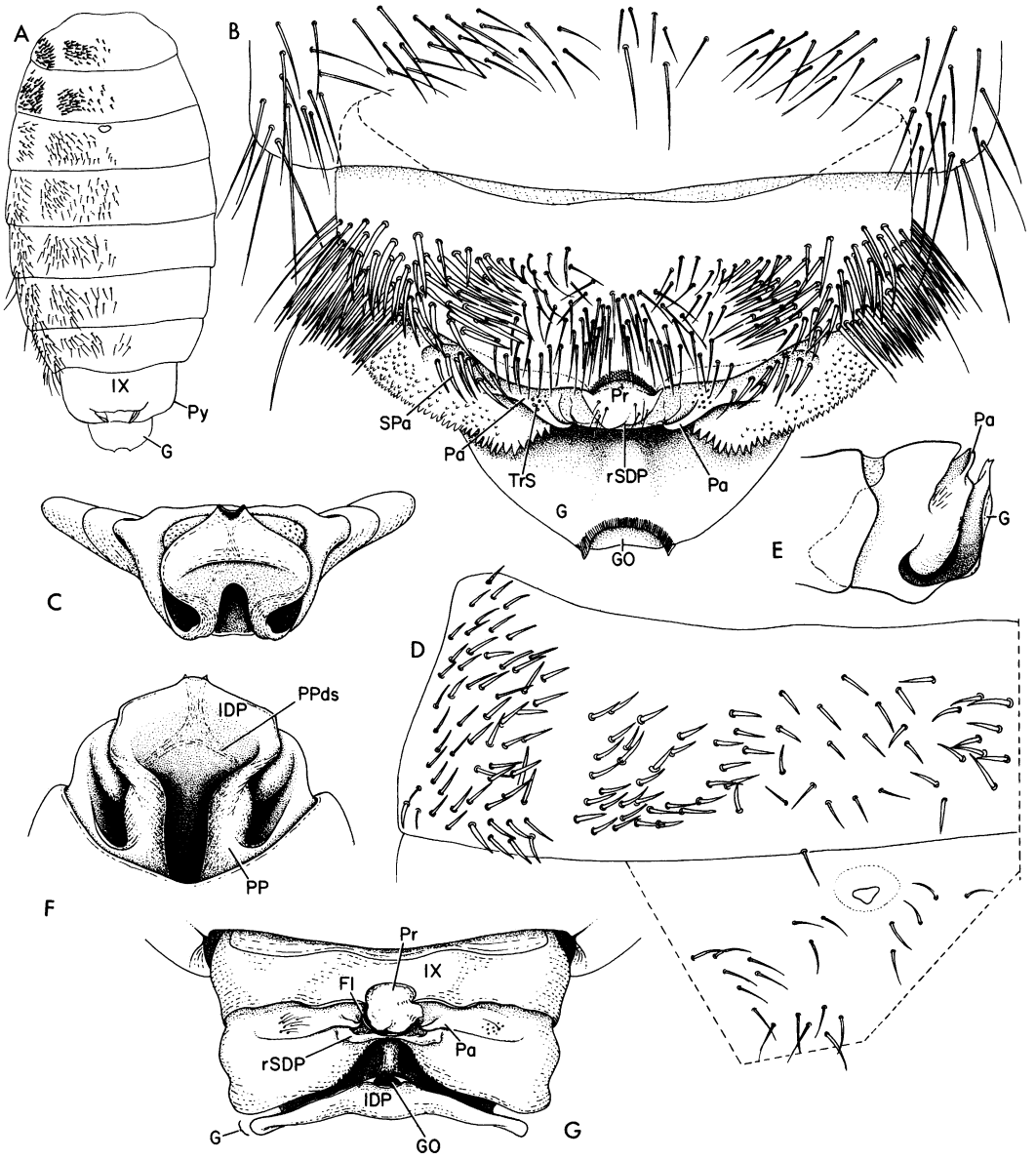


Fig. 100. *Enicocephalus wygodzinskyi*, ♂. **A**. Dorsal view of abdomen (setae of genital region not shown). **B**. Genital region, dorsal view, showing primary dorsal components. **C**. Genital region, posterior view. **D**. Detail of dorsum of abdomen at level of segments III and IV. **E**. Genital region, lateral view. **F**. Genital region, ventral view, showing ventral components. **G**. Genital region, posterodorsal view (see list of abbreviations).

cocephalus (viz. reduced outer claw of forelegs, spines of apex of foretibiae and tarsi, shape of head, etc.).

Hymenocoris Uhler

Hymenocoris Uhler, 1892: 181. — Usinger, 1939: 267. — Jeannel, 1944 (1943): 127–128. — Usinger, 1945 (1944): 322–323, 325, 338. — Štys, 1970a (1968): 448. — Stys, 1978 (1977): 247. — Kritsky, 1978b: 74.

Henicocephalus, Johannsen, 1909: 4. — Usinger, 1932: 146.

Enicocephalus, Bruner, 1924b: 53.

Stenopirates, Jeannel, 1942 (1941): 326–327.

TYPE SPECIES: *Hymenocoris formicinus* Uhler. Fixation by monotypy.

DISTRIBUTION: California south to southern Mexico (fig. 101).

DIAGNOSIS: Males delicate, with foretarsal claws nearly equal in length (figs. 13M, 103A), setae on dorsal surface of abdomen simple, apices of mid and hind tibiae with 2 spines within the circle formed by the bristle combs (figs. 13G, 105B), and frequently with red forewing stigma. Females wingless with membranous abdomen, closed foreacetabula (fig. 102F), spine VI of foretibia molar shaped (fig. 103E), and with basal projection on forefemur (fig. 109).

REDESCRIPTION: Male. Delicate looking, medium size (4.3–6.5 mm). General body color dark brown. Body surface shining; setiferous tubercles absent. All setae simple, slender. Macropterous.

Head with constriction behind eyes well developed (figs. 102A, B). Eyes from medium size to large, almost meeting on ventral surface of head; synthlipsis from slightly wider to distinctly narrower than width of eyes. Ocelli from medium size to large. Antennae with segments II to IV progressively decreasing in length. Rostrum slender. Hind lobe of head subglobose in dorsal view, impressed longitudinally along middle.

Pronotum unarmed (fig. 102A). Median lobe with a simple median longitudinal impression; disc of lateral portions of midlobe lacking sculptural elements. Hind lobe of pronotum fairly short, its hind border straight or slightly emarginated. Mesonotum somewhat exposed before in front of scutellum. Anterior acetabula open behind (fig. 102C). Meso- and metathorax with two grooves above the metathoracic synpleuron accepting costal edge of the wing when at rest (fig. 104B). Metathoraic scent gland auricle flat and tab-shaped, poorly developed (fig. 104B).

Pterostigma of forewings tinged with red. Basal and discal cells present (figs. 6A, 108). Stigmal cell less than half as long as discal cell. Apex of Cu attaining wing margin. 1An extending beyond cu-pcu crossvein. PCu and 1An both developed. Setae arranged in two irregular rows on most veins, mostly in a single row on R+M, and much more numerous on costal margin. Membrane of cells with a moderate number of short setae, especially on distal half of forewing (fig. 104D). Wing coupling device C-shaped (fig. 104E); both arms of "C" with very large microtrichial projections apically, shortest projections on arm of "C" nearest wing edge.

Hind wing with a few setae along veins and on membrane. Costal edge of hind wing bearing foliaceous structures at level of wing coupling device (fig. 104F).

Abdomen with spiracles on ventral connexival plates II–VIII. Tenth tergum small but distinct, semilunar, with an irregular transverse row of about 20 setae (fig. 105E). Guide subrectangular, rounded to nearly truncate apically, perforate (fig. 105D).

Front legs slender. Under surface of coxa and femur lacking tubercles or scalelike cuticular structures. Trochanter without process. Inner apical angle of tibia with a group of seven spines (specimens with more numerous spines unusual); I–IV and VII straight, elongate, V and VI short, conical (fig. 103B). Tarsus slightly longer than width of apical portion of tibia. Tarsal organ situated on inner and close to dorsal surface. Four well-developed, simple tarsal spines (fig. 103C); all conical, I and III stout, II and IV slender. Two claws (fig. 103A), outer one slightly shorter than inner one, the latter nearly as long as tarsus. Mid and hind legs without special characters; apex of tibiae with two closely spaced bristle combs and two large spines (fig. 105B).

Female (fig. 109). Slightly larger than male (6.1–7.3 mm). General body color light brown. Apterous. Setae simple, slender. Setal insertions slightly expanded (fig. 102F).

Head very elongate, subcylindrical, only slightly constricted behind eyes (fig. 102D). Eyes minute, composed of few ommatidia (fig. 102E). Ocelli absent. Rostrum similar to that of male but stouter. Antennae with segments II–IV progressively decreasing in length (fig. 102E).

Pronotum with fore and hind lobes short and narrow (fig. 102D). Median lobe very large, subglobose, with a narrow median longitudinal sulcus, and 1 + 1 slight impressions on lateral portions of discs. Hind lobe transverse, its posterior border either straight, or with a slight backward-directed median point. Mesonotum and metanotum subquadrate, their discs convex (fig. 109). Anterior acetabula closed behind (fig. 102F).

Abdomen physogastrous, almost com-

pletely membranous. External genitalia present but extremely minute (fig. 105F), with a median tab projecting posteriorly from center of hind edge of sternum VIII.

Front legs very stout. Coxa, trochanter, and femur with minute tuberclelike cuticular structures. Femur with stout projection at base (fig. 109). Inner apical angle of tibia with a group of seven stout spines (fig. 103E). I–V and VII elongate, slender, straight, V short and conical, VI molar shaped. Tarsus stout, shorter than width of apical portion of tibia. Tarsal spines and claws as in male, but claws proportionally stouter, and inner claw slightly longer than tarsus. Mid and hind legs with two large spines and two bristle combs apically (fig. 105C); setae in bristle combs stouter and blunter than those of males.

Fifth instar nymph, male (fig. 113B). General shape slender. Eyes obsolescent. Antennae slender. Neck distinct. Mesothoracic wing pads meeting medially, longer than wide, rounded posteriorly. Spines of foretibia as in adult female. Abdomen membranous; terga with short setae of uniform size.

Fifth instar nymph, female (fig. 113A). General shape slender. Eyes obsolescent. Antennae slender. Meso- and metanotum individualized; wing pads absent. Spines of foretibia as in adult female. Abdomen membranous; terga with short setae of uniform size.

DISCUSSION: *Hymenocoris* males display a tremendous range of variation in several characters: length, shape of tibial spine VI, coloration, and head proportions. Delineation of species boundaries is problematical, since there is never good separation between species in all characters simultaneously. Specimens that we have called *brunneocephalus* and *hintoni* are the most consistently separable, but even they overlap *formicinus* in some characters. Character distributions in what we have called *H. formicinus* are variable and are not consistent as to geography, date of collection, or any other factor that we can demonstrate. Thus we have lumped most specimens that are intermediate in the broadly defined species "*formicinus*." In *Hymenocoris*, perhaps more than any other genus, more collecting needs to be done before the alpha taxonomy can be resolved.

The most useful proportion for separating species of *Hymenocoris* seems to be head width across eyes/width of hind lobe of head (fig. 114B). In all measured specimens that we are calling *formicinus*, with the exception of the Adobe Creek specimen, the ratio was 1:1 or 1:1.1; i.e., head width across eyes was equal to, or less than, the width of the hind lobe of the head. *H. brunneocephalus* and the specimens from Guasave that we are presuming to be *hintoni* (see Discussion under latter), were just the opposite. They had ratios of 1: 0.7 or 1:0.8. True *hintoni*, according to Kritsky's measurements, has a ratio of 1:0.7. The specimen from Paso Robles, California, geographically far from the type locality of *hintoni* (Vera Cruz, Mexico), had a ratio of 1: 0.8. We are calling it (probable) *hintoni* on that basis.

The above decisions are well supported by the ratio of head length to width across eyes in figure 114D, but not as clearly supported by the ratio of eye width to synthlipsis (fig. 114C) or length (fig. 114A; see discussion below).

The following characters seem to be scattered in a mosaiclike pattern throughout our material of *Hymenocoris* and don't appear especially reliable in defining species, nor do they seem to be consistent within populations.

For example, the lengths of males thought to be *H. formicinus* varied from 4.6 to 6.3 mm and overlapped lengths of other species (fig. 114A). In most localities, the range fell in a narrower band from 5.5 to 6.2 mm, but in two groups (both consisting of specimens caught on the same day in the same locality) nearly the entire size range was displayed (4.6–6.1 mm and 4.9–6.3 mm).

Shapes of tibial spine VI of the foreleg also varied as shown in figures 111A–D. Evidently this character cannot be used to separate species, or populations either, since we found considerable variation within specimens from a single locality and even found one specimen that had different types of spines on opposite legs (types B and D). Both arrangement and number of tibial spines exhibit frequent teratologies and are not reliable as taxonomic characters.

It is with a slight element of doubt that we include the unique apterous, physogastrous

females described above in the same genus with the males of *Hymenocoris*. In addition to secondary sexual characters and others obviously related to the absence or presence of wings, the two sexes differ also by such important features as the open or closed condition of the forecoxal cavities, the absence or presence of a dorsal projection at the base of the forefemur, and the shape of tibial spine VI. The general structure of the claws of the foretibia and tarsus agrees with that of the males, with the exception of tibial spine VI. It is modified even more than the most modified state of the male (fig. 111E) so that it is distinctly two-lobed.

In the San Bruno Hills near San Francisco, Usinger and Wygodzinsky collected numerous apterous females and many indubitably conspecific nymphs of various stages of both sexes. This material shows that in the last instar male and female nymphs can be distinguished by their size and body shape. Nymphs of both sexes and all instars have tibial spines as typical for the adult female; in the later instars, a dorsal projection at the base of the femur is also present, though larger in the female than in the male nymph. Wygodzinsky was unfortunately unable to rear a male nymph to the adult stage, but a male specimen dying shortly before its last molt permitted extraction of the head of the adult male. This head (fig. 112F–H) was somewhat compressed as it had not yet been freed naturally from the comparatively small nymphal cuticle, a fact to be taken into account when interpreting our illustrations. We believe that the morphology of this teneral head is sufficiently similar to that of the well-preserved males of *Hymenocoris formicinus* to support our hypothesis that the unique apterous female and the winged male *Hymenocoris* are congeneric.

Wings of Males. Our male specimens of *Hymenocoris* display fewer wing teratologies than previous genera we have studied. Out of 57 wings examined, 7 (approximately one-eighth) exhibited teratologies. In *Enicocephalus* (*cubanus*), six out of 24 (one-quarter) were teratological; in *Tornocrusus* 18 percent were teratological.

BIOLOGY: All of our *Hymenocoris* males were caught singly or in small groups. However, Usinger (1939) mentioned that Michelbacher and White discovered them swarming.

See also discussion (Biology) in introductory section.

KEY TO SPECIES OF *HYMENOCORIS* MALES

1. Head width across eyes less than or equal to width of hind lobe of head. Ocelli, though prominent, remote from lateral edge of head (fig. 108) ..... *formicinus* Uhler
   Head width across eyes greater than width of hind lobe of head. Ocelli extremely prominent, on diverging lobes, and attaining or surpassing lateral edge of head (fig. 106) 2
2. Size small, 4.5–4.7 mm. Pronotum light yellowish brown, sharply contrasting with darker head. Abdomen extending beyond wings .. .. *brunneocephalus*, n. sp.
   Size larger, 5.2–6.8 mm. Head, pronotum, and scutellum dark brown. Wings extending well beyond abdomen .... (probable) *hintoni* Kritsky

Hymenocoris brunneocephalus, new species

Figures 101, 106, 107, 114

DISTRIBUTION: Known only from one locality in north central Mexico.

DIAGNOSIS: *Hymenocoris brunneocephalus* differs from the similar *H. formicinus* in the large size of its eyes, the sharp contrast in color between the head and pronotum, and other characters mentioned in the key.

DESCRIPTION: Females unknown. Length of males 4.5–4.7 mm. General body color brown. Texture very smooth and shiny and all body parts moderately clothed with medium length setae. Head dark reddish brown fading to light brown anterior to antenniferous tubercles; eyes and areas around ocelli tinged with red. Antennae and rostrum light to medium brown. Pronotum light to medium brown, sharply contrasting with dark head; scutellum medium brown. Entire thorax and abdomen light to medium brown; genital capsule slightly darker. Wings hyaline with light brown veins; wing base, costa, and stigma tinged with red. Legs light to medium brown, becoming darker toward ends of tibiae and on tarsi.

Head longer than pronotum (1:0.7; fig. 106). Eyes very large: ratio head length to width

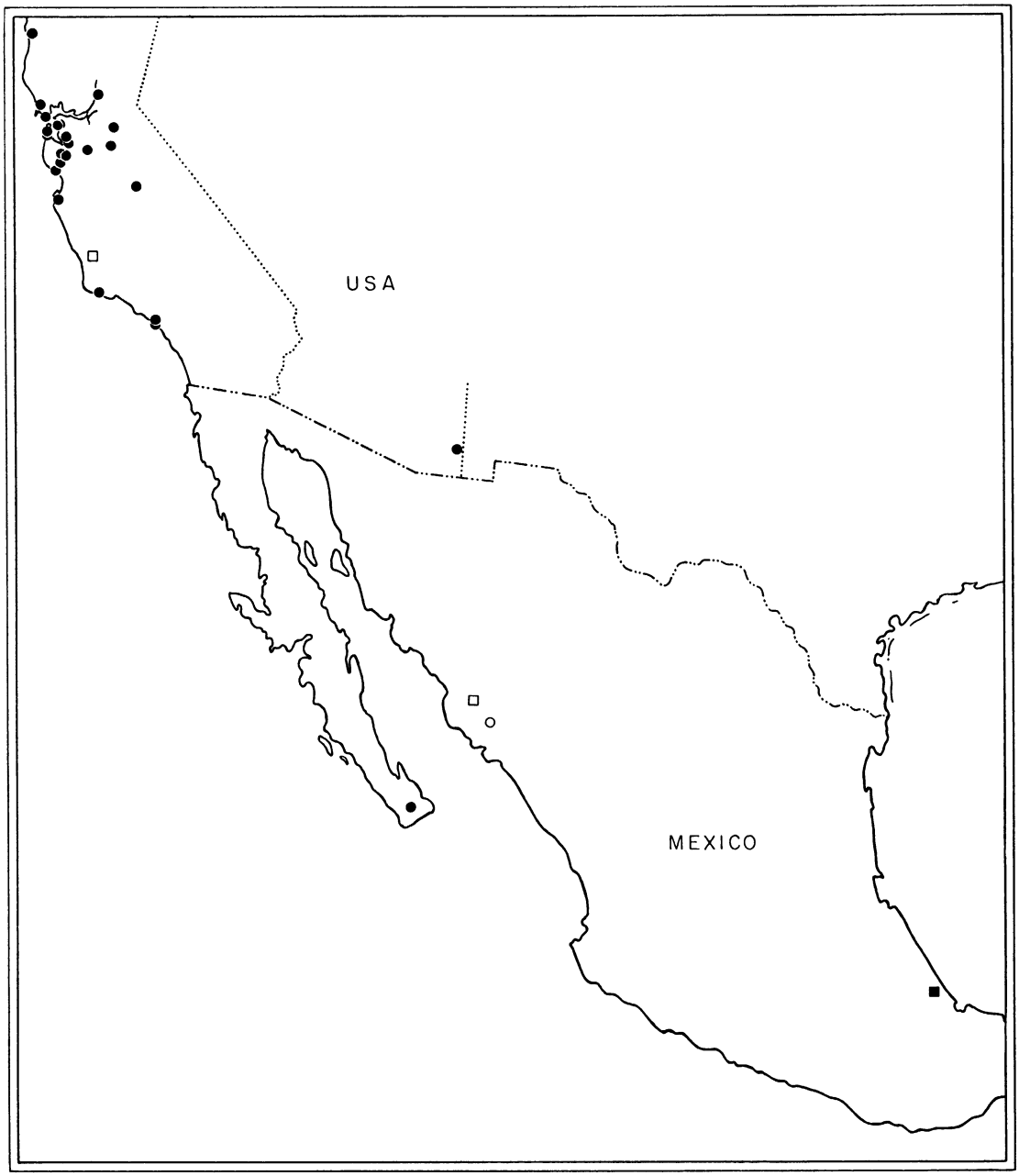


Fig. 101. Distribution of *Hymenocoris*. *H. formicinus* (●). *H. brunneocephalus* (○). *H. hintoni* (■). *H. hintoni* (probable; □).

across eyes 1:0.6; ratio length of eyes to anteocular distance 1:0.7; ratio eye width to synthlipsis 1:0.6; ratio head width across eyes to hind lobe of head width 1:0.8. Ratio length to width of hind lobe of head 1:1.3. Ocelli extremely large, projecting laterally beyond edge of head.

Antennal segments I–III 1:3.2:3.1 with seg-

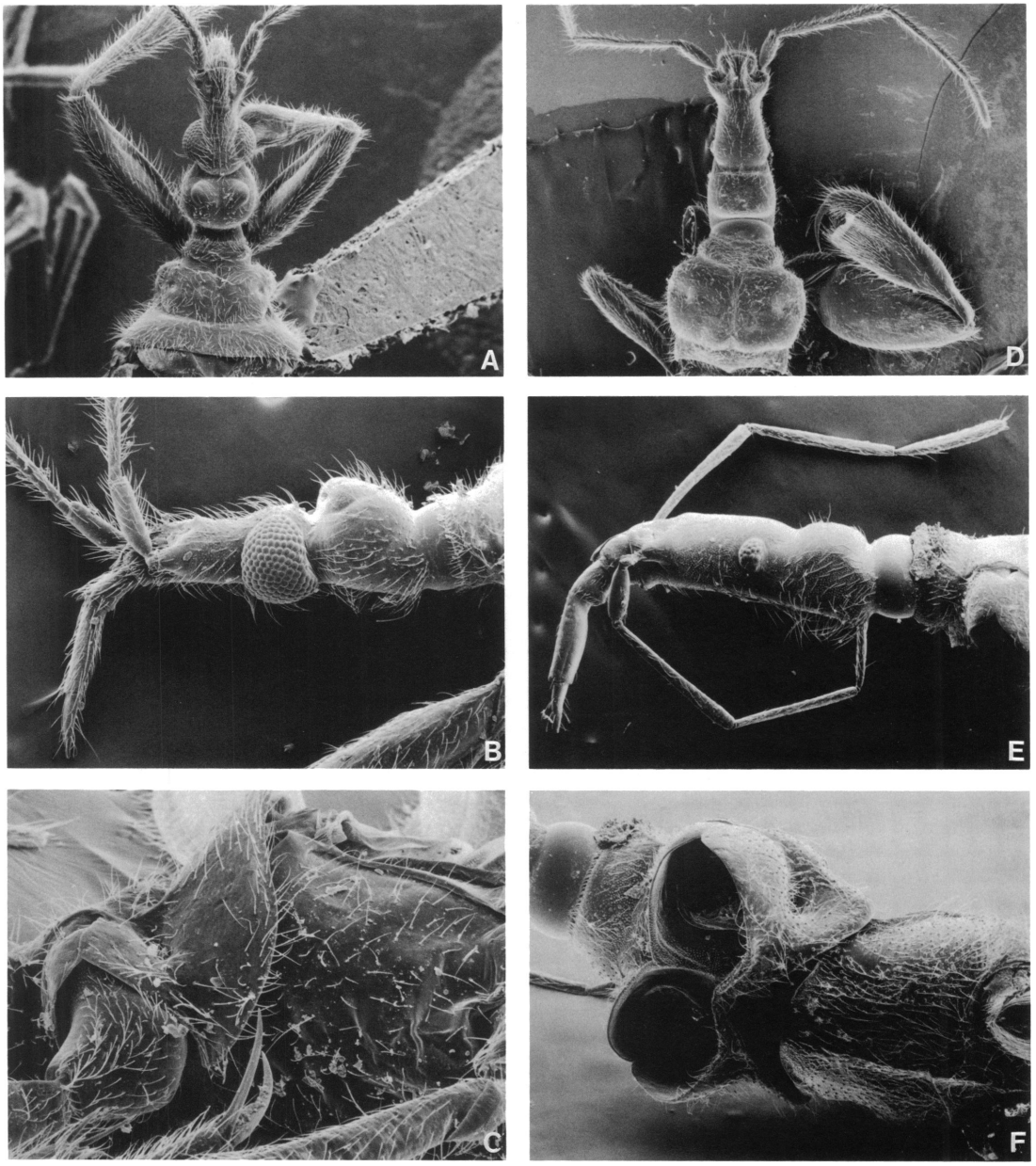


Fig. 102. *Hymenocoris formicinus*. **A–C**. ♂. **D–F**. ♀. **A, D**. Head and pronotum, dorsal view, showing extreme sexual dimorphism. **B, E**. Head, lateral views. **C, F**. Prothorax, ventral view, showing open condition of foreacetabula (C) and closed (F).

ment IV missing in both specimens examined (fig. 106). Antenna much longer than head plus pronotum.

Pronotum as shown in figure 106, with a slightly excavated longitudinal sulcus in the midlobe and a shallow incision between mid and hind lobes. Ratio width of mid to hind lobe 1:1.5, ratio length of mid to hind lobes (measured in center) 1:0.7.

Forewings as shown in figures 106 and 107E

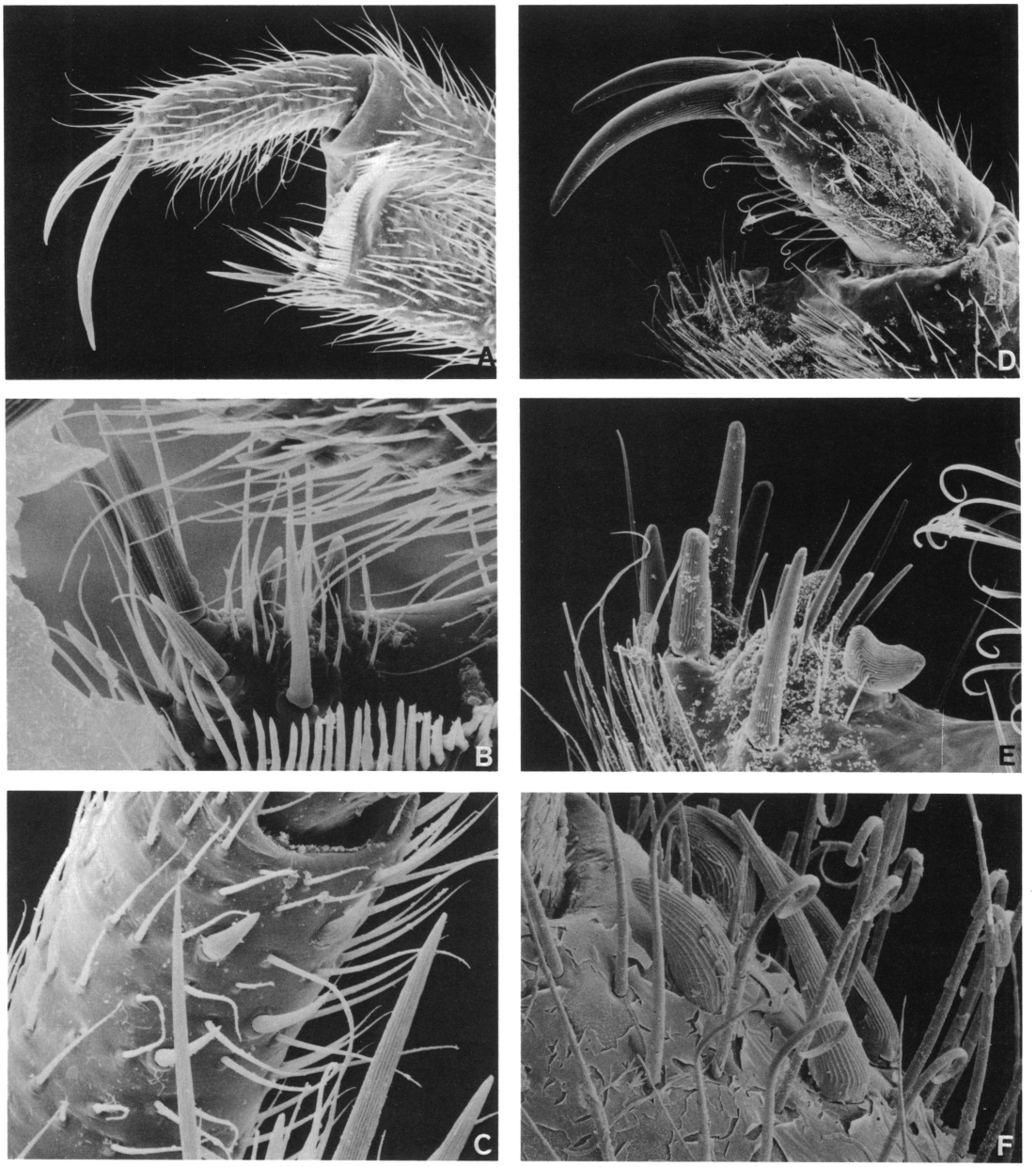


Fig. 103. *Hymenocoris formicinus*. **A–C**. ♂. **D–F**. ♀. **A, D**. Apices of forelegs. **B, E**. Foretibial spines. **C, F**. Foretarsal spines.

with a large discal cell and a smaller basal cell. Short setae roughly two-ranked along veins of disc of forewing; setae slightly longer and randomly arranged towards base of wing. Lumens of cells of disc each containing 12–24 setae.

Abdomen and genitalia as in generic description.

Forelegs as shown in figure 107G. Ratio length to width of forefemur 1:0.26; ratio length to width foretibia 1:0.26.

Foretibia and tarsus bearing spines as in figures 107B–D.

Ratio length to width of hind femur 1:0.20 (fig. 107H).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, MEXICO: **Sinaloa**: 16 mi S of Guamuchil, June 16, 1961 (F. D. Parker; U. C. Davis).

PARATYPE: same data as holotype (AMNH), 1♂.

ETYMOLOGY: From the Latin adjective *brunneus*, meaning brown, plus the noun *cephalus*, meaning head (in reference to its distinctive brown head).

Hymenocoris formicinus Uhler
Figures 101–105, 108–114

Hymenocoris formicina Uhler, 1892: 182. — Usinger, 1939: 267. — Usinger, 1945 (1944): 339. — Kritsky, 1978b: 74–76.
Hymenocoris formicinus, Štys, 1978 (1977): 247.
Henicocephalus formicina, Johannsen, 1909: 4. — Usinger, 1932: 146–147, 156.
Enicocephalus formicina, Bruner, 1924b: 53.
Stenopirates formicinus, Jeannel, 1942 (1941): 326–329.

DISTRIBUTION: Coastal and central California east to Arizona and south to southern Baja California.

DIAGNOSIS: *Hymenocoris formicinus* males can be distinguished from their congeners by their measurements, their narrow head across eyes (equal to or less than hind lobe of head width), and by their ocelli (remote from lateral edge of head). Females are wingless, have small eyes, and are known only from this species.

REDESCRIPTION: Male. Length 4.6–6.3 mm. General body color dark brown to piceous. Body moderately clothed in medium length setae. Texture shiny with stippled quality. Head piceous, with eyes, ocelli, and antenniferous tubercles tinged with red. Antennae and rostrum medium to dark brown. Pronotum, scutellum, meso- and metathorax varying from brown to piceous. Abdomen fuscous; genital capsule slightly darker. Wings fuscous and translucent; wing bases, stigmas, and occasionally costal veins variously tinged with red. Legs fuscous.

Head longer than pronotum (1:0.7; figs. 102A, 108). Eyes of moderate size: ratio head length to width across eyes 1:0.4; ratio length of eyes to anteocular distance from 1:1.1 to 1:1.4; ratio eye width to synthlipsis 1:1.0 to 1:1.4; ratio head width across eyes to hind lobe of head width from 1:1 to 1:1.2. Ratio length to width of hind lobe of head 1:1.3 to 1:1.4. Ocelli of moderate size, not projecting beyond head laterally. Antennal segments I–IV 1:3.5:3.2:2.3; antenna approximately as long as head and pronotum combined.

Pronotum (figs. 102A, 108), with a shallow median longitudinal sulcus on midlobe, and a shallow transverse incision between mid and hind lobes. Ratio width of mid to hind lobes 1:0.7. Anterior coxal cavities open behind.

Forewings as shown in figure 108, with a large discal cell. Short setae roughly two-ranked along veins of disc of forewing; lumens of posterior cells containing many (50–100) short setae (fig. 104D).

Abdomen and genitalia as in generic description and as shown in figures 105D, E, 110F, H, I, L (see also discussion in introduction under: Genitalia, Homologies, and the Phylogeny of the New World Taxa). Abdomen not extending beyond wingtips.

Forelegs as shown in figure 111F. Ratio length to width of forefemur 1:0.25 to 1:0.20. Ratio length to width of foretibia 1:0.26 to 1:0.23. Foretibia and tarsus bearing spines as in figures 103B, C, 111A–K (see Discussion below).

Ratio length to width of hind femur 1:0.18 to 1:0.13 (fig. 111L).

Female. Length 6.1–7.3 mm (specimens in alcohol; pinned material may be shorter due to shrinkage).

General body color light brown. Head and all legs uniform light brown; pronotum, meso- and metathorax slightly darker. Antenna and abdomen white. Body with a textured shine and sparsely to moderately clothed in medium length setae.

Head longer than pronotum (1:0.8; figs. 102D, 109). Eyes minuscule, very sparsely pigmented, and consisting of about only a dozen ommatidia clustered toward the front and top (fig. 102E). Ratio of eye length to anteocular distance 1:4.2. Ocelli absent.

Antennal segments I–IV 1:2.7:2.6:2.1, combined slightly longer than head plus pronotum (1:0.8).

Thorax as in generic description. Ratio length to width of pronotum 1:0.9.

Forelegs extremely stout (fig. 112C). Ratio length to width of forefemur 1:0.40. Minute cuticular granules present on anterior edge of forefemur and coxa, and a stout basal process present as in generic description. Foretibia and tarsus armed with spines as in figures

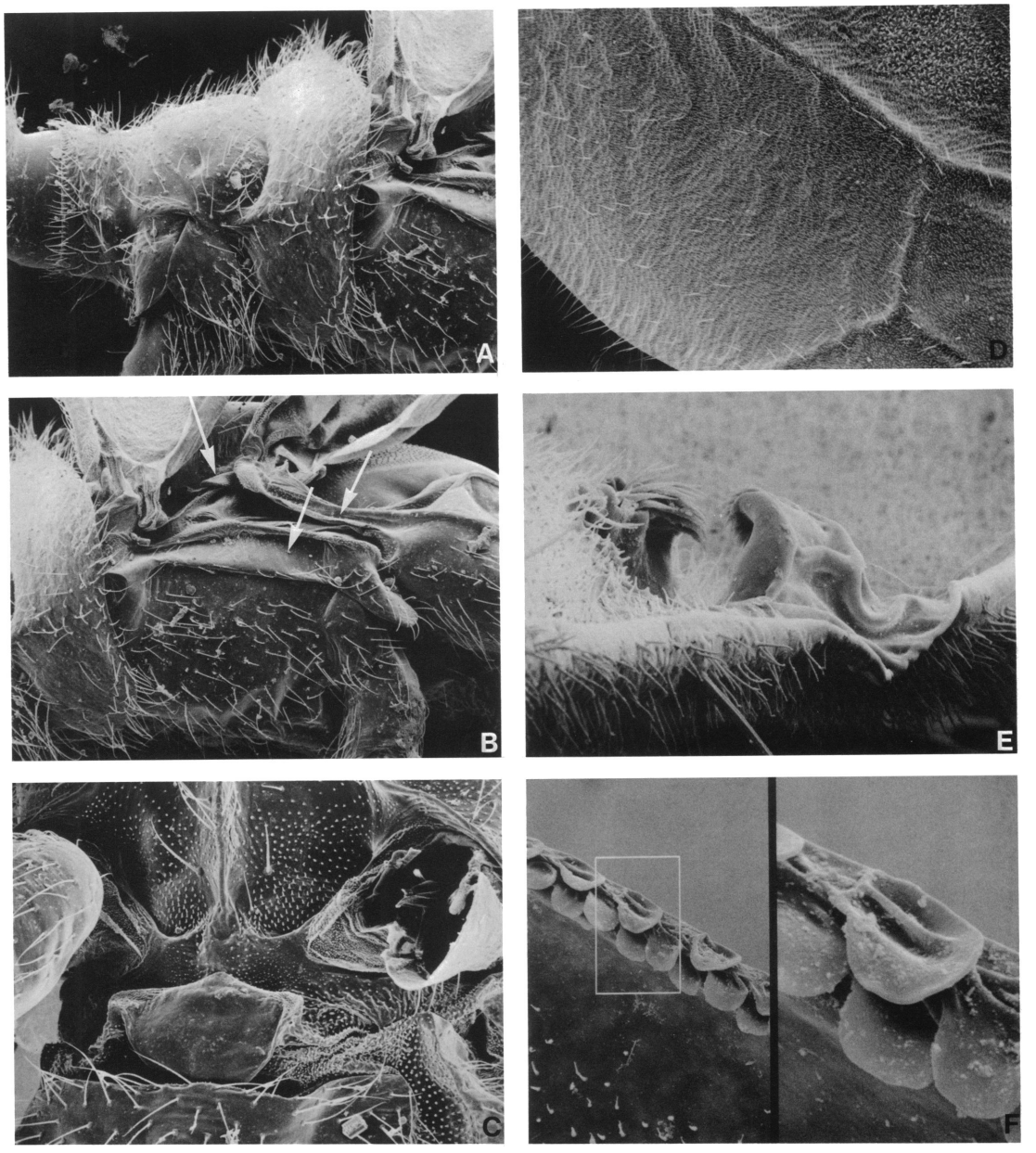


Fig. 104. *Hymenocoris formicinus*, ♂. **A**. Prothorax, lateral. **B**. Meso- and metathorax, lateral (left arrow points to scent gland auricle, middle arrow to forewing-to-body coupling groove, and right arrow to hind wing-to-body coupling groove). **C**. Thoracicoabdominal junction, ventral. **D**. Surface of forewing, showing setae in cell lumens. **E**. Wing coupling mechanism under hind edge of forewing. **F**. Hind wing edge at level of wing coupling mechanism, showing foliaceous structures.

103E, F, 112D, E. Ratio length to width of foretibia 1:0.40.

Ratio length to width of hind femur 1:0.30.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, USA: **California**: *Los Angeles Co.*: no date (Coquillett collection; USNM); examined. This specimen is labeled "lectotype" and is missing its head and one foreleg.

MATERIAL EXAMINED: MEXICO. – **Baja**

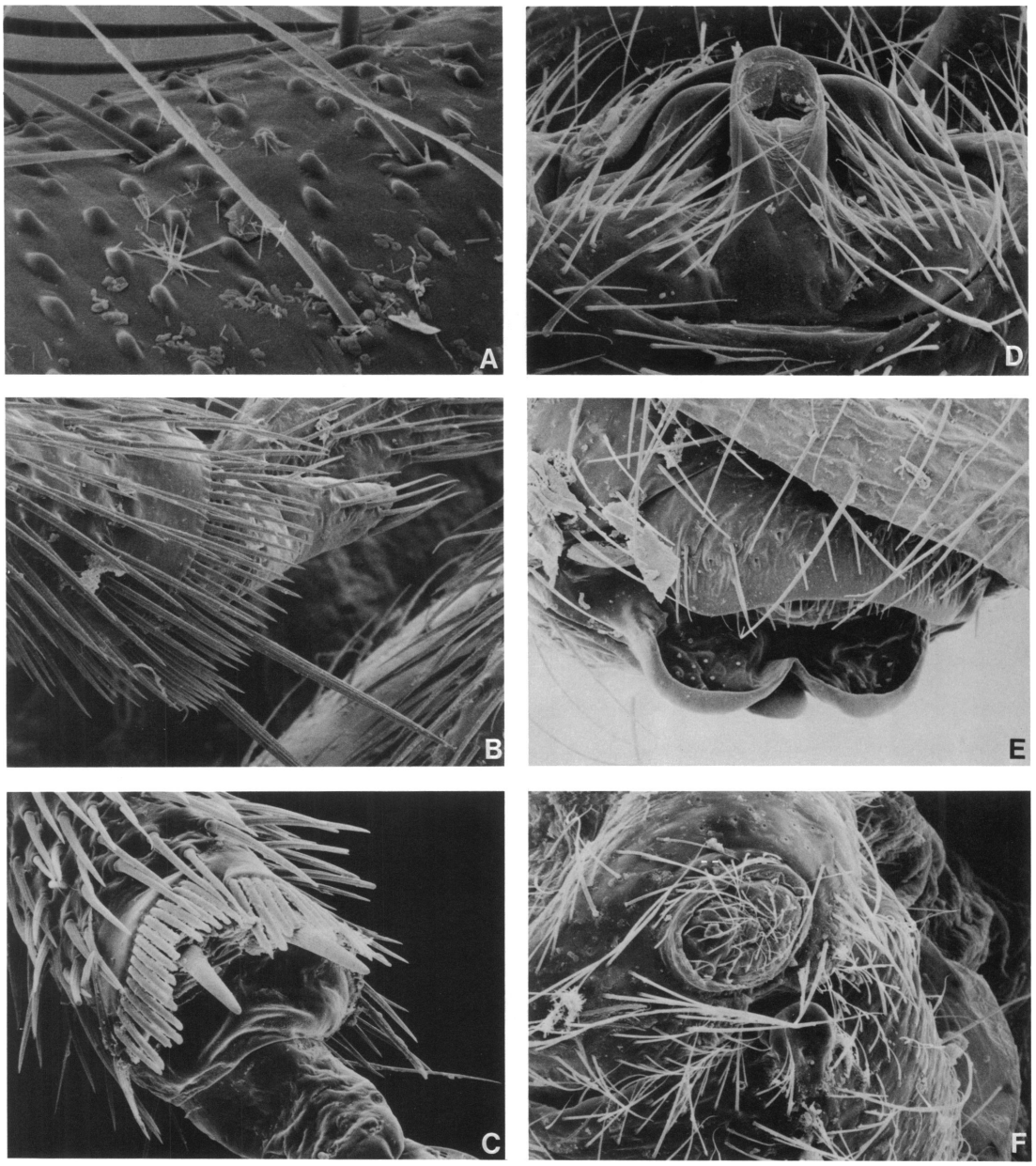


Fig. 105. *Hymenocoris formicinus*. **A**. Inner (ventral) surface of forefemur, ♀. **B**, **C**. Apices of hind tibiae, ♂ and ♀, respectively, showing two narrowly separated bristle combs and two spines each. **D**, **E**. Genitalia, ♂, posterior and dorsal views, respectively. **F**. Genitalia, ♀, oblique ventral view.

California Sur: Sierra La Laguna, 1770–1850 m, light trap near stream, August 29, 1977 (E. Fisher and R. Westcott; CAS), 1♂. USA. – **Arizona**: *Cochise Co.*: Southwest Research Station near Portal, 5400 ft (1650 m), at lights, 4:30 AM, no date (V. Roth; AMNH), 1♂; Stewart Camp, 1 mi S of Portal, malaise trap, August 26–29, 1971 (J. Doyen; Essig Mus.), 1♂. **California**: *Alameda Co.*: Berkeley Hills, November 12, 1959 (P. Ashlock; Ashlock collection), 1♂; Niles, at light, November 21, 1961 (W. H. Tyson; AMNH), 2♂; Berkeley Hills, back of University of California, in bee tunnel, May 24, 1959 (R. W. Thorp; AMNH),

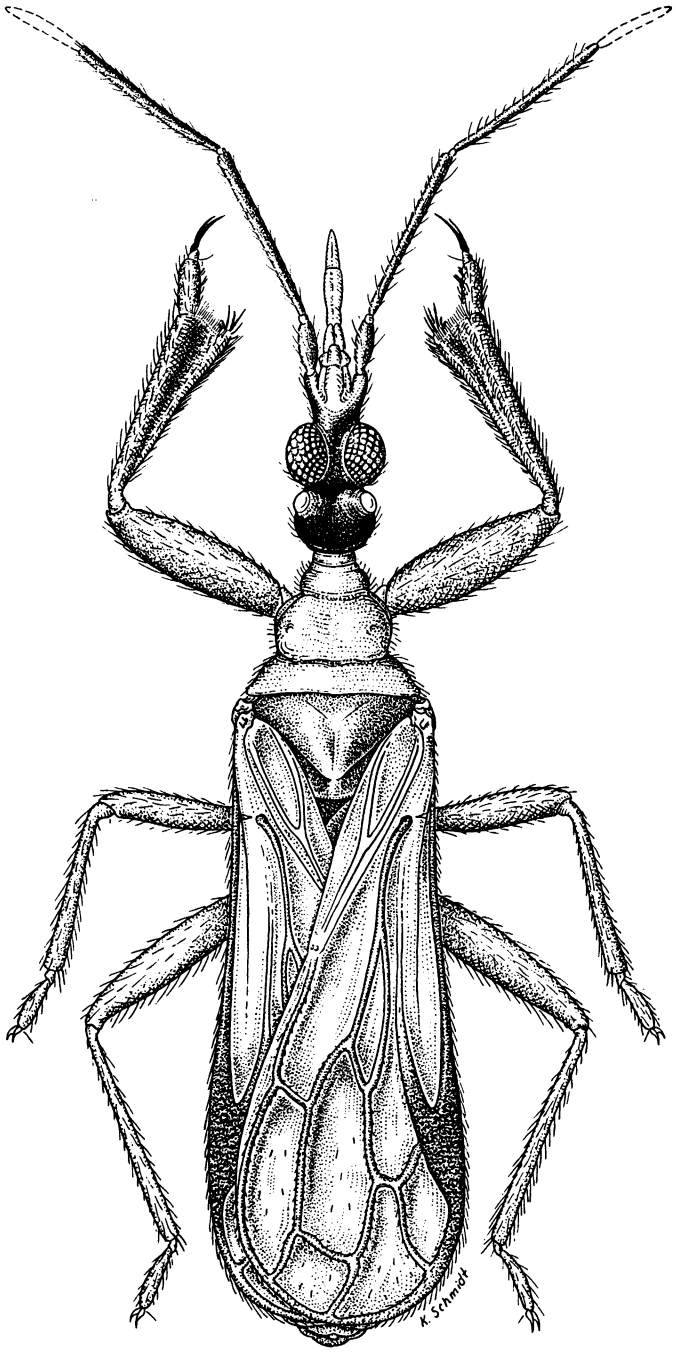


Fig. 106. *Hymenocoris brunneocephalus*, ♂, dorsal view.

2♀ (used for SEM). *Calaveras Co.:* 4 mi E of Murphys, 3000 ft (917 m), July 16, 1963 (P. Quyle; AMNH), 1♂. *Contra Costa Co.:* Berkeley, Tunnel Road, light trap, July 6, 1931 (R. L. Usinger; AMNH), 1♂; 1946 (J. W. MacSwain; AMNH), 1♂; Lafayette, in swimming pool, September 21, 1968 (G. M. Buxton; AMNH), 4♂; 3 mi NE of Orinda, flying

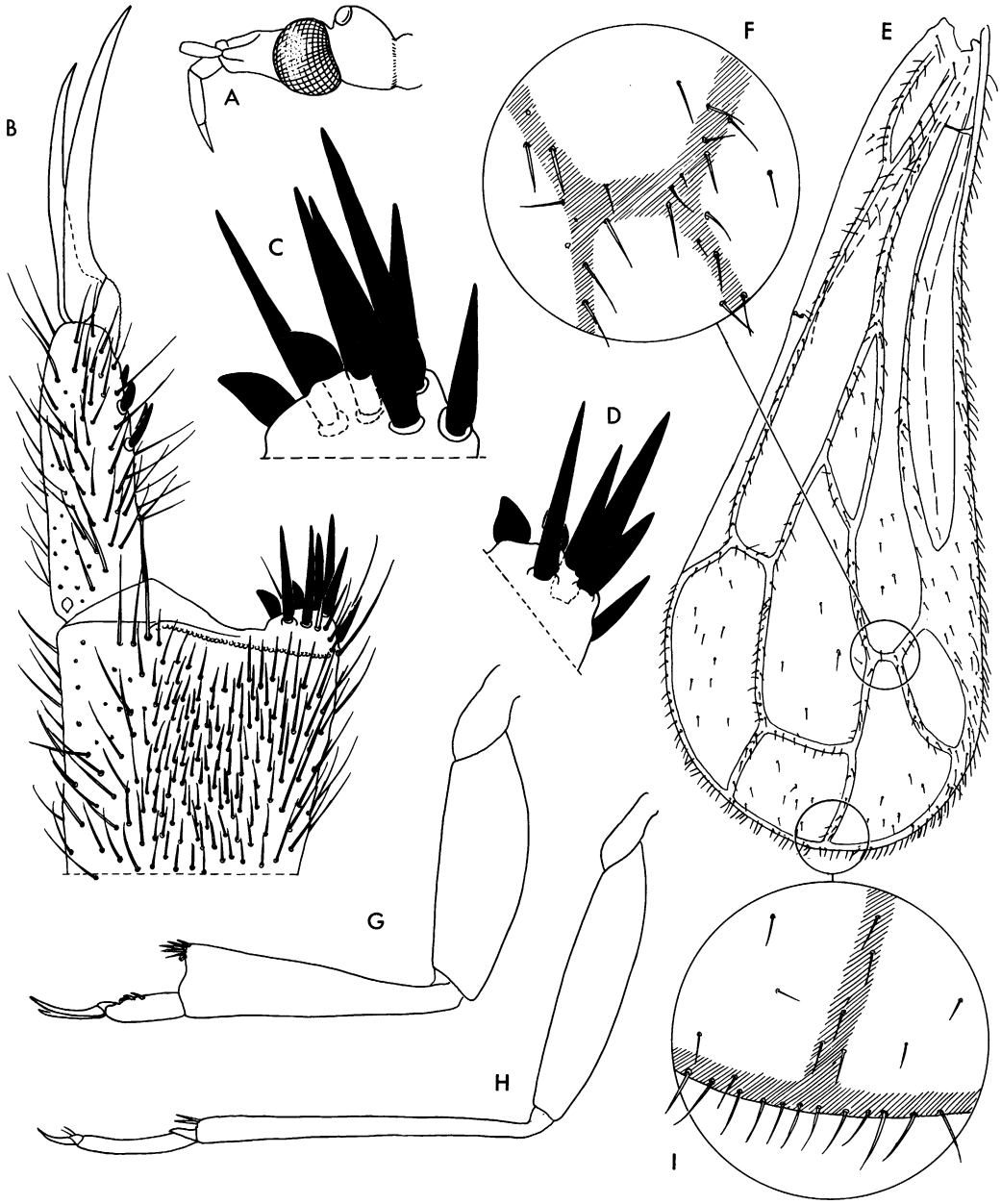


Fig. 107. *Hymenocoris brunneocephalus*, ♂. **A**. Head, lateral view. **B**. Apex of foreleg, inner view. **C**. Tibial spines, showing atypical number (8) and configuration, outer view, **D**. Tibial spines, usual number (7), outer view. **E**. Forewing. **F**. Detail of forewing. **G**. Foreleg. **H**. Hind leg. **I**. Detail of apex of forewing.

at 6:30 AM, October 1, 1961 (W. Ferguson; AMNH), 1♂; Walnut and Creek (San Ramon Cr. x SPRR), at light, October 9, 1966 (J. Powell; AMNH), 1♂; Kensington, flying at 7: 30 AM, October 20, 1976 (H. V. Daly; AMNH), 1♂. *Fresno Co.:* Auberry, October 20, 1962 (no collector; AMNH), 1♂. *Humboldt Co.:* Richardsons Grove, black light, September 5, 1968 (R. A. Belmont; AMNH), 2♂. *Los Angeles Co.:* Glendale, October 8,

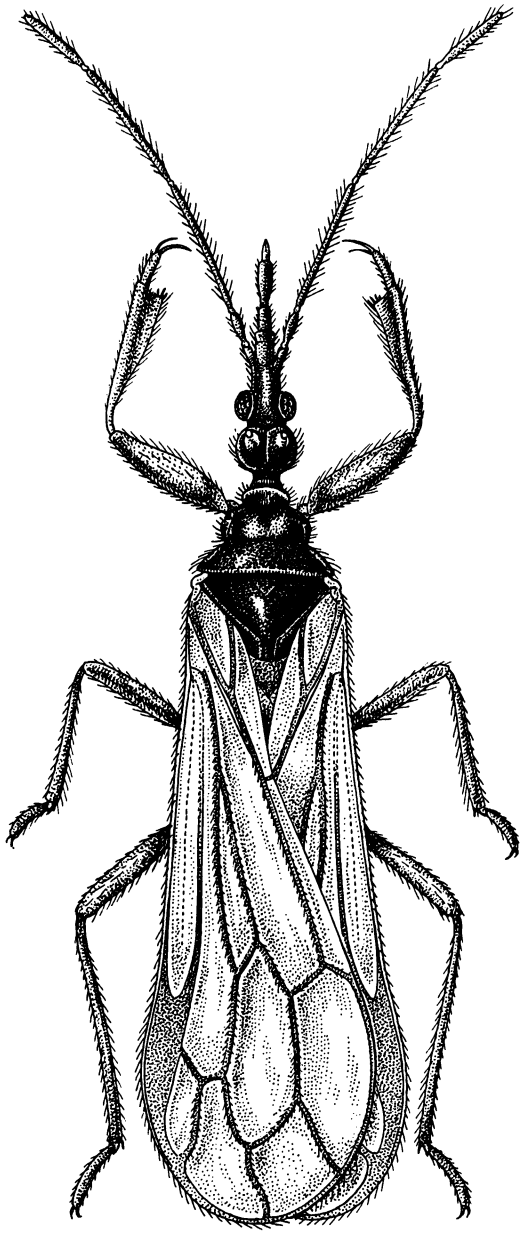


Fig. 108. *Hymenocoris formicinus*, ♂, dorsal view.

1951 (W. M. Schlinger; U. C. Davis), 1♂; Griffith Park, December 24, 1930 (E. C. Van Dyk; AMNH), 1♂. *Marin Co.:* Corte Madera, August 5–18, 1972 (D. Baldwin; U. C. Davis), 3♂; Marshall, trapped in spider web, October 16, 1964 (R. O. Sanders; AMNH), 1♂; Mill Valley, November, 1947 (E. S. Ross; AMNH), 1♂; October 8–11, 1965 (P. H. Arnaud; CAS), 2♂; Fairfax, May 19, 1919 (F. E. Blaisdell; AMNH), 1♀; Mill Valley, Ross residence, un-

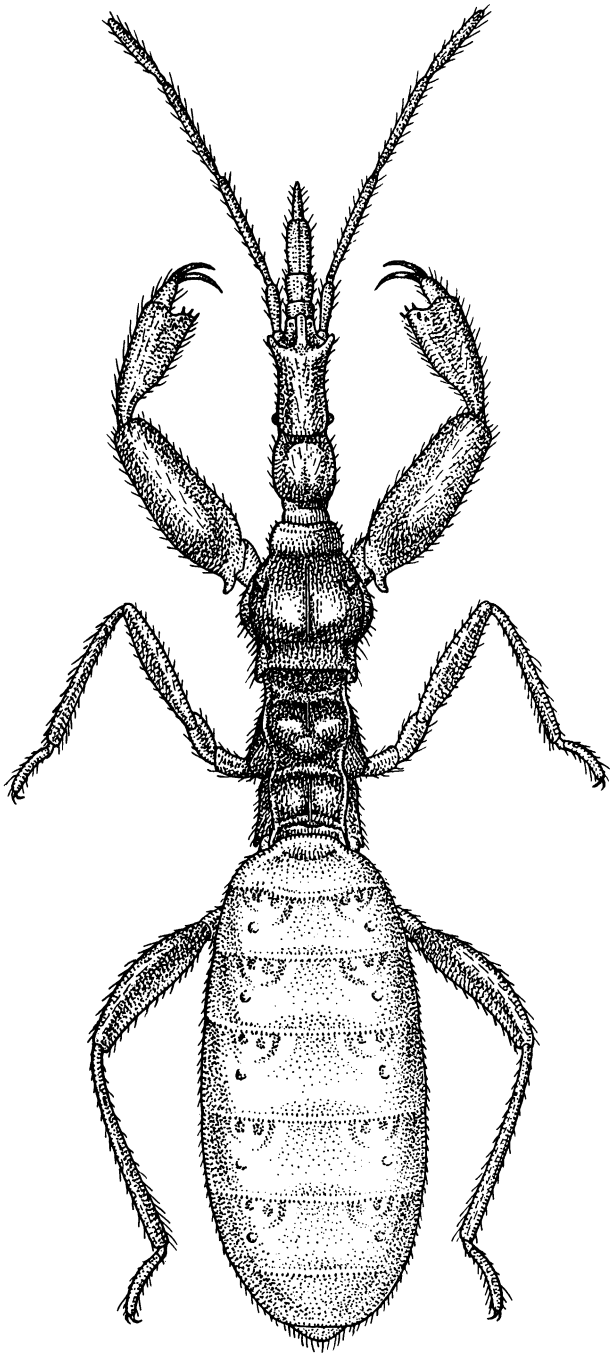


Fig. 109. *Hymenocoris formicinus*, ♀, dorsal view.

der deep stone, July 6, 1961 (collected), August 25, 1961 (died) (E. S. Ross; AMNH), 1 nymph. *Monterey Co.:* Carmel Valley, under rock in soil, April 1, 1961 (Steve Johnson; AMNH), 1♀. *Sacramento Co.:* Sacramento, Arden Park, at light, August 7–17, 1968 (R. A. Belmont; AMNH), 3♂; Sacramento, June 16, 1968 (no collector; AMNH), 1♂; Sacramento, August 14, 1968 (R. A. Belmont; AMNH), 1♂. *San Mateo Co.:* San Bruno

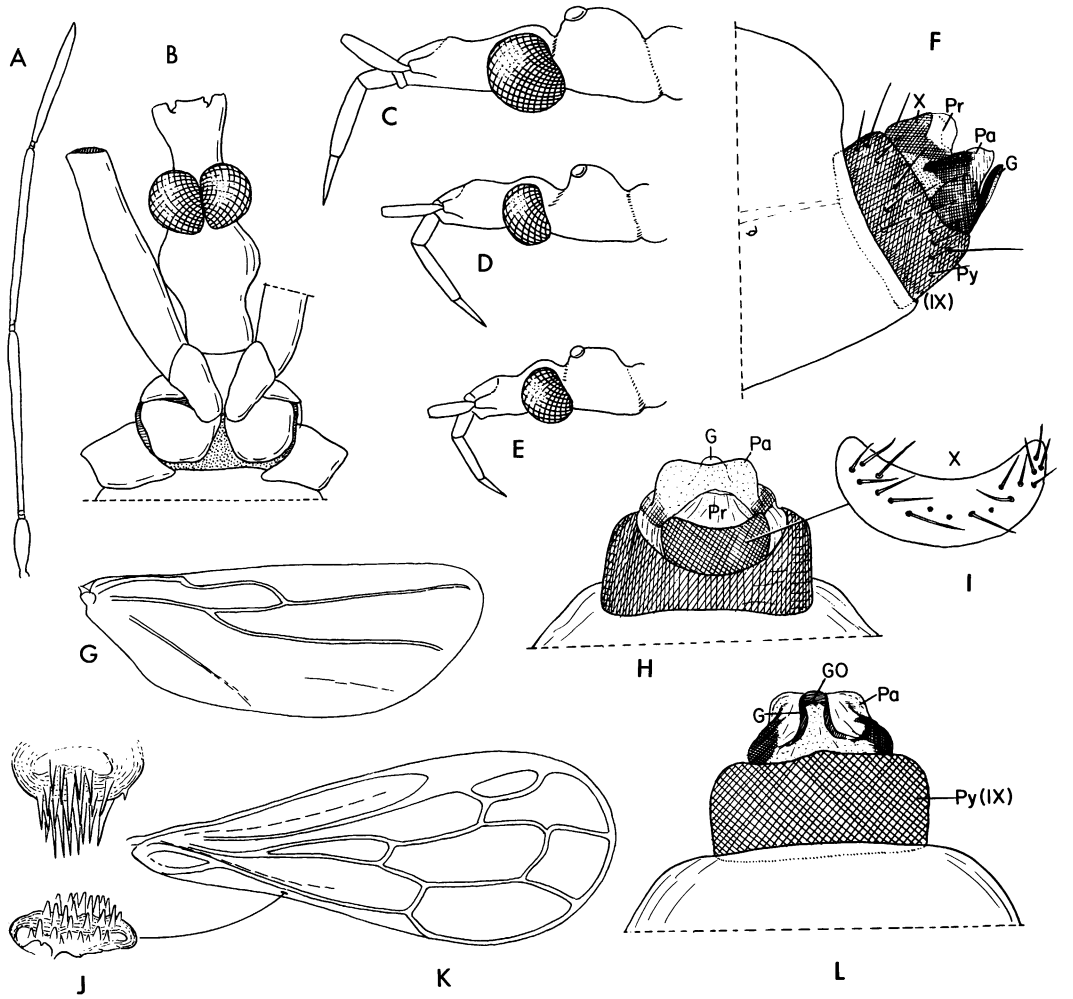


Fig. 110. *Hymenocoris formicinus*, ♂. **A**. Antenna (Los Gatos). **B**. Head and prothorax, ventral (Los Gatos). **C–E**. Lateral views of heads (Adobe Creek, Los Gatos and Glendale, respectively). **F**. Genital region, lateral view (Santa Cruz). **G**. Hind wing (Los Gatos). **H**. Genital region, dorsal view (Santa Cruz). **I**. Detail of tergum X. **J**. Wing coupling mechanism on hind edge of forewing. **K**. Forewing (Los Gatos). **L**. Genital region, ventral view (Santa Cruz).

Mountains, February 28 and March 10, 1961 (Wygodzinsky; AMNH), 3♀ and 6 nymphs; no date (Usinger and Wygodzinsky; AMNH), 1♀; no date (no collector; AMNH), 2♀, 1 nymph, eggs; March 30, 1962 (R. L. Usinger; AMNH), 1♀; rocks behind Daly City, March, 1957 (Bandar; AMNH), 1♀. *Santa Barbara Co.:* 3 mi N of Refugio Beach, June 20–28, 1965 (J. Powell; AMNH), 2♂. *Santa Clara Co.:* East Los Gatos foothills, October 9, 1966 (some used for SEM); October 8, 16–19, 23, 25, 29, 31, 1967; November 4, 6–8, 11, 14–15, 1967; December 19, 1967 (R. M. Vierhus, AMNH), 63♂; San José at light, June 3, 1933 (L. W. Saylor; AMNH), 1♂. *Santa Cruz Co.:* Santa Cruz, light trap, July, 1948 (R. Coleman; AMNH), 2♂. *Stanislaus Co.:* Adobe Creek, 22 mi W of Patterson, August 29, 1952 (H. B. Leech and J. W. Green; CAS), 1♂; La Grange, black light, June 2, 1970 (R. P. Allen; AMNH), 1♂.

DISCUSSION: Males of *H. formicinus* vary tremendously and thus this species has a broad definition (see Discussion under genus

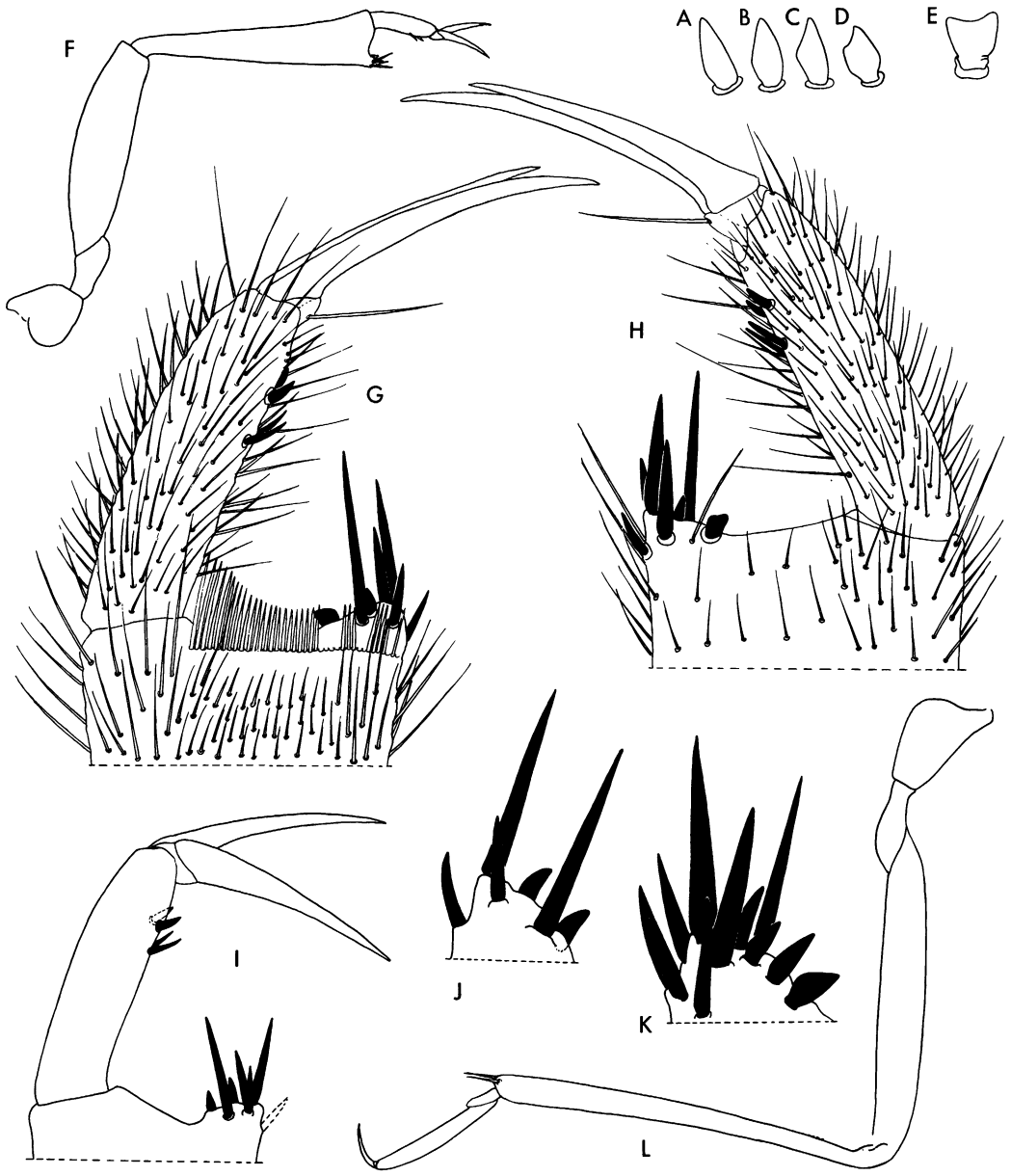


Fig. 111. *Hymenocoris formicinus*, ♂. **A–D**. Variations in shape of tibial spine VI. **E**. Comparison with tibial spine VI of female. **F**. Foreleg. **G–K**. Variation in shape, number, and placement of foretibial spines. **G**. Santa Cruz, inner surface. **H**. Santa Cruz, outer surface. **I**. Glendale, inner surface. **J**, **K**. Los Gatos, opposite forelegs from one individual. **L**. Hind leg.

Hymenocoris). Specimens that are intermediate in some characters have been included here. The specimen from Adobe Creek (Stanislaus County, California) has its head width across eyes greater than the width of the hind lobe of its head, and a slightly wider head than most *formicinus* specimens, but fits in with this species in other characters. This specimen and one from Auberry (Fresno County, California) both have light-colored pronota.

Color in *H. formicinus* varies mostly in the

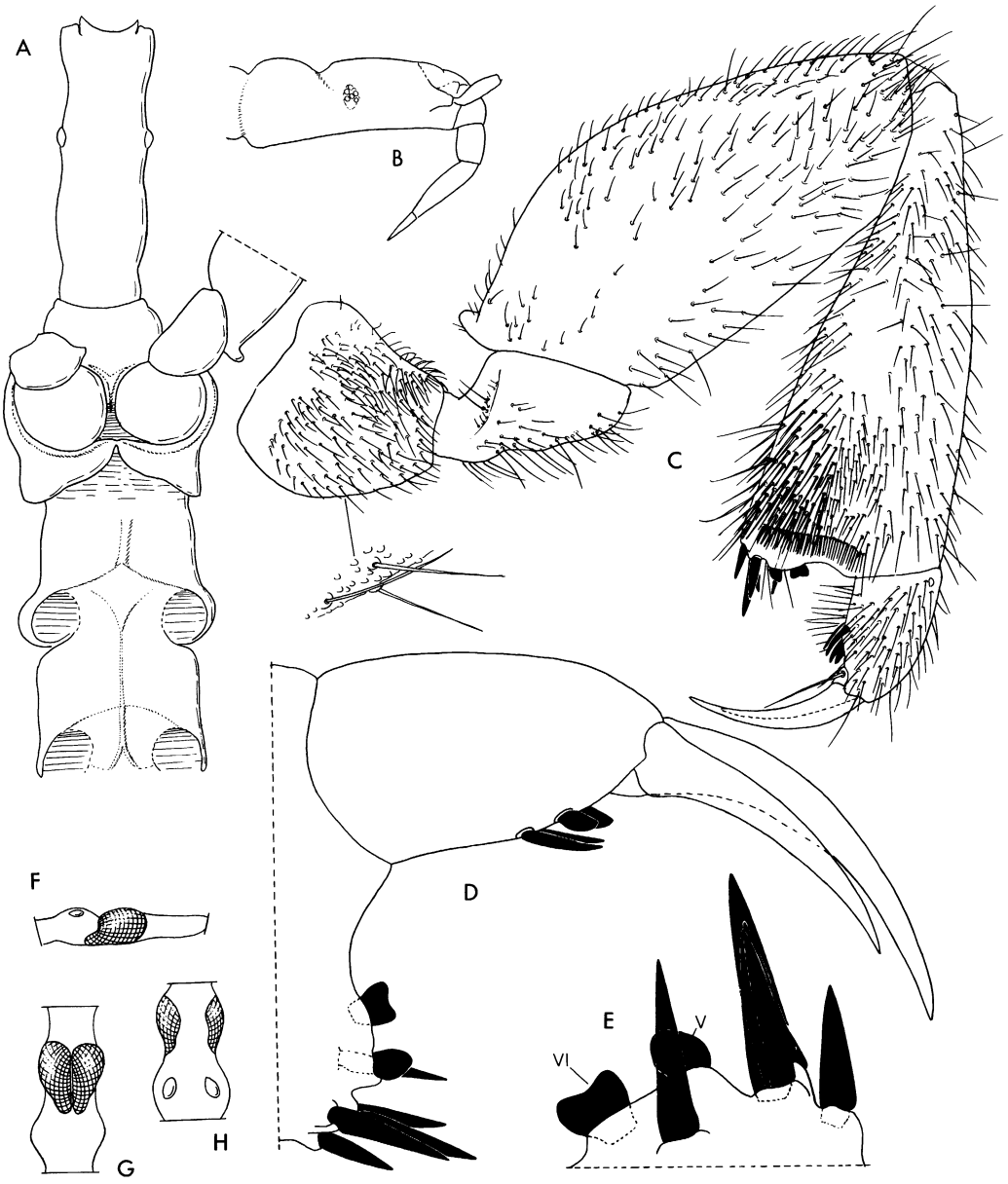


Fig. 112. *Hymenocoris formicinus*. **A–E**. ♀ from San Bruno, California. **A**. Ventral view of head and thorax, mid- and hind legs removed. **B**. Lateral view of head. **C**. Foreleg, inner surface. **D**. Apex of foreleg, inner surface. **E**. Detail of foretibial spines, outer view (note short tibial spines V and VI). **F–H**. ♂, nymph from San Bruno, lateral, ventral and dorsal views, respectively.

pronotum, although there are slight differences in the head and scutellum. The most common condition is: piceous head, pronotum, and scutellum with dark fuscous legs.

Three additional specimens have been found in localities quite far from most *H. formicinus* localities and differ slightly from the others. Specimens from Arizona (Cochise County) are fairly small (5.1 mm), and the specimen from southern Baja California is

very dark brown and shiny. We do not have enough material from these localities to determine their specific status for certain, so include them in *H. formicinus* until more information is available.

Hymenocoris hintoni Kritsky
Figures 101, 114

Hymenocoris hintoni Kritsky, 1978b: 74

DISTRIBUTION: Mexico; Vera Cruz, and possibly north to southern California (see Discussion).

HOLOTYPE: According to Kritsky (1978), the holotype and seven paratypes are deposited in the California Academy of Sciences. However, they are apparently not there, nor are they at Tri-State University where the work was done. They are not at the Illinois Natural History Survey, where types of other species were deposited by Kritsky, nor at the U.S. National Museum. We are unwilling to declare them lost at this time, and feel they will turn up eventually.

MATERIAL EXAMINED: MEXICO. – **Sinaloa**: 11 mi S of Guasave, 200 ft (61 m), UV light, December 16, 1963 (L. R. Obrien; J. A. Slater collection), 2♂; (L. R. Obrien; Ashlock collection), 2 ♂. USA. – **California**: *San Luis Obispo Co.*: Paso Robles, July 19, 1931 (C. H. Hicks; AMNH), 1♂

DISCUSSION: The type series has been misplaced (see holotype, above), so we have not seen the holotype. We have five specimens that may be *H. hintoni*: four from Sinaloa, Mexico, and one from southern California. There is a conflict in Kritsky's (1978b) paper concerning eye size, which seems to be an important character. According to the text, the ratio of head width across eyes to hind lobe of head width is 1:0.7. However, the drawing shows the two measurements to be approximately equal. Until the holotype can be located, our inclusion of the above five specimens in this species is, at best, speculative.

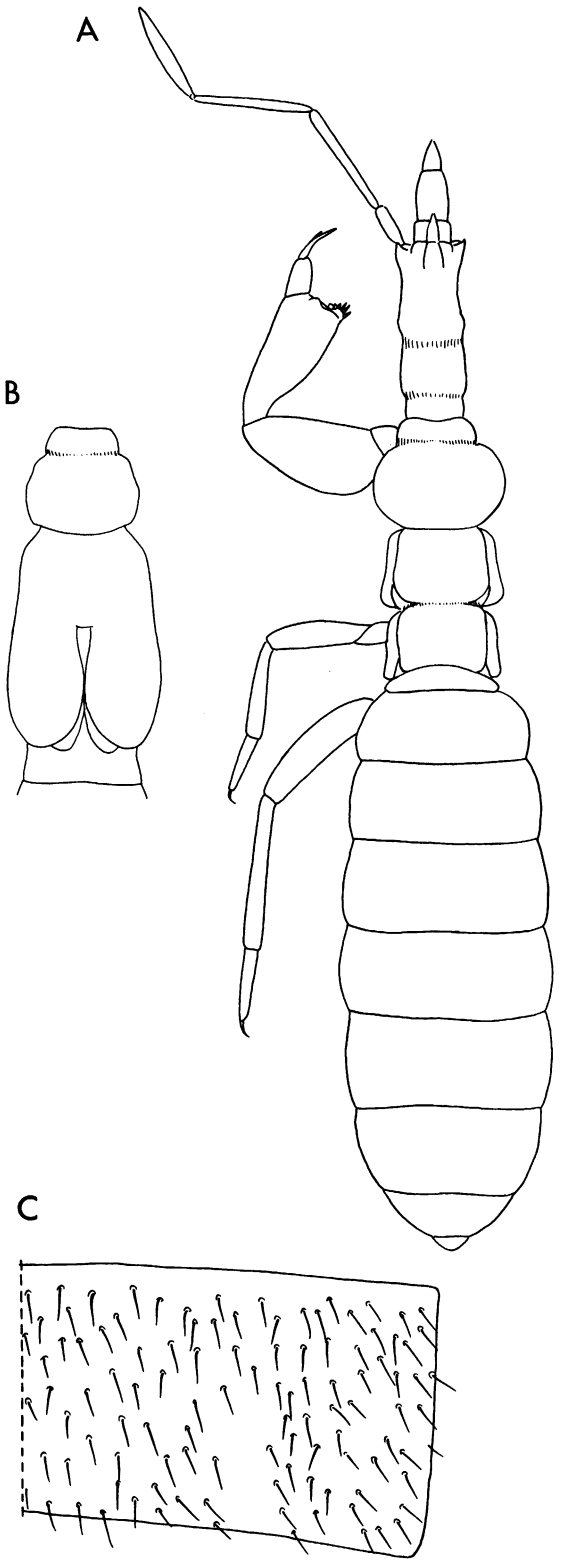


Fig. 113. *Hymenocoris formicinus*, fifth instar nymphs. **A**. Dorsal view ♀. **B**. Pronotum and wingpads ♂. **C**. Detail of tergum VI ♀.

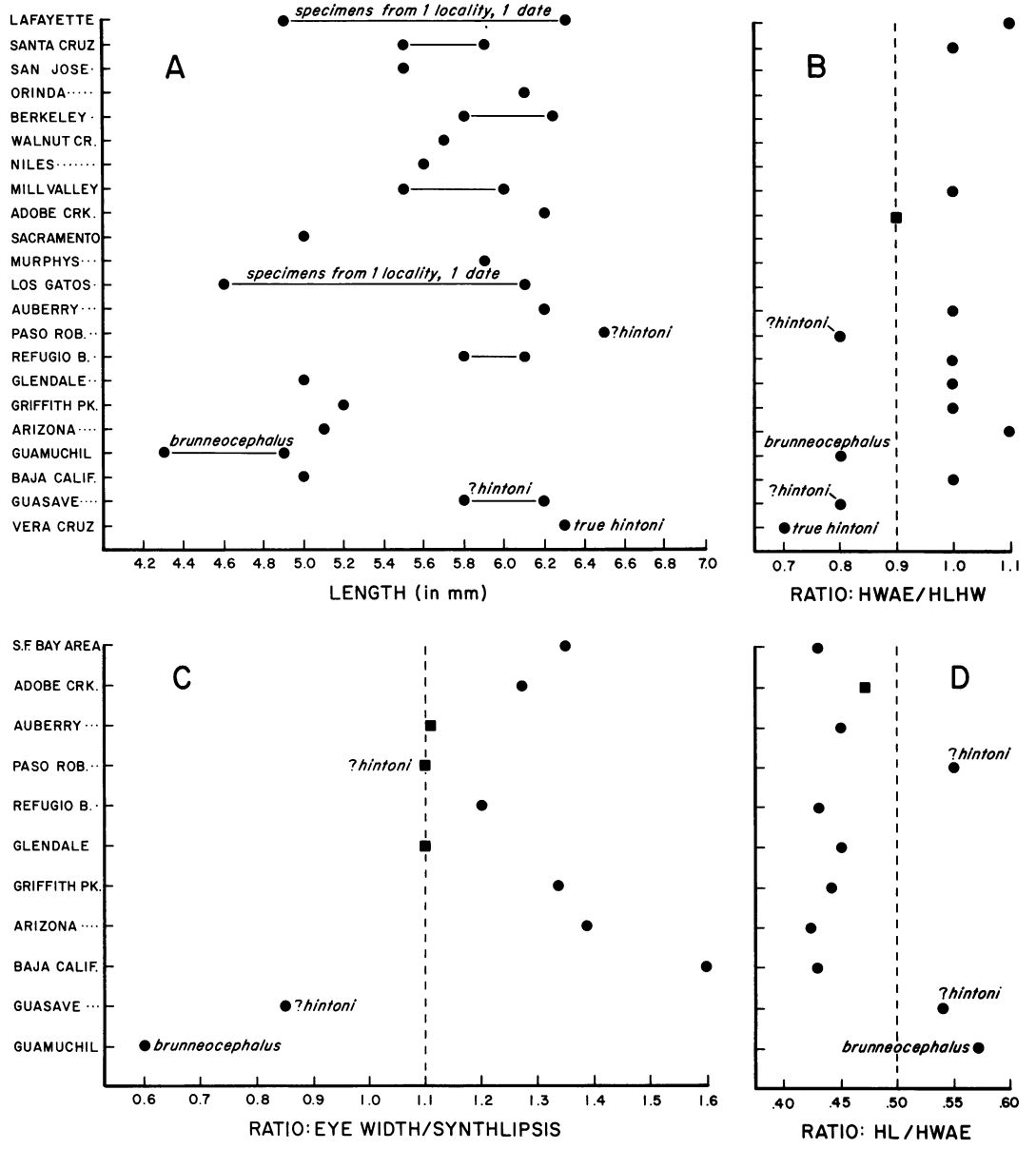


Fig. 114. Graphic representation of four characters in three species of *Hymenocoris* males. All data points are *H. formicinus* unless otherwise indicated. **A.** Horizontal bars represent ranges within lots; true *hintoni* figures are based on the original description (type could not be located); ? *hintoni* are specimens we examined and presumed to be *hintoni* based on description. **B.** HWAE = head width across eyes; HLHW = hind lobe head width. **B, D.** ●, probably distinct species, ■, specimens with many intermediate characters. **D.** HL = head length.

Lysenicocephalus, new genus

TYPE SPECIES: *Lysenicocephalus chemsaki*, new species.

DISTRIBUTION: Known from Baja California and Texas (fig. 115).

DIAGNOSIS: *Lysenicocephalus* is one of three small genera (including *Brevidorsus* and *Urnacephala*), which lack a basal cell in the forewing (fig. 117E). This genus can be distinguished by the presence of a closed discal cell, exceptionally large ocelli (fig. 116B), the pres-

ence of five to seven large spines on the foretibia (figs. 116E, 117F, G), the narrowly tongue-shaped phallus (fig. 116I, 117H) which is rounded apically, and the tenth tergum, which is convex posteriorly (figs. 117H).

DESCRIPTION: Male. Small size (3.0–3.7 mm), extremely delicate insects. General body color very light brown. Body surface somewhat shining, lacking setiferous tubercles. All setae simple, slender. Macropterous.

Head with constriction behind eyes well developed (fig. 116B). Eyes very large; synthlipsis narrower than width of eye. Ocelli very large. Antennae with second and third segments subequal in length (fig. 116A; fourth missing in all specimens examined). Rostrum slender (fig. 117B). Hind lobe of head transverse, shorter than wide, sides rounded.

Pronotum unarmed (fig. 116B). Median lobe with a simple median longitudinal impression; disc of lateral portions of midlobe lacking sculptural elements. Hind lobe of pronotum very short, almost ribbon-shaped, its posterior border emarginate. Scutellum widely exposed. Anterior acetabula open behind.

Front legs of moderate proportions (figs. 116F, 117C). Coxa and femur with or without minute irregularly arranged cuticular structures (figs. 116G, 117D). Trochanter lacking process. Inner apical angle of tibia with a group of five to seven strong, straight spines of various lengths (figs. 116E, 117G). Tarsus approximately as long as width of apical portion of tibia. Tarsal organ situated on inner lateral surface of tarsus. Four well-developed, simple tarsal spines (figs. 116E, 117F): I and III stout, II and IV more slender and more pointed. Two claws, outer one only two-thirds as long as inner one, the latter approximately as long as tarsus. Middle and hind legs without special characters; apex of tibiae with two bristle combs and two large setae.

Forewings lacking basal cell; discal cell closed (fig. 116D, 117E). Stigmal cell over half as long as discal cell. Apex of Cu attaining wing margin. Two anal veins developed; PCu extending beyond level of cu-pcu crossvein, attaining wing margin. Setae arranged on veins in two irregular rows, but only in a single row on R+M, and much more numerous on costal margin. Membrane of cells with short setae in moderate numbers, especially on apical half of wing. Hind wings not examined in detail; with a few setae along anterior margin and on membrane.

Abdomen with spiracles on ventral connexival plates.

Tenth tergum present, with a slight convexity at its posterior edge, possibly representing tergum 11 (fig. 117H). Guide tongue-shaped, rounded apically (fig. 117H).

Female unknown, probably wingless.

ETYMOLOGY: From the Greek *lysis*, meaning loosing or splitting, plus *Enicocephalus*, in reference to three superficially similar genera, which we split apart.

DISCUSSION: For a discussion of possible females of this genus, see Discussion under *Urnacephala*.

KEY TO SPECIES OF *LYSENICOCEPHALUS*

1. Ocelli extending laterally beyond edge of hind lobe of head (fig. 116B); hind lobe of head transverse, ratio length to width 1:1.7; apex of foretibia with five spines (fig. 116E); forefemur with microscopic cuticular tubercles (116G) ..... *chemsaki*, n. sp.
   Ocelli not extending laterally beyond sides of hind lobe of head (fig. 117A); hind lobe of head somewhat rounder, ratio length to width 1:1.5; apex of foretibia with seven spines (figs. 117F, G); forefemur lacking microscopic cuticular tubercles (fig. 117D) ..... *macneili*, n. sp.

Lysenicocephalus chemsaki, new species

Figures 115, 116

DISTRIBUTION: Known only from San Antonio, Texas.

DIAGNOSIS: *Lysenicocephalus chemsaki* can be distinguished by its ocelli which extend laterally beyond the edge of the head, by the proportions of the hind lobe of the head and by details of the forelegs mentioned in the key.

DESCRIPTION: Females unknown. Length of male 3.2 mm. General body color light brown. Head brown, with dark reddish brown eyes and red surrounding ocelli. Rostrum and entire thorax light yellowish brown. Antenna, legs, wings, and abdomen yellowish white. Genital area slightly darker. Body generally shiny; wings densely covered with mircrotri-

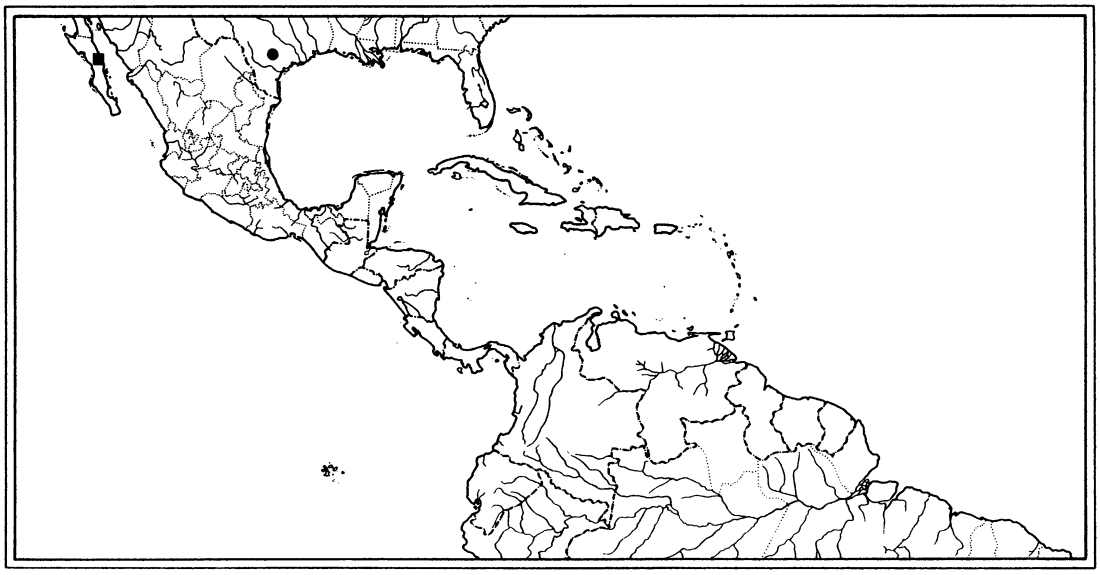


Fig. 115. Distribution of *Lysenicocephalus*. *L. chemsaki* (●); *L. macneil* (■).

chiae, giving them a dull appearance. Medium length setae sparse on all areas of body.

Head longer than pronotum (1:0.7; fig. 116B). Ratio head length to width across eyes 1:0.7. Ratio length of eyes to anteocular distance 1:0.5; ratio eye width to synthlipsis 1:0.7. Ratio width of hind lobe of head to head width across eyes 1:1.2. Ratio length to width of hind lobe of head 1:1.7. Ocelli extremely large, slightly over half length of hind lobe of head, and extending laterally beyond border of lobe. Rostrum as in figure 116C. Antennal segments I–III 1:2.6:2.8, segment IV missing (fig. 116A).

Pronotum as shown in figure 116B. Ratio length of fore to mid to hind lobes measured along midline 1:2:0.6; ratio width of fore to mid to hind lobes 1:1.5:2.1. Scutellum as in figure 116B.

Abdomen lightly sclerotized. Tenth tergum present, with a straight or slightly convex posterior border, but no obvious median tab (fig. 116I). Guide tongue-shaped, rounded at apex (fig. 116I).

Forewings poorly sclerotized, veins difficult to see. Venation as in figure 116D. Setae of medium length, most numerous along costal margin and apex of wing, sparser toward center of wing and in lumens of cells (fig. 116D). Wing coupling mechanism as in figure 116H. Hind wings setose apically.

Forelegs as in figures 116F. Forefemur bearing setae of one length; cuticular surface with microscopic granules (fig. 116G). Ratio length to width of forefemur 1:0.30. Ratio length to width of hind femur 1:0.24 (fig. 116J). Ratio length to width of foretibia 1:0.30, the apex bearing five long straight spines as in figure 116E. Foretarsus stout, only twice as long as wide, and bearing four spines (fig. 116E). Outer claw short, approximately two-thirds length of inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, USA: Texas: *Bexar Co.*: October 5, 1942 (E. S. Ross; AMNH).

ETYMOLOGY: The species is named for Dr. John A. Chemsak, curator of the California Insect Survey Collection at Berkeley.

Lysenicocephalus macneili, new species

Figures 115, 117

DISTRIBUTION: Known only from Baja California, Mexico.

DIAGNOSIS: *Lysenicocephalus macneili* can be distinguished by its ocelli, which do not extend laterally beyond the edge of the head by the proportions of the hind lobe of the head, and by details of the foreleg mentioned in the key.

DESCRIPTION: Female unknown. Length of

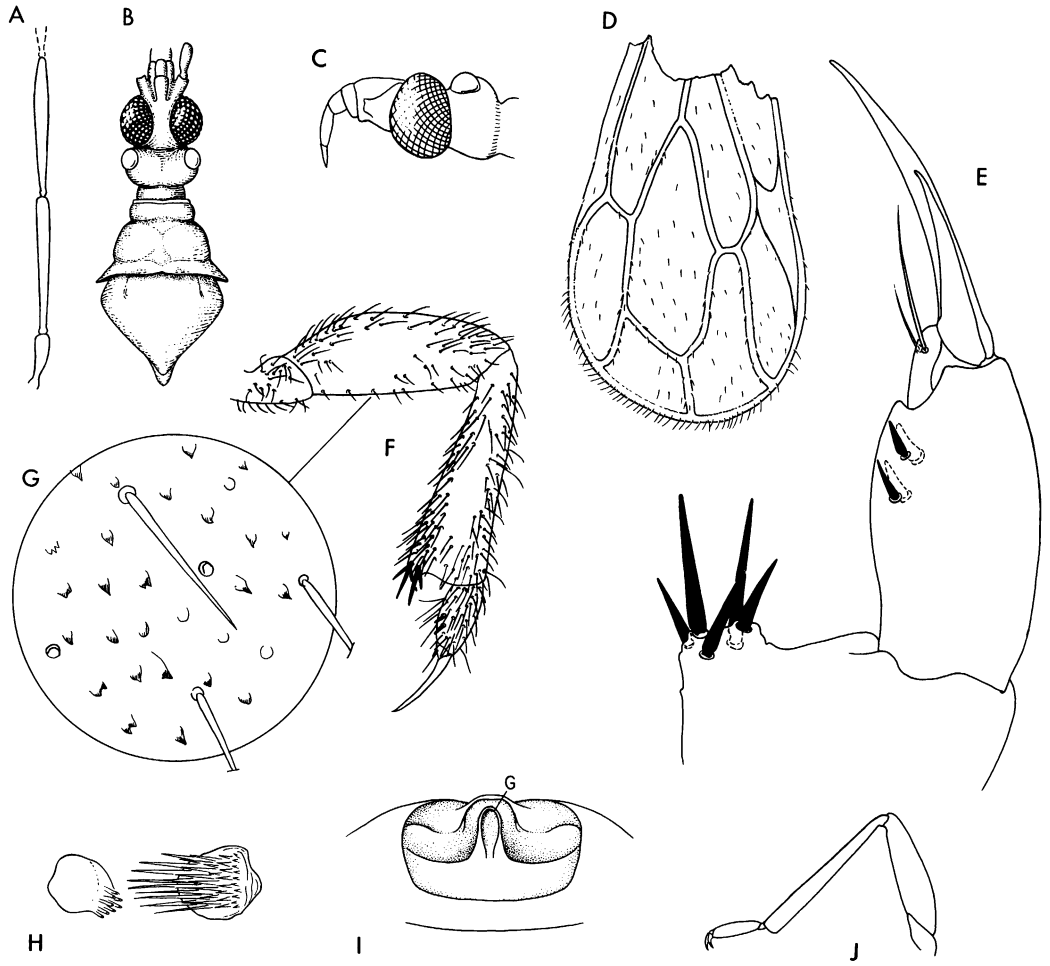


Fig. 116. *Lysenicocephalus chemsaki*, ♂. **A**. Antenna. **B**. Head, pronotum and scutellum, dorsal. **C**. Lateral view of head. **D**. Forewing. **E**. Apex of foreleg, outer surface. **F**. Foreleg. **G**. Detail of inner (ventral) surface of forefemur. **H**. Wing coupling mechanism **I**. Genital region, ventral view. **J**. Hind leg.

male 3.5 mm. General body color light brown. Head, eyes, and ocelli dark reddish brown. Rostrum and entire thorax brown; scutellum slightly darker. Legs light brown. Abdomen moderately sclerotized, dusky brown, with darker genital area. Wings extremely transparent and shiny. Body shiny and sparsely clothed with short to medium length setae.

Head longer than pronotum (1:0.7; fig. 117A). Ratio head length to width across eyes 1:0.6. Ratio length of eyes to anteocular distance 1:0.5. Ratio eye width to synthlipsis 1: 0.5. Ratio width of hind lobe of head to head width across eyes 1:1.2. Ratio length to width of hind lobe of head 1:1.5. Ocelli very large, about half as long as hind lobe of head, but not projecting laterally beyond the borders of the lobe. Rostrum as in figure 117B. Antennae missing on holotype.

Pronotum as in figure 117A. Ratio length of fore to mid to hind lobes measured along midline 1:1.6:0.5; ratio width of fore to mid to hind lobe 1:1.4:2. Scutellum as in figure 117A.

Forewings hyaline, sparsely covered with short setae (fig. 117E). A few setae in lumens of cells, especially at apex of wing. Veins light brown.

Abdomen lightly sclerotized. Tenth tergum present, with convex border, possibly

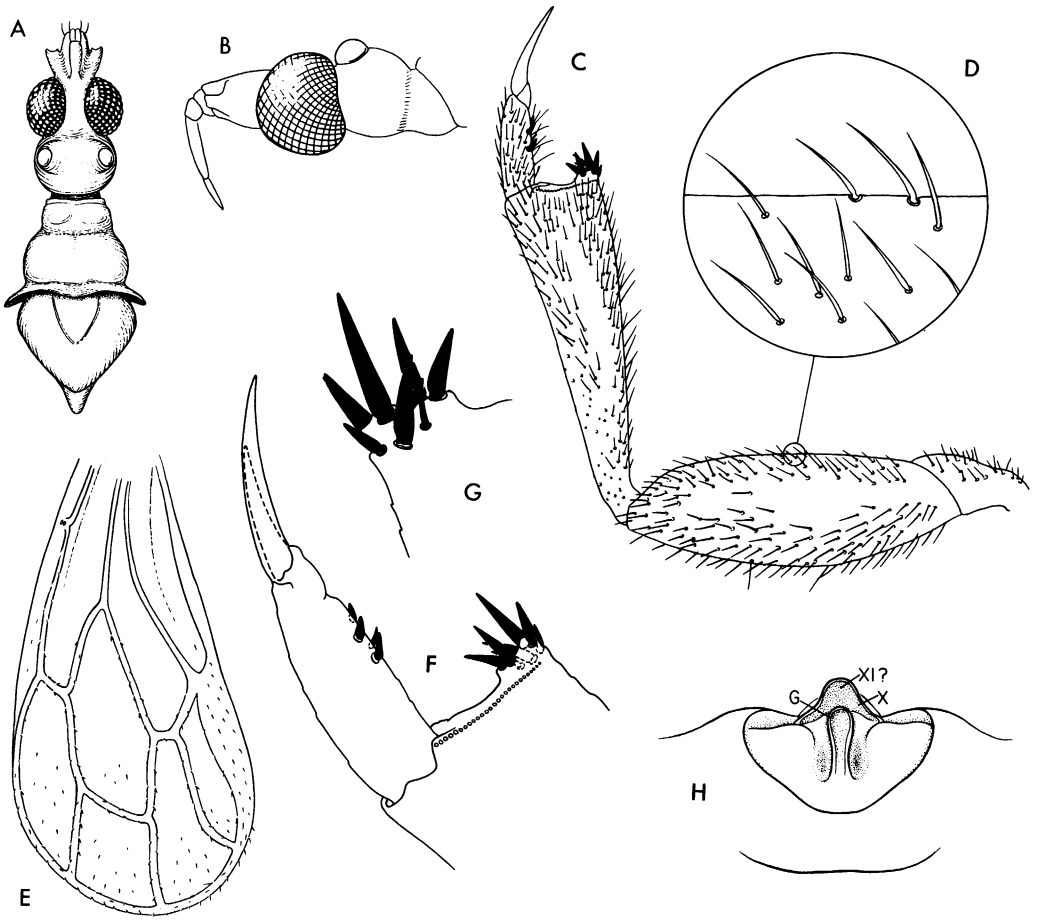


Fig. 117. *Lysenicocephalus macneili*, ♂. **A**. Head, pronotum and scutellum, dorsal. **B**. Lateral view of head. **C**. Foreleg, inner surface. **D**. Detail of inner (ventral) surface of foreleg. **E**. Forewing. **F**. Apex of foreleg, inner surface. **G**. Detail of foretibial spines, outer view. **H**. Genital region, ventral view.

tergum XI (fig. 117H). Guide narrowly spoon-shaped, with a rounded apex (fig. 117H).

Forelegs as in figure 117C. Forefemur bearing setae of uniform length and without microscopic granules on cuticle (fig. 117D). Ratio length to width of forefemur 1:0.32. Hind legs missing. Ratio length to width of foretibia 1:0.27, the apex bearing seven spines as in figure 117G. Foretarsus three times as long as wide, bearing four spines as in figure 117F. Outer claw short, two-thirds as long as inner claw.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, MEXICO: Baja California Sur: Concepcion Bay, Coyote Cove, June 29, 1938 (Michelbacher and Ross; AMNH).

ETYMOLOGY: This species is named for Dr. C. D. Macneil.

Neoncylocotis, new genus

Enicocephalus of authors (in part).
Stenopirates (*Hymenocoris*): Jeannel, 1942 (1941): 329 (in part).
Hymenocoris: Jeannel, 1944 (1943): 127 (in part).
Oncylocotis: Usinger, 1945: 332 (in part).

TYPE SPECIES: *Neoncylocotis albovenosus*, new species.

DISTRIBUTION (fig. 118): *Oncylocotis*, as understood here, is restricted to the Old

World, *Neoncylocotis* to the Western Hemisphere. The genus occurs in Central America, but is absent from the Antilles; it has numerous species in South America, where it attains southern Brazil and northwestern Argentina. *Neoncylocotis* has not been found in Chile.

DIAGNOSIS: Among the American genera, *Neoncylocotis* comes closest to *Enicocephalus*. The two genera can be separated by the different development of the claws of the forelegs, the quite different spines of the apex of the foretibia, and the scalelike setae on the abdominal terga. *Neoncylocotis* can be separated from the Old World *Oncylocotis* by the key characters given in the following discussion section.

DESCRIPTION: Small to medium-size species (2.7–6.3 mm). Body surface from slightly shining to dull. Setae slender or more or less flattened, very rarely capitate, except in *clavisetosus* males. All known species macropterous, but wings of female caducous in at least one species.

Head with deep constriction behind eyes (figs. 119A, B). Postocular portion of head from subglobular to distinctly transverse, its sides convex, longitudinally sulcate in center of dorsal surface. Eyes sexually dimorphic; eyes of males larger than those of females, attaining level of under surface of head in males only (figs. 119C, D). Antennae with third and/or fourth segment conspicuously thinner than first and second (fig. 119C, 123A).

Protonum unarmed (figs. 119A, B). Median lobe with a central longitudinal impression on anterior half, widened posteriorly into a deep transverse fovea, not attaining suture dividing mid and hind lobe. Sides of disc of median lobe with 1 + 1 simple longitudinal impressions. Hind border of pronotum distinctly emarginate. Scutellum with elevated portion constricted subapically, transversely dilated at apex. Anterior acetabula open behind. Prothorax unkeeled laterally (fig. 122A). Segments above metathoracic synpleuron (of Štys, 1981b) forming a weak wing to body coupling groove (fig. 122B).

Forelegs sexually dimorphic, slightly stouter in females than in males. Coxae, trochantera, and especially femora with minute cuticular elements varying from microtrichiae, through spines, to tuberclelike structures, in addition to ordinary setae. Apex of central portion of inner surface of foretibia with a more or less conspicuous field of short stout setae (fig. 120A). Inner apical angle of foretibia with seven spines (fig. 120B). Spines I–IV and VII straight, conical; V and VI shorter, curved toward tarsus. Foretarsus longer than wide; tarsal organ situated on dorsal surface of tarsus. Tarsus with four spines (fig. 120C): I and III short, conical, very slightly curved; II and IV spiniform, elongate, straight. Foretarsus with two claws of equal length (fig. 120A). Apex of mid and hind tibiae with two or three spines and two bristle combs (fig. 122C). Mid and hind tarsi two-segmented, their claws of identical size.

Forewings with basal and discal cell, the latter variable in length. Setae of forewing of approximately uniform size, sometimes interspersed with microtrichiae. Setae arranged in two rows on veins of apical half of wing including apical marginal vein, but more numerous on costal margin, R+M, and basal half of Cu; in only one species (*stannardi*) setae on R+M and Cu arranged in two rows. Lumens of cells with setae, from very sparse to numerous. Wing coupling mechanism as in figure 120E.

Apical portion of "cell" of hind wing, beyond insertion of posterior free vein, about five times as long as wide. Anal lobe lacking free apical portion. Hind wings with setae on base of anterior vein. Hind wing edges simple, as in figure 120F.

Abdomen of male well sclerotized; in some cases divisions between sternites and ventral connexival plates not obvious. Abdomen of female mostly membranous, bearing regularly arranged sclerotized plates (fig. 137I, N). In both sexes spiracles on ventral connexival plates II–VIII (figs. 121D, E). Abdominal sterna with slender pointed setae, interspersed with either smaller setae or large microtrichiae (fig. 123I). Terga with modified flattened setae (figs. 121A, C, 123H). In addition to setae and microtrichiae, both surfaces with one to four-toothed cuticular tubercles interspersed among larger structures mentioned above. Entire abdomen with minute, bare, circular areas (probably evapora-

toria), each with a central hole (figs. 121A, B, D–F).

Genitalia of male small. Guide fused to pygophore, subrectangular, truncate apically. Tenth tergum present (fig. 122 D, E).

Fifth instar nymph (fig. 138). General shape stout. Eyes well developed. Antennae slender. Neck distinct. Mesothoracic wing pads meeting medially, longer than wide, rounded posteriorly. Abdomen membranous but in many species with sclerotized areas; if so, segments of abdominal dorsum with 1 + 1 small submedian and 2 + 2 sublateral sclerotized plates. Abdominal terga with ordinary setae and short hairlike cuticular processes.

DISCUSSION: *Neoncylocotis* comes closest to *Oncylocotis* Stål, where the New World species heretofore described had been formerly included. The two genera can be distinguished by the characters given in the following key. However, Stys (personal commun.), indicates that these characters may not be diagnostic for certain Oriental, Australian, and Pacific species of *Oncylocotis* upon which he is currently working.

1. Hind lobe of head distinctly depressed or sulcate longitudinally along middle; apex of foretibia with spines I–IV and VII long, straight, V and VI short, curved toward tarsus (fig. 123-O). Setae on dorsal surface of abdomen flattened and scale-shaped (fig. 123H) .... *Neoncylocotis*, n. gen.
   Hind lobe of head not depressed or sulcate above; apex of foretibia with six or seven spines, all long and straight except III which is very short and conical. Setae on dorsal surface of abdomen normal and slender .. .. *Oncylocotis* Stål

As in the related *Enicocephalus*, we find in *Neoncylocotis* amazing intraspecific variability, mainly regarding the forewing venation. Previous workers have occasionally used proportions of forewing basal and discal cells as specific characters. In keeping with our premise that enicocephalid wings show a high rate of variability and teratology, we measured 13 male specimens (one wing each) of *N. clavisetosus* from a single series and found that the length of the basal cell was greater than that of the discal cell in four specimens, equal to the discal cell in five, and less than the discal cell in four. Considering this variability, basal and discal cell proportions cannot be used as specific characters.

Another teratology which appears frequently in *Neoncylocotis* is an open discal cell.

KEY TO SPECIES OF *NEONCYLOCOTIS*

1. Extremely large, length 5.4 mm or greater 2
   Less than 5.0 mm in length 3
2. Length 5.5 to 6.3 mm. Uniform dark brown. Ventral surface of abdomen with uniform length setae interspersed with one-toothed microtrichiae (fig. 137H). Many setae (20 in discal cell) in lumens of wing cells (fig. 137M) ..... *weyrauchi*, n. sp.
   Length 5.4 to 5.6 mm. Head and pronotum piceous, contrasting with translucent brown wings. Ventral surface of abdomen with two-length setae interspersed with one to four-toothed microtrichiae (fig. 127C). A moderate number of setae (7 in discal cell) in lumens of wing cells (fig. 127D). Males bearing clavate hairs on forelegs (figs. 126D, F, 127E) ..... *clavisetosus*, n. sp.
3. Extremely small, length 3.1 mm or less .. 4
   Intermediate in size, length 3.3 to 5.0 mm 5
4. Length 2.7 to 2.8 mm. Uniform light to medium brown with lighter grayish-brown legs and antennae. Veins on underside of forewings brown as rest of wing. Scales of dorsal surface of abdomen spoon-shaped (fig. 132D). Protonum shallowly emarginate (fig. 132B) ..... *pisinnus*, n. sp.
   Length 3.1 mm. Not uniform brown; head dark brown tinged with red on eyes and around ocelli, fading to orange on tylus and yellowish brown on rostrum; fore and mid lobes of pronotum orange-brown, hind lobe dusky brown; wings translucent dusky brown; veins on underside of forewing white, contrasting with membranous areas. Pronotum moderately emarginate (fig. 124B). Males with setae of forefemur clavate (fig. 124D, E) ..... *alvarengai*, n. sp.
5. Legs bright scarlet. Head and pronotum piceous, tinged with red. Wings lighter dusky brown ..... *rubripes*, n. sp.
   Legs yellow, brown, or tinged with red, but never bright scarlet 6
6. Length 4.0 mm or greater 7
   Length less than 3.8 mm 11
7. Delicate looking species with slender heads (fig. 125A, B); ratio length of head to width of hind lobe 1:0.50 or greater; ratio length

of forelobe of head to synthlipsis 1:0.45 or greater. Head and pronotum dark chestnut brown. Hind lobe of head in side view not salient, its height 1.1 times the distance between the posterior border of eye and limit between head and neck (fig. 131C) 8

Slightly shorter, stouter species (figs. 130B, 135A); ratio of head length to width of hind lobe 1:0.55 or less; ratio length of forelobe of head to synthlipsis 1:0.50 or less. Head and pronotum medium brown. Hind lobe of head in side view moderately salient, its height 1.3 times the distance between posterior border of eye and limit between head and neck (fig. 135B) 10

8. Veins on underside of forewings white, sharply contrasting with membranous areas. A large (4.7 mm or greater) dark brown species ..... *albovenosus*, n. sp.

Veins on underside of forewings brown as rest of membrane 4.7 mm or less in length 9

9. Hind legs, and usually mid and forelegs and base of Sc of forewing, tinged with red. Yellowish at tibiofemoral joints (knees). Head and pronotum darker than wings. Forecoxal setae evenly distributed and not grouped into a tuft ..... *montanus*, n. sp.

Legs uniform dark brown. Tibiofemoral joints and base of Sc occasionally slightly lighter. Head, body, and wings uniform dark brown. Forecoxae with tuft of setae medially .... *annulipes* (Champion)

10. Setae on head and pronotum short, hooked at tips, and somewhat widened and scale-shaped. Veins on underside of forewing brown as rest of wing .... *concolor* (Champion)

Setae on head, pronotum, and wings long, slender, curved at tips or straight, and not widened or scale-shaped. Veins on underside of forewing white, sharply contrasting with rest of wing .... *meridionalis*, n. sp.

11. Setal insertions, especially on head, expanded and appearing like sand grains on cuticular surface (fig. 136E) 12

Setal insertions normal, not conspicuous 13

12. Setal insertions expanded on head and pronotum but not on forefemora. Veins on underside of forewing white, sharply contrasting with membranous areas. Quite a few setae in lumens of forewing cells .... *mexicanus* (Kritsky)

Setal insertions expanded on head, pronotum, and forefemora. Veins on underside of forewing brown as rest of wing. Very few setae in lumens of forewing cells .... *stannardi* (Kritsky)

13. Most setae on body, wings, and some on legs short, curved, and scale-shaped. Hind lobe of head in side view conspicuously salient below, the height 1.4 times the distance form the posterior edge of the eye to the line between head and neck. On underside of forewing, Sc white and all other veins brown ..... *slateri*, n. sp.

Setae normal, not scale-shaped. Hind lobe of head in side view not conspicuously salient, its height not much more than distance from posterior border of eye to line between head and neck. Underside of forewing with all veins brown as rest of wing .... *rhyparus* (Stål)

Neoncylocotis albovenosus, new species

Figures 118–123

DISTRIBUTION: Colombia.

DIAGNOSIS: *Neoncylocotis albovenosus* most closely resembles *N. clavisetosus* but has gray-white veins under its forewings and is smaller.

DESCRIPTION: Length of males and females 4.7–5.0 mm.

General body color piceous. Legs brown. Apical segments of rostrum, antennae, tibiae, and all tarsi whitish. Base of Sc varying from whitish to light brown. Abdomen medium brown with rosy coloring on posterior edge of segments and male genital capsule. Undersides of veins of forewings grayish white, sharply contrasting with brown of membrane.

Head approximately equal in length to pronotum in both sexes (figs. 119A, B, 123B, E). Ratio head length to width across eyes 1:0.5 in both sexes. Ratio length to width of hind lobe of head 1:1.5 in both sexes. Ratio length of eyes to anteocular portion 1:0.9 in males, 1:1.3 in females; ratio width of eyes to synthlipsis 1:2.2 in males, 1:2.6 in females. Posterior lobe of head not especially salient below, its height only slightly more (1.1 times) than distance from posterior border of the eye to limit between head and neck (figs. 123C, D).

Antennal segments I–IV 1:2.1:2.9:2.2 in males, 1:2.4:2.3:1.9 in females, combined shorter than head plus pronotum (1:1.3 in males, 1:1.4 in females).

Protonum as shown in figures 119A, B, 123B, E, moderately incised behind. Propor-

Fig. 118. Distribution of *Neoncylocotis*. Described species (●); undescribed (■).

tional width of mid to hind lobes 1:1.7 in males, 1:1.8 in females.

Forewings 3.2–3.3 mm long in males, 3.0–3.2 mm in females. Veins as in figure 123G, bearing setae of two lengths (fig. 123F).

Abdomen bearing microtrichiae between setae, each with from one to four teeth (figs. 123H, I). Setae on ventral surface of abdomen slender and normally shaped, but of two sizes; those on dorsal surface of abdomen of one length but scale-shaped with sharp tips as in figure 123H.

Forelegs as shown in figures 123J, K. Ratio length to width of forefemur 1:0.21 in males,

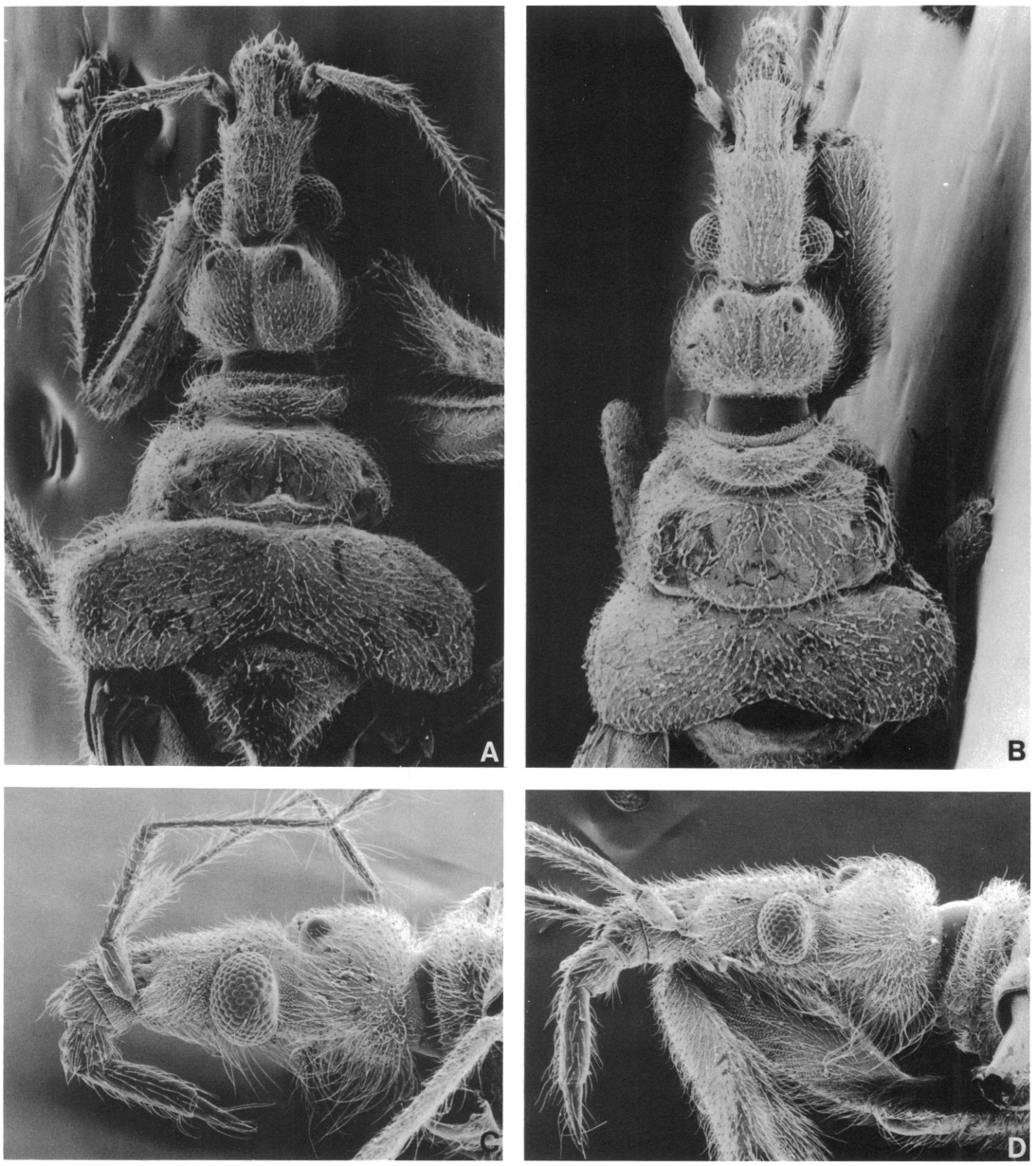


Fig. 119. *Neoncylocotis albovenosus*. **A**, **B**. Dorsal view of head and pronotum, ♂ and ♀, respectively. **C**, **D**. Lateral view of head, ♂ and ♀, respectively. Note wider hind pronotal lobe and larger eye of ♂.

1:0.26 in females. Setae on forefemur of two sizes, with minute hairs scattered among larger setae (fig. 123N). Cuticular surface with narrow band of small granules along inner surface of article (fig. 123N). Ratio length to width of hind femur 1:0.18 in males, 1:0.23 in females (figs. 123Q, M). Ratio length to width of foretibia 1:0.28 in males, 1:0.33 in females. Foretibia and tarsus bearing spines as shown in figures 120B, C, 123L, O. Longest setae on opposing surfaces of tibiae and femora curved at tips in males, straight in females.

MEASUREMENTS: See Appendix.

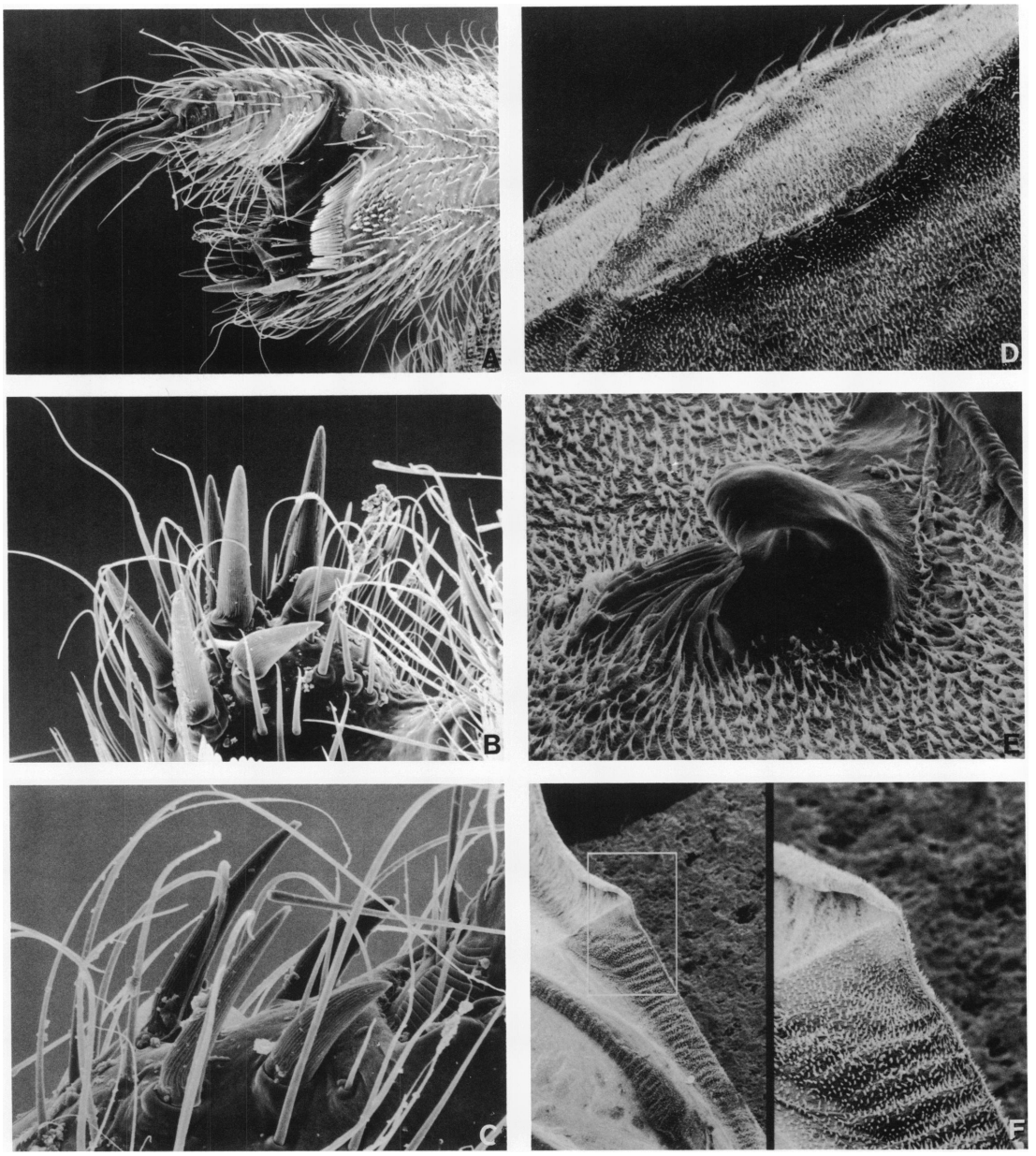


Fig. 120. *Neoncylocotis albovenosus*. **A**. Apex of foreleg, ♀. **B**. Foretibial spines, ♀. **C**. Foretarsal spines, ♀. **D**. Forewing surface, ♂. **E**. Wing coupling mechanism under hind edge of forewing. **F**. Hind wing edge at level of wing coupling mechanism.

HOLOTYPE: Male, COLOMBIA: Sierra Nevada de Santa Marta, San Sebastian de Rabago, 2000 m, April 1–14, 1968 (Malkin; AMNH).

PARATYPES AND NYMPHS: Same data as holotype (AMNH), 6♂ and 3♀ (1♂ and 1♀ used for SEM); 5 nymphs.

ABERRANT SPECIMENS: COLOMBIA: **Cundinamarca**: Finca San Pablo, 8 km N of Alban, 1800 m, August 1–12, 1967 (Wygodzinsky, AMNH), 1♂; Bogota, 2700–2900 m, October 14, 1956 (collector unknown; AMNH), 1♂.

See also Material Examined under *N. clavisetosus*.

ETYMOLOGY: The specific name *alboveno-*

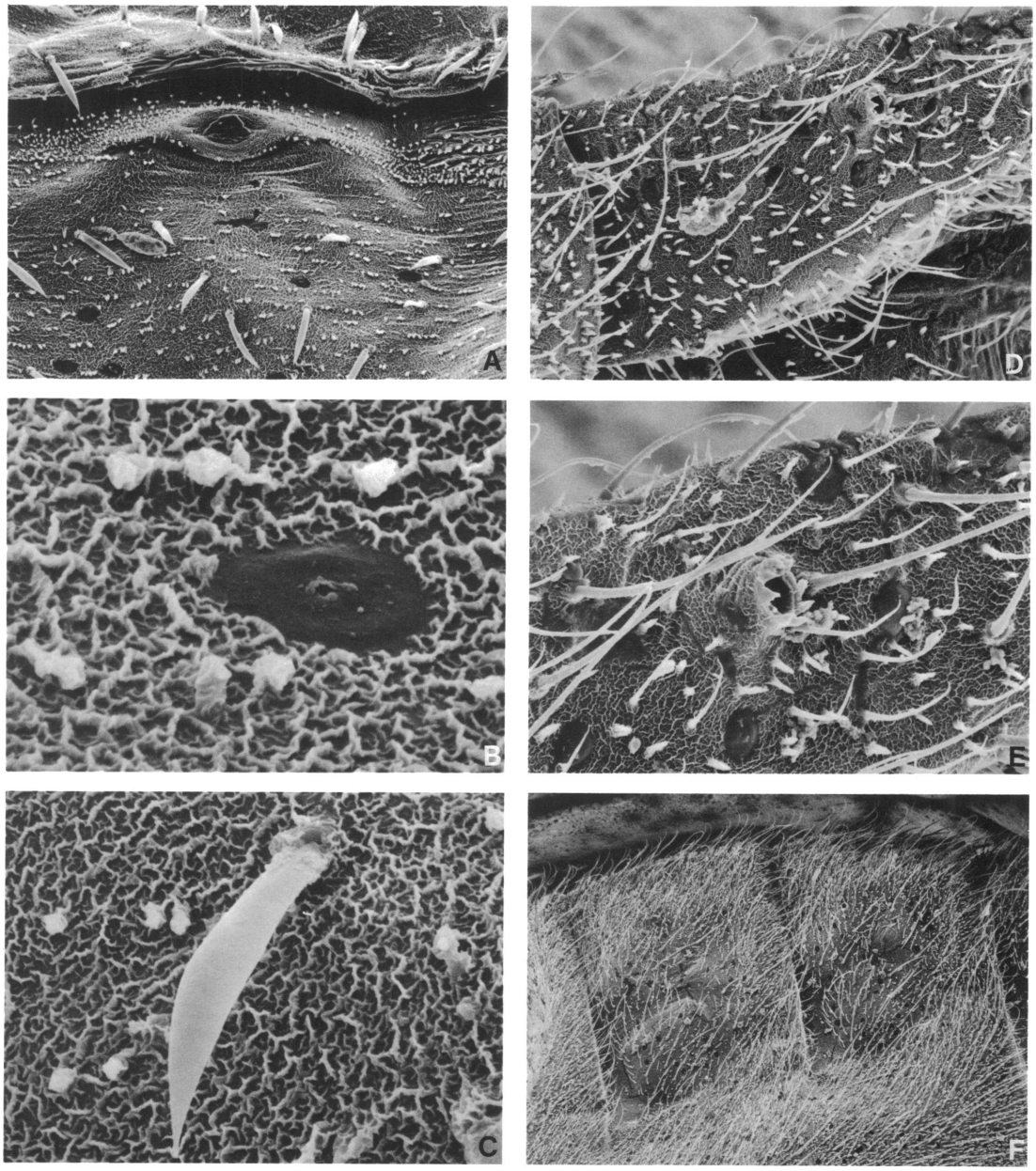


Fig. 121. *Neoncylocotis albovenosus*. **A**. Tergum IV, ♂ showing median scent gland orifice and scalelike setae. **B**. Close-up of a dark circular spot, above, ♂. **C**. Close-up of scalelike seta, ♂. **D**. Ventral connexival plate III, showing setae of two lengths, spiracle, and surface structures, ♂. **E**. Same, close-up of surface. **F**. Abdominal sterna VI and VII and corresponding ventral connexival plates,♀, showing sclerotized patches.

sus refers to the white veins on the undersides of the forewings of this species.

DISCUSSION: *Neoncylocotis clavisetosus* and *N. albovenosus* resemble one another quite closely but differ according to the characteristics listed in table 13.

Although these differences are consistent within most of our specimens, there are three problem specimens with intermediate characters. One exhibits all characters of *N. clavisetosus*, but has white veins on the underside of one forewing and brown on the other. An-

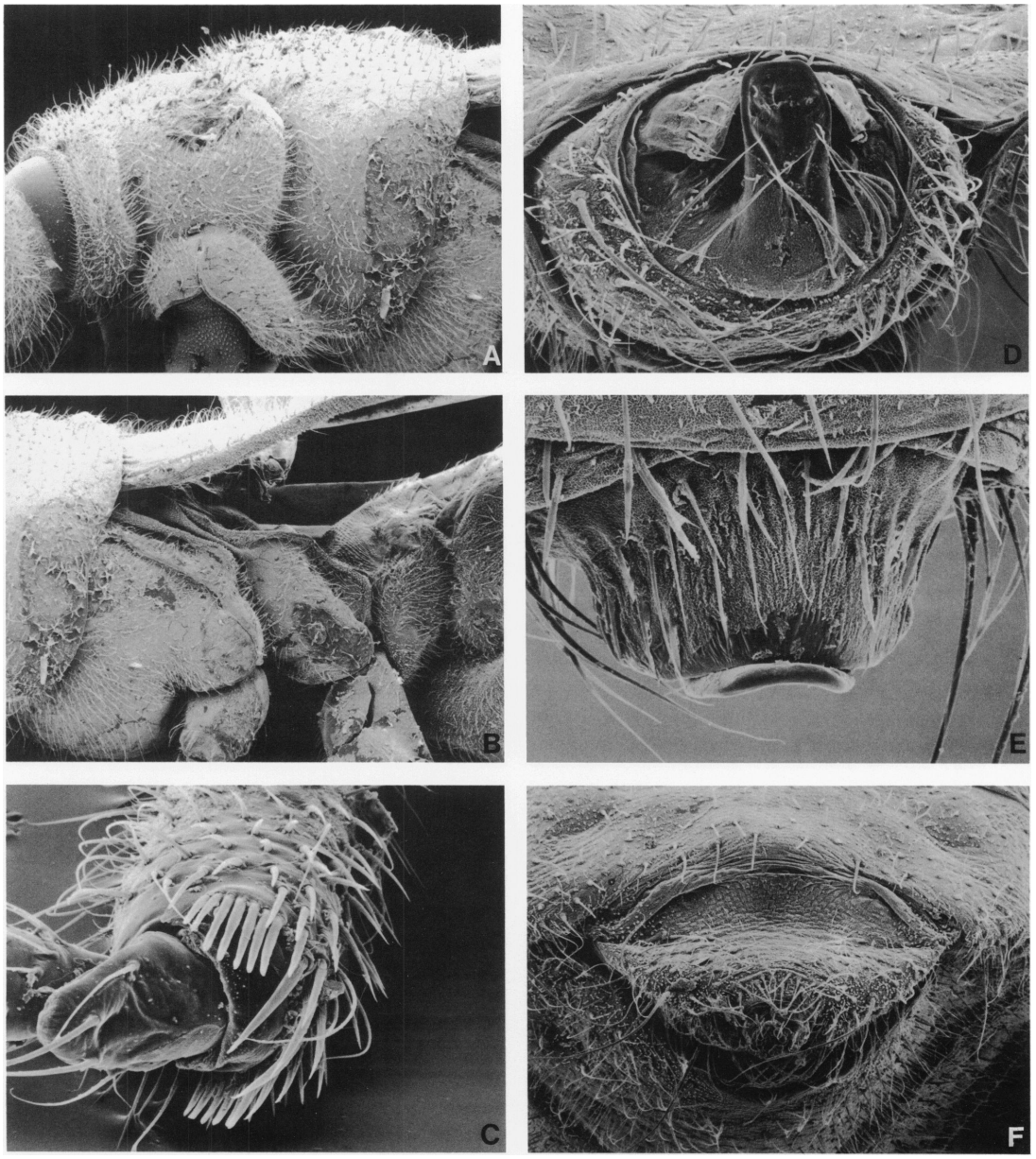


Fig. 122. *Neoncylocotis albovenosus*. **A**. Pronotum, lateral, ♀. **B**. Meso- and metanotum, lateral, ♀. **C**. Apex of hind tibia, ♀. **D**, **E**. Genital capsule, ♂, posterior and dorsal views, respectively. **F**. Genital area, ♀.

other has the length and vein coloration of *clavisetosus* and the leg proportions and coloration of *albovenosus*. The third has all characters of *clavisetosus*, but with white veins underneath the forewings. These may cast doubt on the reliability of our characters or on our decision to recognize two species (from fairly widely separated localities in Colombia). The differences as shown in the table are otherwise consistent, so we have decided to describe two species until more information becomes available.

TABLE 13
Differences between *Neoncylocotis clavisetosus* and *N. albovenosus*

	clavisetosus	*albovenosus*
Length	longer 5.3–5.9 mm	shorter 4.7–5.0 mm
Antennal proportions	male 1:2.5:2.4:1.8	male 1:2.1:2.9:2.2
	female 1:2.4:2.3:1.9	female 1:2.6:3:2.4
Legs	Longer, thinner (see Description)	shorter, thicker (see Description)
Wings	undersides of forewing veins brown	undersides of forewing veins white
Tarsi	light to dark brown	whitish
Abdomen	segments uniformly brown	segments rose on apical borders
Hairs	abdominal hairs scalelike and blunt at tips	abdominal hairs scalelike and pointed at tips
Genitalia	uniformly piceous	rose to crimson basally, bordered with dark brown
Foreleg hairs	curved and expanded at tips	curved at tips, not expanded
Color	light to dark brown antennal tips, rostrum tip, apex of tibiae, tarsi, and Sc vein	whitish antennal tips, rostrum tip, base of Sc, tarsi, and tips of all tibiae

Neoncylocotis alvarengai, new species
Figures 118, 124

DISTRIBUTION: Interior of Brazil.

DIAGNOSIS: This species can be distinguished by the following combination of characters: orange-tinted tylus, ocelli, femora, and protonum; white veins on undersides of forewings; a unicolorous light brown abdomen; and small size (3.1 mm).

DESCRIPTION: Females unknown. Length of male 3.1 mm.

General body color brown tinged with orange. Head dark chestnut brown behind antennal insertions, lightening to orange on tylus and then yellowish brown on rostrum. Ocelli surrounded by orange area; eyes reddish-brown. Antennal segments I–IV light brown, fading to whitish on segment IV. Anterior and midlobes of pronotum orange-brown; hind lobe and scutellum darker dusky brown. Abdomen and forewings light dusky brown. Veins of forewing lighter and more opaque than membrane, and on underside of wing, strikingly white. Forelegs brown; tinged with orange on femur, yellowish at tibiofemoral joints, and dusky brown on tibia and tarsus. Mid and hind legs light yellowish brown, very slightly tinged with orange on femora.

Head and pronotum equal in length (fig. 124B). Ratio head length to width across eyes 1:0.6. Ratio length to width of hind lobe of head 1:1.8. Ratio length of eyes to anteocular portion 1:0.8; ratio width of eyes to synthlipsis 1:2.0. Hind lobe of head moderately salient below, height in side view 1.4 times length from posterior edge of eye to limit between head and neck (fig. 124F).

Antennal segments I–IV 1:1.6:2.1:1.8 (fig. 124A), combined shorter than head plus pronotum (1:1.3).

Pronotum as in figure 124B, with a moderate posterior incision. Proportional width of mid to hind lobes 1:1.4.

Forewings as shown in figure 124H. Basal cell shorter than discal cell. Setae along wing veins short, sparse, two-ranked along all inner veins of disc, and interspersed with microtrichiae. Very few setae in lumens of cells.

Abdomen bearing scale-shaped setae dorsally, normal setae ventrally.

Forelegs as shown in figure 124D. Ratio length to width of forefemur 1:0.23. Setae on forefemur of two sizes and interspersed with microtrichiae and both smooth and toothed granules (fig. 124E). Ratio length to width of hind femur 1:0.19 (fig. 124G). Foretibia and tarsus bearing spines as shown in figure 124C. Longer setae on foretibia slightly curved at tips. Ratio length to width of foretibia 1:0.29.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BRAZIL: Mato Grosso, Lat. 12°31′ Long. 55°37′, Sinop, October, 1974 (Alvarenga; AMNH).

ETYMOLOGY: *Neoncylocotis alvarengai* is named after Moacir Alvarenga, who collected the only known specimen of this species.

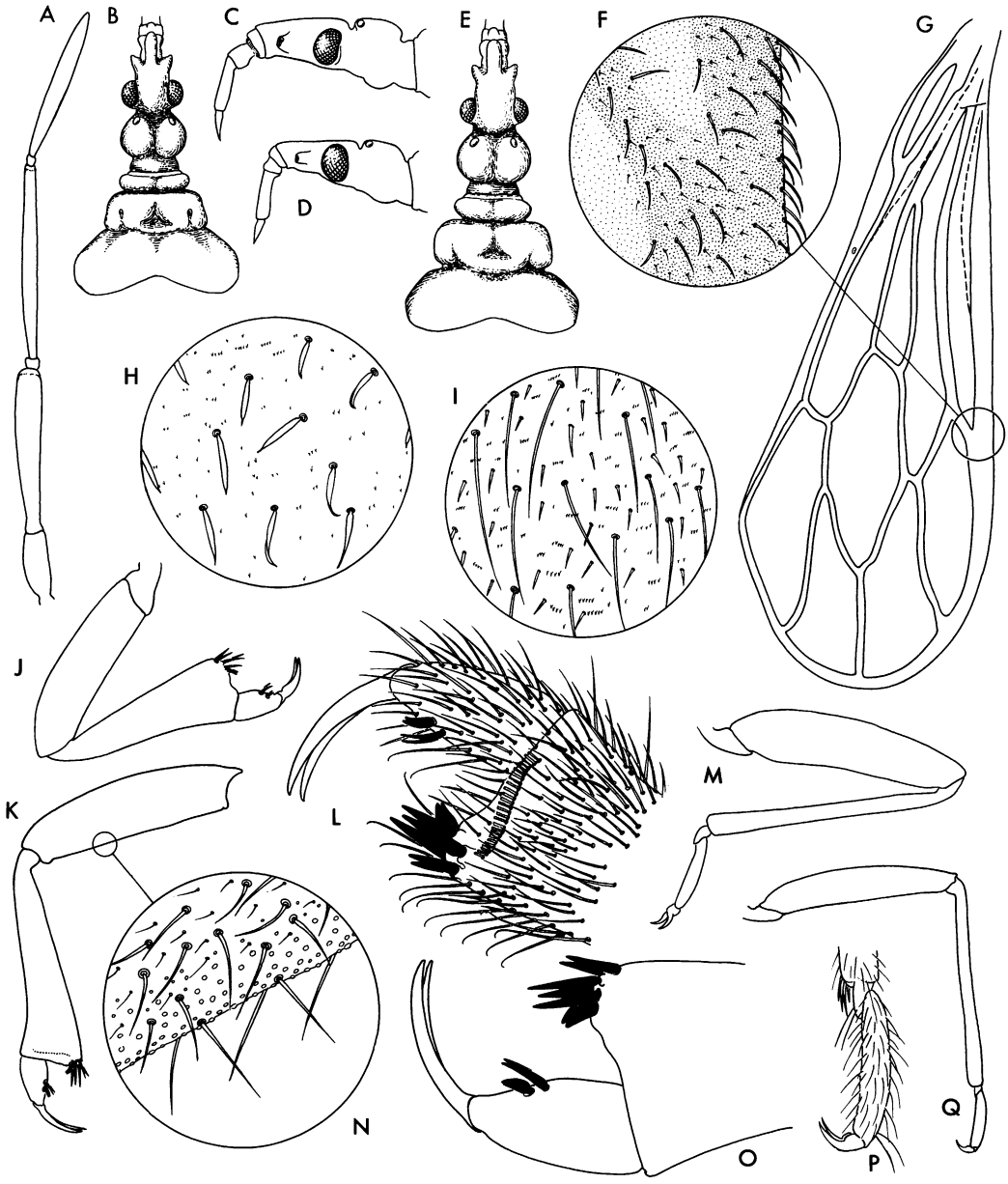


Fig. 123. *Neoncylocotis albovenosus*. **A**. Antenna. **B**. Head and pronotum, ♂. **C**, **D**. Lateral view of head, ♀ and ♂, respectively. **E**. Head and pronotum, ♀. **F**. Detail of forewing. **G**. Forewing. **H**, **I**. Details of abdomen, showing scalelike and normal setae and microtrichiae, dorsal and ventral surfaces, respectively. **J**. Foreleg, outer surface. **K**. Foreleg, inner surface. **L**. Apex of foreleg, inner view. **M**. Hind leg, ♀. **N**. Detail of inner (ventral) surface of forefemur. **O**. Apex of foreleg, outer surface. **P**. Hind tarsi, ♂. **Q**. Hind leg, ♂.

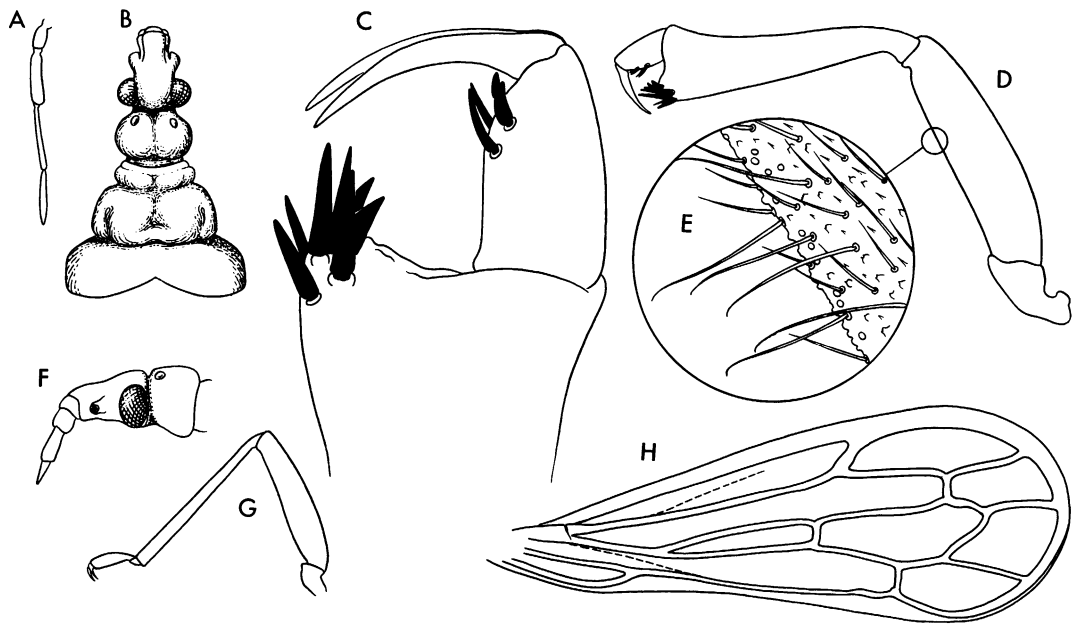


Fig. 124. *Neoncylocotis alvarengai*, ♂. **A**. Antenna. **B**. Head and pronotum. **C**. Apex of foreleg. **D**. Foreleg. **E**. Detail of inner (ventral) surface of forefemur, showing cuticular microstructures. **F**. Lateral view of head. **G**. Hind leg. **H**. Forewing.

Neoncylocotis annulipes (Champion), new combination
Figures 118, 125

Henicocephalus annulipes Champion, 1898: 160.
Stenopirates (*Hymenocoris*) *annulipes*: Jeannel, 1942 (1941): 330.
Oncylocotis annulipes: Usinger, 1945: 333. — Kritsky, 1978c: 194.

DISTRIBUTION: Panama.

DIAGNOSIS: *Neoncylocotis annulipes* can be distinguished from its congeners by its uniform dark brown color, and by the presence of a median tuft of setae on each forecoxa.

REDESCRIPTION: Males unknown. Length of females 4.2–4.5 mm.

General body color dark brown. Head, pronotum, and scutellum piceous. Rostrum and antennae dark brown, slightly lighter at apices. Legs with all femora chestnut-colored, fading to light brown at knees. Foretibia chestnut-colored on apical two thirds; foretarsus light brown. Mid and hind tibiae light brown at knees, dark brown on apical two thirds and on tarsi.

Head slightly longer than pronotum (1:0.9; fig. 125A). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular portion 1:1.3; ratio width of eyes to synthlipsis 1:3.3. Posterior lobe of head not especially salient below, its height in side view 1.1 times length from posterior edge of eye to limit between head and neck (fig. 125B).

Antennal segments I–IV 1:2.2:2.3:2, combined shorter than head plus pronotum (1:1.4).

Protonum as shown in figure 125A, with shallow to moderately emarginate incision. Midlobe with deep triangular depression in center. Proportional width of mid to hind lobes 1:1.4.

Forewings 2.5 mm in length, their venation as in figure 125C. Setae of forewings long and slender, randomly arranged on veins on basal half of wing and two-ranked on inner veins of disc. Long setae interspersed with smaller slender setae.

Forelegs as shown in figure 125E. Ratio length to width of forefemur 1:0.26. Long

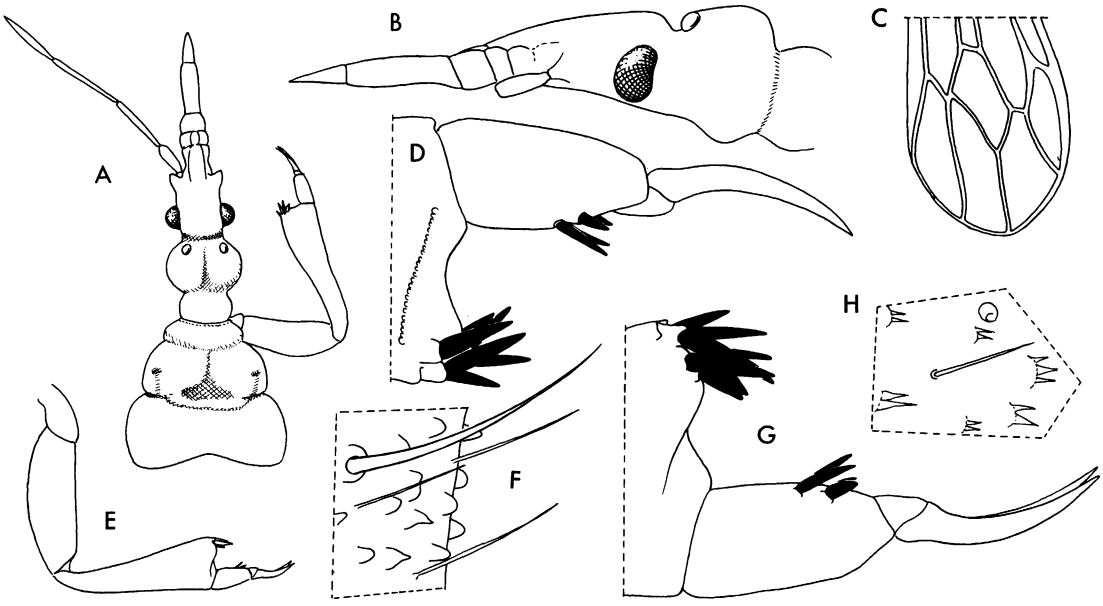


Fig. 125. *Neoncylocotis annulipes*, ♀ (lectotype). **A**. Dorsal view. **B**. Lateral view of head. **C**. Apex of forewing. **D**. Apex of foreleg, inner surface. **E**. Foreleg. **F**. Detail of inner (ventral) surface of forefemur, showing cuticular granules. **G**. Apex of foreleg, outer surface. **H**. Detail of cuticular microstructures at base of forefemur.

setae interspersed with smaller setae (fig. 125F). Granular structures present on anterior surface of forefemur (fig. 125F) gradually changing to two or three-toothed structures on dorsal surface. Foretibia and tarsus bearing spines as in figures 125D, G; ratio length to width of foretibia 1:0.29. Ratio length to width of hind femur 1:0.21.

MEASUREMENTS: See Appendix.

LECTOTYPE: Female, PANAMA, Volcan de Chiriqui, below 4000 ft (Champion; BM); examined.

MATERIAL EXAMINED: Same data as lectotype (BM), 1♀.

DISCUSSION: In accordance with a suggestion by W. R. Dolling of the British Museum, we designate as lectotype the specimen bearing the red "type" label. There is no evidence that a holotype was previously designated. This specimen agrees closely with the original description and illustration (Champion, 1898), though the hind border of the pronotum (fig. 125A) is more conspicuously emarginate than shown by Champion.

Neoncylocotis clavisetosus, new species

Figures 118, 126, 127

DISTRIBUTION: Colombia.

DIAGNOSIS: *Neoncylocotis clavisetosus* can be distinguished from *N. albovenosus* by its larger size (5.3–5.9 mm vs. 4.7–5.0 mm), its thinner legs (see table 13 in Discussion section of *N. albovenosus*), its more uniform brown color, and lack of white veins on the undersides of the forewings.

DESCRIPTION: Female unknown (See Discussion). Length of male 5.4–5.6 mm.

General body color piceous, fading to light brown at joints and ends of appendages. Undersides of veins of forewings brown as rest of wing. Male genitalia uniformly piceous.

Head slightly longer than pronotum (1:0.9). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.3. Ratio length of eyes to anteocular portion 1:0.9; ratio width of eyes to synthlipsis 1:2.1. Posterior lobe of head not especially salient below, the height of the lobe in side view 1.1

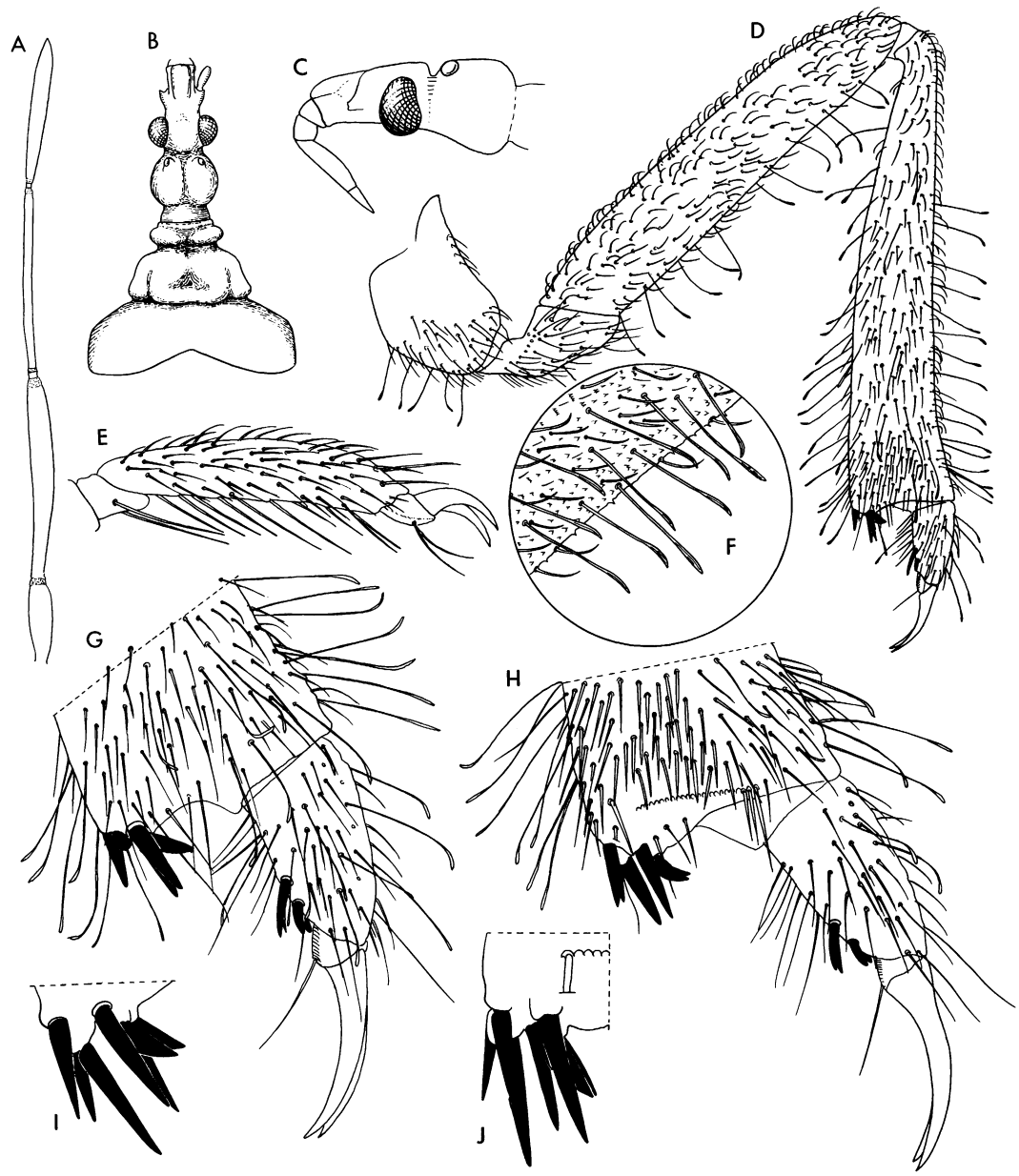


Fig. 126. *Neoncylocotis clavisetosus*, ♂. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Foreleg. **E**. Hind tarsus **F**. Detail of inner (ventral) surface of forefemur, showing two types of setae and various microtrichiae. **G**, **H**. Apex of foreleg, outer and inner surfaces, respectively. **I**. Foretibial spines, outer view. **J**. Foretibial spines, inner view.

times distance between posterior border of eye and limit between head and neck (fig. 126C).

Antennal segments I–IV 1:2.5:2.4:1.8 (fig. 126A), combined shorter than head plus pronotum (1:1.3).

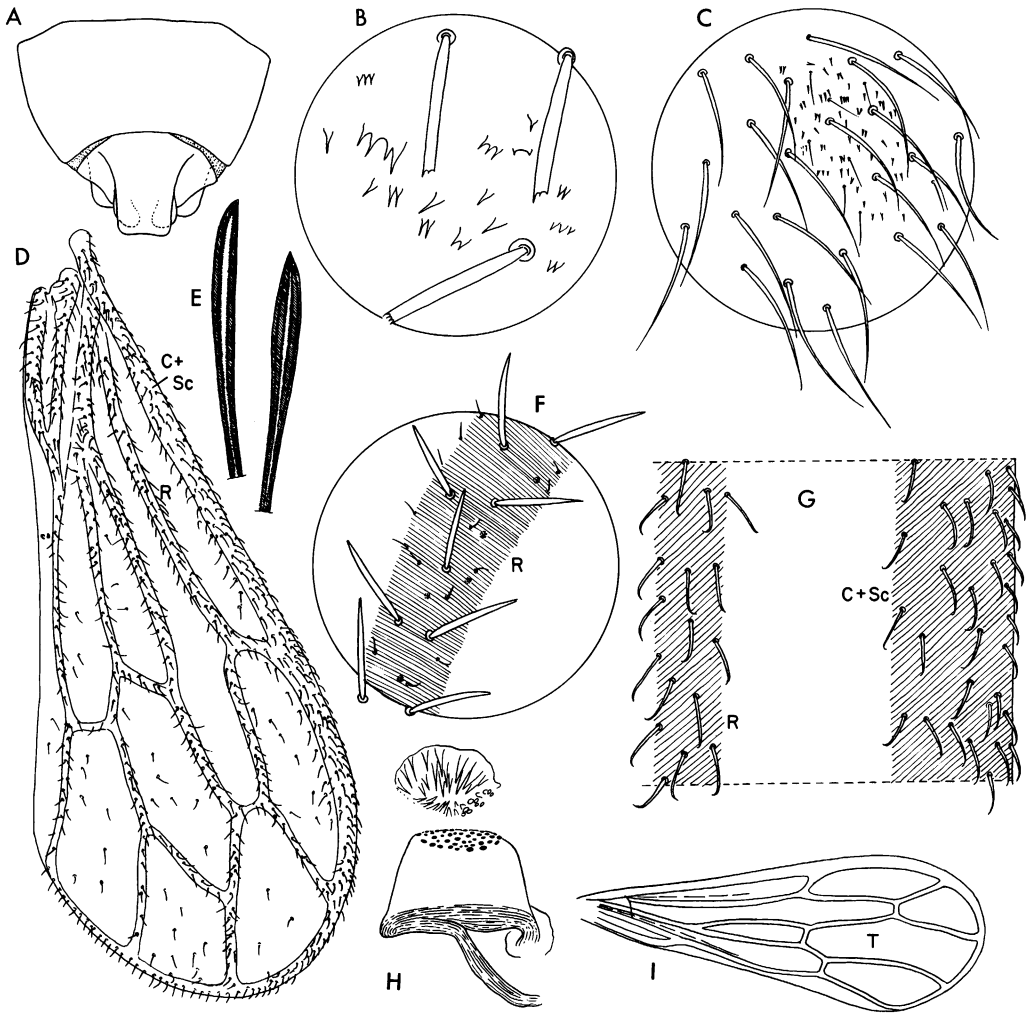


Fig. 127. *Neoncylocotis clavisetosus*, ♂. **A**. Genital segments from below. **B**, **C**. Details of abdomen, dorsal and ventral, respectively, showing setae and microtrichiae. **D**. Forewing. **E**. Capitate setae of foretibia. **F**. Detail of radius of forewing at level of basal cell. **G**. Detail of C+Sc and R of forewing, same level. **H**. Wing coupling mechanism, and edge of forewing. **I**. Teratological forewing.

Pronotum as shown in figure 126B, with a moderate posterior incision. Proportional width of mid to hind lobes 1:1.7.

Forewings 3.8 mm long with veins arranged as in figure 127D. Setae arranged as in figures 127F, G; inner veins of wing with smaller hairs interspersed among setae.

Abdomen bearing microtrichiae between setae, each with from one to four teeth (figs. 127B, C). Setae on ventral surface of abdomen slender and normal shaped but of two sizes (fig. 127C); those on dorsal surface of abdomen of one length but scale-shaped with blunt tips as in figure 127B. Male genitalia as in figure 127A.

Foreleg as shown in figure 126D. Ratio length to width of forefemur 1:0.20. Setae on forefemur of three lengths (fig. 126F), the longest ones clavate, the medium and shortest ones simple. Cuticular surface bearing many toothed microtrichiae (fig. 126F). Ratio length to width of hind femur 1:0.15. Ratio length to width of foretibia 1:0.21. Foretibia and tarsus bearing spines as shown in

figures 126G–J. Longest hairs on opposing surfaces of tibia and femur curved at tips (fig. 126D).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, COLOMBIA: Cundinamarca, 12 mi SE Bogota, 2930 m, March 13, 1955 (Schlinger and Ross; CAS).

PARATYPES: Same data as holotype (CAS), 12♂ (11 pinned, 1 slide), paratypes; (AMNH), 4♂ (2 pinned, 2 slides) paratypes. COLOMBIA: **Cundinamarca**: Monserrate, Bogota, 3100 m, July 1, 1965 (P. & B. Wygodzinsky; AMNH), 1♂.

ABERRANT SPECIMEN: COLOMBIA: **Cundinamarca**: 15 km E Bogota, Paramo, 3300 m [no date] (Herman; AMNH), 1♀. (See also *N. albovenosus*.)

ETYMOLOGY: The specific name *clavisetosus* refers to the clavate setae on the foretibia and femur.

DISCUSSION: The aberrant specimen mentioned above has white veins under one forewing and brown veins under the other.

Neoncylocotis concolor (Champion), new combination

Figures 118, 128

Henicocephalus concolor Champion, 1898: 160.
Stenopirates (*Hymenocoris*) *concolor*: Jeannel, 1942 (1941): 329.
Hymenocoris concolor: Jeannel, 1942 (1941): 329; 1944 (1943): 127.
Oncylocotis concolor: Usinger, 1945: 334; Kritsky, 1978c: 196.

DISTRIBUTION: Guatemala. This species was described from Guatemala and Panama (Volcan de Chiriqui). Jeannel (1942) selected the Guatemalan specimen as type, and also reported the species from Costa Rica and Ecuador. It is highly doubtful that *concolor* has such a wide distribution; most enicocephalids have a much smaller range (See Discussion.)

DIAGNOSIS: *Neoncylocotis concolor* is a uniformly brown species from Central America with 1 + 1 raised tubercles (fig. 128A) on the top of the anterior pronotal lobe and a conspicuously salient hind lobe of the head below (fig. 128B).

REDESCRIPTION: Males unknown. Length of female 4.6 mm (measurements are of holotype).

General body color dark brown. Rostrum and antennal segments I and II light brown (III and IV missing in type). Forewings translucent brown with slightly darker veins. Abdominal segments tinged with rose at edges and posterior borders. Eighth segment and genital capsule brown. Forefemur and basal half of foretibia dark brown; apical half of foretibia and tarsus light yellowish brown. Mid and hind legs light yellowish brown.

Head slightly longer than pronotum (1:0.9; fig. 128A). Ratio head length to width across eyes 1:0.6. Ratio length to width of hind lobe of head 1:1.6. Ratio length of eyes to anteocular portion 1:1; ratio width of eyes to synthlipsis 1:2.5. Posterior lobe of head moderately salient below, its height in side view 1.3 times distance between posterior border of eye and limit between head and neck (fig. 128B).

Ratio of lengths of antennal segments I and II, 1:2.6 (missing from holotype; fig. 128A). According to the original description, segments III and IV are much narrower than the first two.

Pronotum as in figure 128A, with moderate posterior incision. Anterior lobe bearing 1 + 1 tubercules on dorsum; midlobe with a deep central triangular depression and 1 + 1 lateral sulci accentuating height of the lateral lobes. Proportional width of mid to hind lobes 1:1.4.

Forewings 2.9 mm in length, their venation as in figure 128D. Setae slightly expanded and scalelike, distinctly two-ranked on all interior veins and randomly present in lumens of cells. Setae interspersed with smaller hairs.

Forelegs as shown in figures 128F. Ratio length to width of forefemur 1:0.30. Ratio length to width of hind femur 1:0.21. Foretibia and tarsus bearing spines as in figures 128C, E; ratio length to width of foretibia 1: 0.31.

Most setae on head, pronotum, legs, and wings expanded and scalelike.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, GUATEMALA: Guatemala City (Champion; BM); examined.

SPECIMENS OF UNCERTAIN IDENTIFICATION: PANAMA: **Chiriqui**: Volcan de Chiriqui, 2500–4000 ft (781–1250 m) (Champion; BM), 1♀; Barca Arca, Finca Lerida near Boquete, 5650 ft, March 14, 1959 (H. S. Dybas;

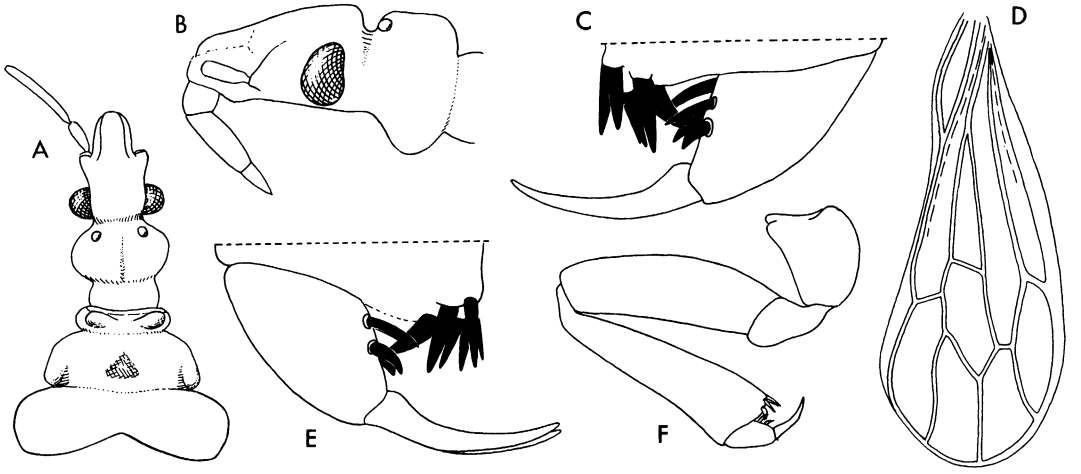


Fig. 128. *Neoncylocotis concolor*, ♀ (holotype). **A**. Head and pronotum. **B**. Lateral view of head. **C**. Apex of foreleg, outer surface. **D**. Forewing. **E**. Apex of foreleg, inner surface. **F**. Foreleg.

AMNH), 1♂, 1♀; Finca Lerida, near Boquete, Casita Alfa, 7750 ft (2422 m), March 17, 1959 (H. S. Dybas; AMNH), 1♀.

DISCUSSION: The type of *concolor* agrees well with Champion's original description (1898). We have added some characters in our redescription. The other specimen, from Volcan de Chiriqui, Panama, which Champion mentions, differs from the type in the following ways: it has uniformly light brown legs, antennae, and rostrum and the color on the abdomen is chestnut rather than rose. We also have in our possession three more Panamanian specimens (two females and one male) which are similar to the type in color with the exception of the abdomens. They vary from whitish to chestnut in our specimens, but are never rose. Their proportions are similar to those of the type, but their overall size and all measurements are 10–20 percent smaller.

Experience with other species of *Neoncylocotis* having longer series of specimens leads us to believe that size and coloration is more constant within a species than is the case for the material examined here, and that specimens from such widely separated localities are usually not conspecific. We have therefore decided not to consider the Panamanian specimens as *N. concolor* until more material can be examined and the extent of variation in this genus can be more fully understood.

We have also seen the specimen from Loja, Ecuador, identified by Jeannel (1944) as *concolor*; it represents an undescribed species close to *weyrauchi*.

Neoncylocotis meridionalis, new species

Figures 118, 129

DISTRIBUTION: Argentina.

DIAGNOSIS: This is a medium-size brown *Neoncylocotis* that can be distinguished by its opaque yellow-brown veins and femora, and the strikingly white veins on the undersides of the forewings.

DESCRIPTION: Males unknown. Female 4.2 mm in length.

General body color brown. Eyes and ocelli very slightly tinged with red. Foreacetabula slightly darker than rest of pronotum. Antennae light brown; rostrum light yellowish brown. Femora opaque light brown, banded with chestnut distally. Tibiae light brown; distal ends of tibiae and entire tarsus yellowish. Veins of forewing opaque light brown, contrasting with translucent smokey color of membrane. Veins on underside of forewing and of hindwing white, in striking contrast to membrane.

Head equal in length to pronotum (fig. 129B). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.7. Eyes equal in length to anteocular distance; ratio width of eyes to synthlipsis 1:

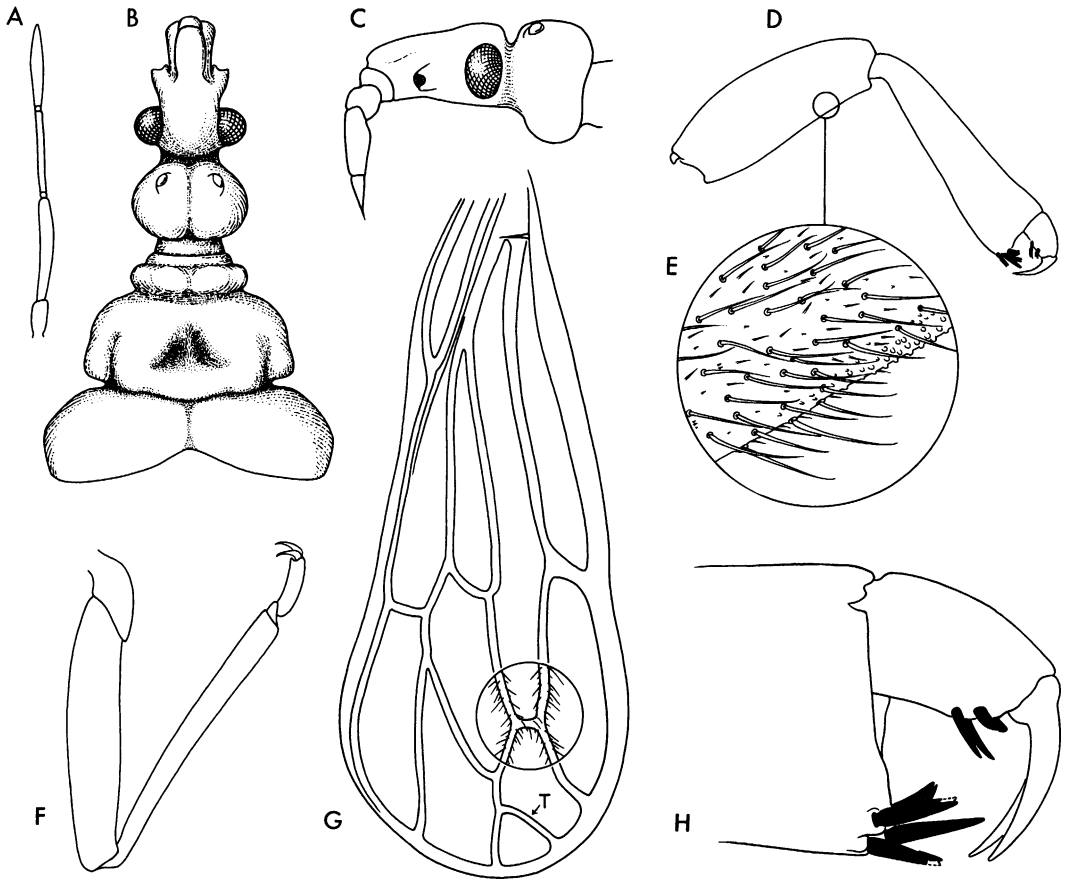


Fig. 129. *Neoncylocotis meridionalis*, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Foreleg. **E**. Detail of inner (ventral) surface of forefemur, showing setae and cuticular structures. **F**. Hind leg. **G**. Forewing. **H**. Apex of foreleg.

2.3. Posterior lobe of head moderately salient below, its height in side view 1.3 times length from posterior edge of eye to limit between head and neck (fig. 129C).

Antennal segments I–IV 1:2.5:2.1:2 (fig. 129A), combined much shorter than head plus pronotum (1:1.4).

Pronotum as shown in figure 129B, with a moderate posterior incision. In addition to the usual median triangular depression in the center of the midlobe, also with a very slight median sulcus on the posterior lobe. Proportional width of mid to hind lobes 1:1.4.

Right forewing of holotype with teratological venation (fig. 129G; at arrow); left wing normal. Setae in normal arrangement, interspersed with smaller hairs, and present occasionally in lumens of cells.

Setae on ventral surface of abdomen of normal shape, but of two lengths; those on dorsal surface of one length, but scale-shaped.

Forelegs as shown in figure 129D. Ratio length to width of forefemur 1:0.33. Setae on forefemur interspersed with smaller hairs and microtrichiae (fig. 129E). A few cuticular granules present distally on the forefemur (fig. 129E). Ratio length to width of hind femur 1:0.21 (fig. 129F). Foretibia and tarsus bearing spines as in figure 129H. Ratio length to width of foretibia 1:0.29.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, ARGENTINA: Tucumán, Cerro de San Javier, 1000 m, Nov., 1957 (Wygodzinsky; AMNH).

ETYMOLOGY: The specific name *meridionalis*, meaning southernmost, refers to the fact

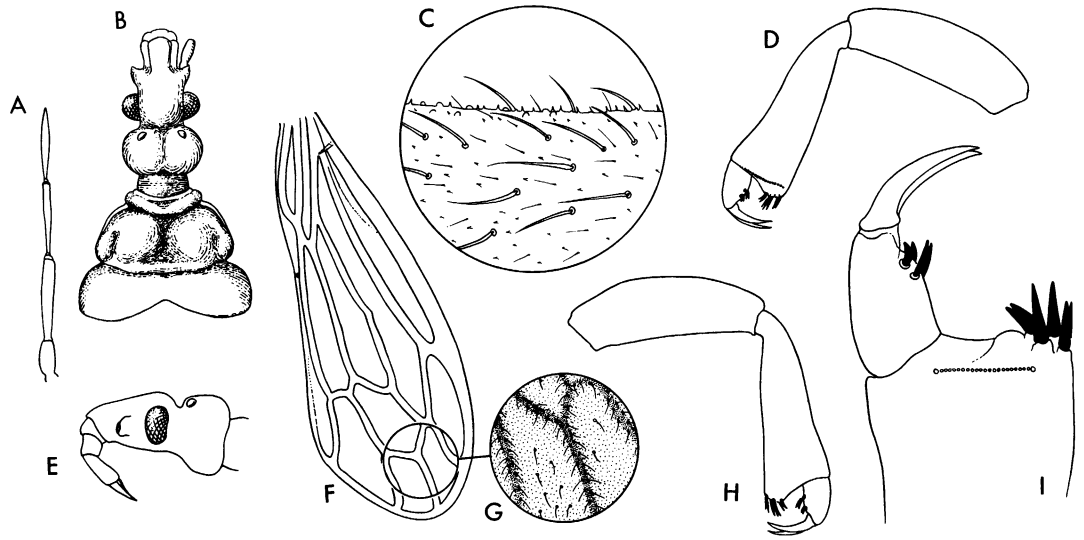


Fig. 130. *Neoncylocotis mexicanus*, ♀ (all but figures C and I are drawn from holotype). **A**. Antenna. **B**. Head and pronotum. **C**. Detail of inner (ventral) surface of forefemur. **D**. Foreleg, inner surface. **E**. Lateral view of head. **F**. Forewing. **G**. Detail of forewing. **H**. Foreleg, outer surface. **I**. Apex of foreleg, inner surface.

that this is one of the two southernmost species in the genus.

Neoncylocotis mexicanus (Kritsky), new combination
Figures 118, 130

Oncylocotis mexicanus Kritsky, 1978c: 195.

DISTRIBUTION: Southern Mexico.

DIAGNOSIS: This is a small, uniformly brown *Neoncylocotis* similar to *stannardi* in its expanded setal insertions over much of its body, and its areas of red around the ocelli. It differs by lacking expanded setal insertions on the forefemur; they are present in *stannardi*.

ADDITION TO DESCRIPTION: We have examined the holotype of *Neoncylocotis mexicanus* and add to Kritsky's original description the following information in order to be consistent with other parts of this work. It based on two additional specimens plus the holotype.

Males unknown.

General body color uniform medium brown, appendages lighter. Area around ocelli red.

Ratio head length to pronotum length 1:0.9 (fig. 130B). Ratio head length to width across eyes 1:0.6. Ratio length of eyes to anteocular portion 1:1.2; ratio width of eyes to synthlipsis 1:3.1. Ratio length to width of hind lobe of head 1:1.9. Hind lobe of head moderately salient below, its height 1.3 times distance from posterior border of eye to division between head and neck (fig. 130E).

Antennal segments I–IV 1:2:2:2, combined much shorter than head plus pronotum (1:1.4)

Forefemur as in figures 130D, H, with setal insertions not expanded, and with a very few minute tubercles along inner edge only (fig. 130C). Microtrichiae near anterior edge of forefemur in two sizes in roughly equal numbers. Ratio length to width of forefemur 1:0.29; of foretibia 1:0.27; of hind femur 1:0.19.

Forewings with setae two-ranked on veins of disc (fig. 130F, G) and with setae in lumens of cells.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, MEXICO: Chiapas, Tapachula, May, 1902 (Cook and Collins; USNM), examined.

MATERIAL EXAMINED: MEXICO. – **Chiapas**: 20 mi NE of Tuxtla Gutierrez, August

TABLE 14
Leg Proportions of Two Groups of *Neoncylocotis montanus* Collected in Different Years
Proportions are figured from average measurements (see measurements and ranges in Appendix)

	N	Total length	L to W forefemur	L to W hind femur	L to W foretibia
1945 spec.	(4)	4.4–4.7 mm	1:0.22	1:0.19	1:0.29
1953 spec.	(3)	4.1–4.3 mm	1:0.19	1:0.15	1:0.26

18, 1966 (J. and W. Ivie; AMNH), 1♀ (probably). **Vera Cruz**: Cordoba, August 4, 1969 (J. Peck; AMNH), 1♀.

DISCUSSION: The two specimens from localities other than the type locality are slightly darker than the holotype but otherwise agree remarkably well in overall appearance and proportions. The major difference is that these specimens lack the "deep median diverging suture" described in Kritsky's (1978c) key and evident on the holotype. After examining the suture closely, we noticed that it was slightly asymmetrical and we believe that it is teratological. We see no reason why these specimens should not be treated as conspecific.

Neoncylocotis montanus, new species
Figures 118, 131

DISTRIBUTION: Venezuela.

DIAGNOSIS: A delicate brown *Neoncylocotis* from Venezuela with reddish brown femora, and whitish femorotibial joints ("knees") and forewing bases.

DESCRIPTION: Female unknown. Length of males 4.1–4.7 mm.

General body color medium brown. Head and pronotum dark brown; hind lobe of head and scutellum sometimes slightly lighter. Eyes red to dark reddish brown. Rostrum and antennae brown basally, apical segment of each whitish. Abdomen medium brown with lighter brown sclerotized areas, and reddish lateral and posterior borders. Guide red. All femora reddish distally turning white at "knee" joints. All tibiae medium brown with white at "knee" joints. Tarsus light to medium brown.

Head and pronotum equal in length (fig. 131B). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular portion 1:1.1; ratio width of eyes to synthlipsis 1:2. Posterior lobe of head not especially salient below, height of lobe 1.1 times distance between posterior border of eye and limit between head and neck (fig. 131C).

Antennal segments I–IV 1:2.2:2.7:1.9 (fig. 131A), combined length shorter than head plus pronotum (1:1.4).

Pronotum as shown in figure 131B, with a moderate posterior incision. Proportional width of mid to hind lobes 1:1.7.

Forewings 2.6–3.2 mm long with veins arranged as in figure 131M. Setae of uniform length on wing veins, not present in lumens of cells, and two-ranked on all inner veins of disc (fig. 131J). Microtrichiae along edges of some veins.

Dorsal surface of abdomen bearing setae of uniform length but scalelike in their structure (fig. 131H) and curved at tips. Ventral side of abdomen with setae of two lengths, but unmodified in their structure. Both surfaces bearing one to several-toothed microtrichiae.

Hind wings as shown in figure 131L.

Forelegs as shown in figures 131D. Ratio length to width of forefemur 1:0.22 to 1:0.19 (see Discussion). Setae of forefemur interspersed with shorter setae (fig. 131E); anterior surface with granular structures in a narrow band along edge, fading to minute toothed microtrichiae dorsally (fig. 131E). Ratio length to width of hind femur 1:0.19 to 1:0.15 (fig. 131K). Ratio length to width of foretibia 1: 0.29 to 1:0.26. Foretibia and tarsus bearing spines arranged as in figures 131F, G.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, VENEZUELA: Aragua, Rancho Grande, 1100 m, May 24, 1953 (F. Fernandez; AMNH).

PARATYPES: Same data as holotype (AMNH), 3♂.

Fig. 131. *Neoncylocotis montanus*, ♂. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Foreleg. **E**. Detail of inner (ventral) surface of forefemur. **F**, **G**. Apex of foreleg, outer and inner surfaces, respectively. **H**, **I**. Details of abdomen, showing setae and microtrichiae, dorsal and ventral, respectively. **J**. Detail of forewing. **K**. Hind leg. **L**. Hind wing. **M**. Forewing.

ADDITIONAL MATERIAL EXAMINED: VENEZUELA. – **Aragua**: Rancho Grande, April 22, 1945 (no collector; AMNH), 3♂.

ETYMOLOGY: The specific name *montanus* refers to the relatively high altitude at which these specimens were collected.

DISCUSSION: We examined two groups of specimens, both from Rancho Grande, Venezuela, but collected in two different years. They seem identical in everything but their overall length and leg proportions, which are summarized in table 14. The specimens are

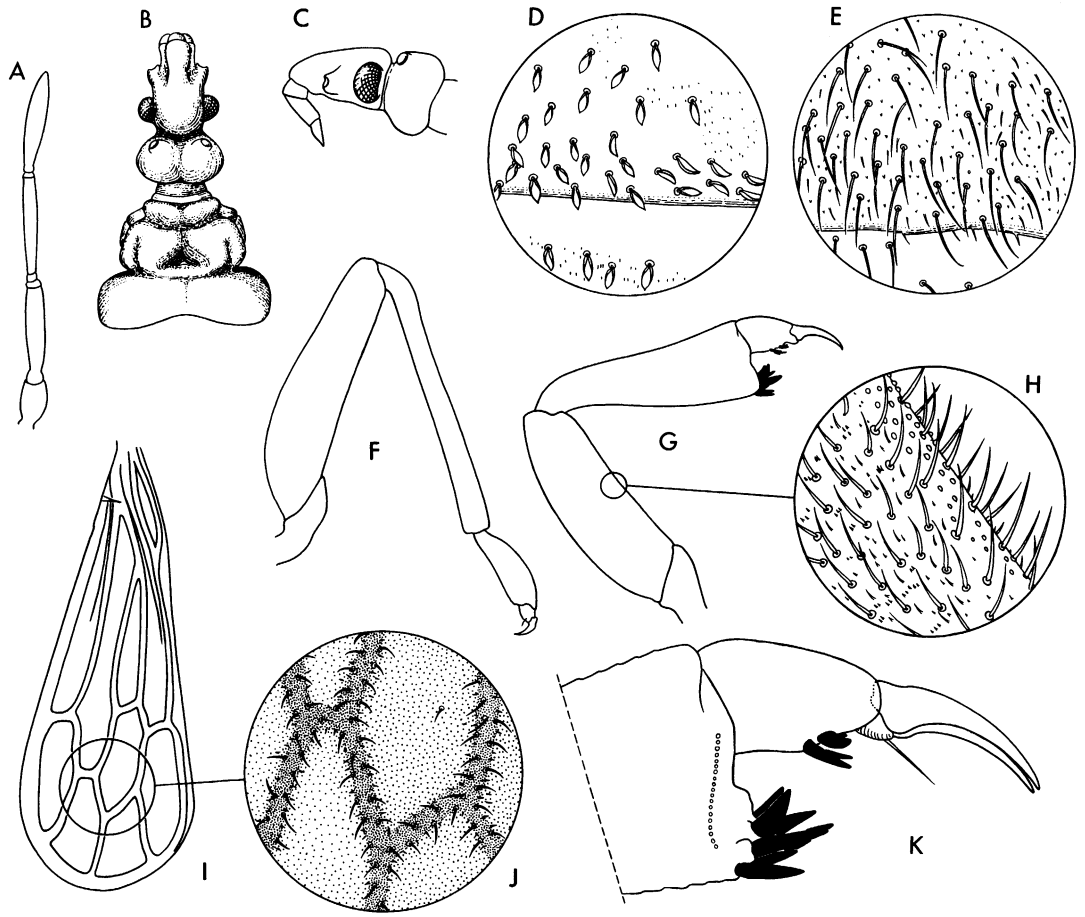


Fig. 132. *Neoncylocotis pisinnus*, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**, **E**. Details of abdomen, showing setae and microtrichiae, dorsal and ventral, respectively. **F**. Hind leg. **G**. Foreleg. **H**. Detail of inner (ventral) surface of forefemur, showing cuticular granules and setae. **I**. Forewing. **J**. Detail of above. **K**. Apex of foreleg, inner surface.

otherwise so similar that we must conclude that they are conspecific.

Neoncylocotis pisinnus, new species

Figures 118, 132

DISTRIBUTION: Northern Brazil.

DIAGNOSIS: This uniformly brown *Neoncylocotis* can be distinguished by its extremely small size of not more than 2.8 mm.

DESCRIPTION: Males unknown. Females very small, 2.7–2.8 mm in length.

General body color uniform light brown. Head, hind lobe of pronotum, and scutellum slightly darker than fore and midlobe of pronotum. All appendages light yellowish brown. Eyes and ocelli tinged with crimson.

Head slightly longer than pronotum (1:0.9; fig. 132B). Ratio head length to width across eyes 1:0.6. Ratio length to width of hind lobe of head 1:1.9. Ratio length of eyes to anteocular portion 1:1; ratio width of eyes to synthlipsis 1:3. Posterior lobe of head conspicuously salient below, its height in side view 1.5 times length from posterior edge of eye to limit between head and neck (fig. 132C).

Antennal segments I–IV 1:1.8:2:2 (fig. 132A), combined length much shorter than head plus pronotum (1:1.5).

Pronotum as shown in figure 132B, with a relatively shallow posterior incision (less than

half total length of hind lobe). In addition to usual triangular depression in center of midlobe, also a very slight median sulcus on posteror lobe of most specimens. Proportional width of mid to hind lobes 1:1.3.

Forewings with setae two-ranked on all inner veins of disc, and with a few in lumens of cells (fig. 132J). Microtrichiae interspersed between setae on veins of wing.

Abdomen bearing simple nontoothed microtrichiae interspersed among setae (figs. 132D, E). Setae on ventral surface of normal shape but of two lengths (smaller ones may be microtrichiae (fig. 132E); setae on dorsal surface uniform in size but short and scale-shaped (fig. 132D).

Forelegs as shown in figure 132G. Ratio length to width of forefemur 1:0.33. Setae on forefemur interspersed with smaller setae and microtrichiae (fig. 132H). A few cuticular tubercles distally on forefemur (fig. 132H). Ratio length to width of hind femur 1:0.24 (fig. 132F). Foretibia and tarsus bearing spines as in figure 132K. Ratio length to width of foretibia 1:0.34.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRAZIL: Pará; 8 km E Belém, Ananindeua, May 30, 1973 (R. T. Schuh; AMNH).

PARATYPES: Same data as holotype (AMNH), 3♀ (2 pinned and 1 slide).

ETYMOLOGY: This is the smallest known *Neoncylocotis* and is named *pisinnus*, meaning "small" in Latin.

Neoncylocotis rhyparus (Stål), new combination
Figures 118, 133

Henicocephalus rhyparus Stål, 1860: 82. — Bergroth, 1889: 319.
Stenopirates (*Hymenocoris*) *rhyparus*: Jeannel, 1942 (1941): 331.
Hymenocoris rhyparus: Jeannel, 1944 (1943): 128.
Oncylocotis rhyparus: Usinger, 1945: 334.

DISTRIBUTION: Southern Brazil (see Discussion).

DIAGNOSIS: *Neoncylocotis rhyparus* can be distinguished by its overall dull light brown color, translucent wings with opaque veins, normal shaped setae, wide hind pronotal lobe, and other characters as stated in the Description and Key.

ADDITION TO DESCRIPTION: Length of male 3.7 mm.

General body color dull light brown. Forewings translucent with opaque veins. Head longer than pronotum (1:0.6); (fig. 133B). Ratio length of eyes to anteocular distance 1:0.9. Ratio length to width of hind lobe of head 1:1.5. Ratio of width of mid to hind pronotal lobes 1:1.7.

Antennae as in figure 133B.

Forelegs as in figure 133F. Ratio length to width of forefemur 1:0.24. Forefemur with setae of two lengths, interspersed with microscopic cuticular granules and spines (fig. 133D). Foretibia with spines as in figures 133E, G. Ratio length to width 1:0.23.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BRAZIL: Rio de Janeiro (no collector; Stockholm Museum), examined.

DISCUSSION: Jeannel (1944 [1943]) reported this species–with some doubts—from Costa Rica and Bolivia; we share those doubts, and believe this species to be restricted to southeastern Brazil. We have examined Jeannel's specimen from Bolivia; it belongs to an undescribed species of *Neoncylocotis*. We have also examined Kritsky's (1978c) *rhyparus* from Peru, which does not represent the same species, since the specimens are nearly black, and a full millimeter longer than the holotype.

Neoncylocotis rubripes, new species
Figures 118, 134

DISTRIBUTION: Peru.

DIAGNOSIS: This is the only *Neoncylocotis* with bright scarlet legs.

DESCRIPTION: Females unknown. Length of male 3.9–4.2 mm.

General body color brown tinged with red or orange. Head piceous tinged with red, especially eyes, tylus, and area around ocelli; underside of head brownish orange. First segment of antenna red, second and third segments light brown, and fourth whitish. Rostrum light brown. Pronotum and scutellum piceous; underside of thorax dark brown tinged with orange. Membrane of forewings translucent dusky brown with veins slightly more orange veins; base of forewings whitish to apex of scutellum. Abdomen and genital area dark brown with posterior edge of segments tinged with red. Legs scarlet; coxae, trochantera, tarsi, and claws brown.

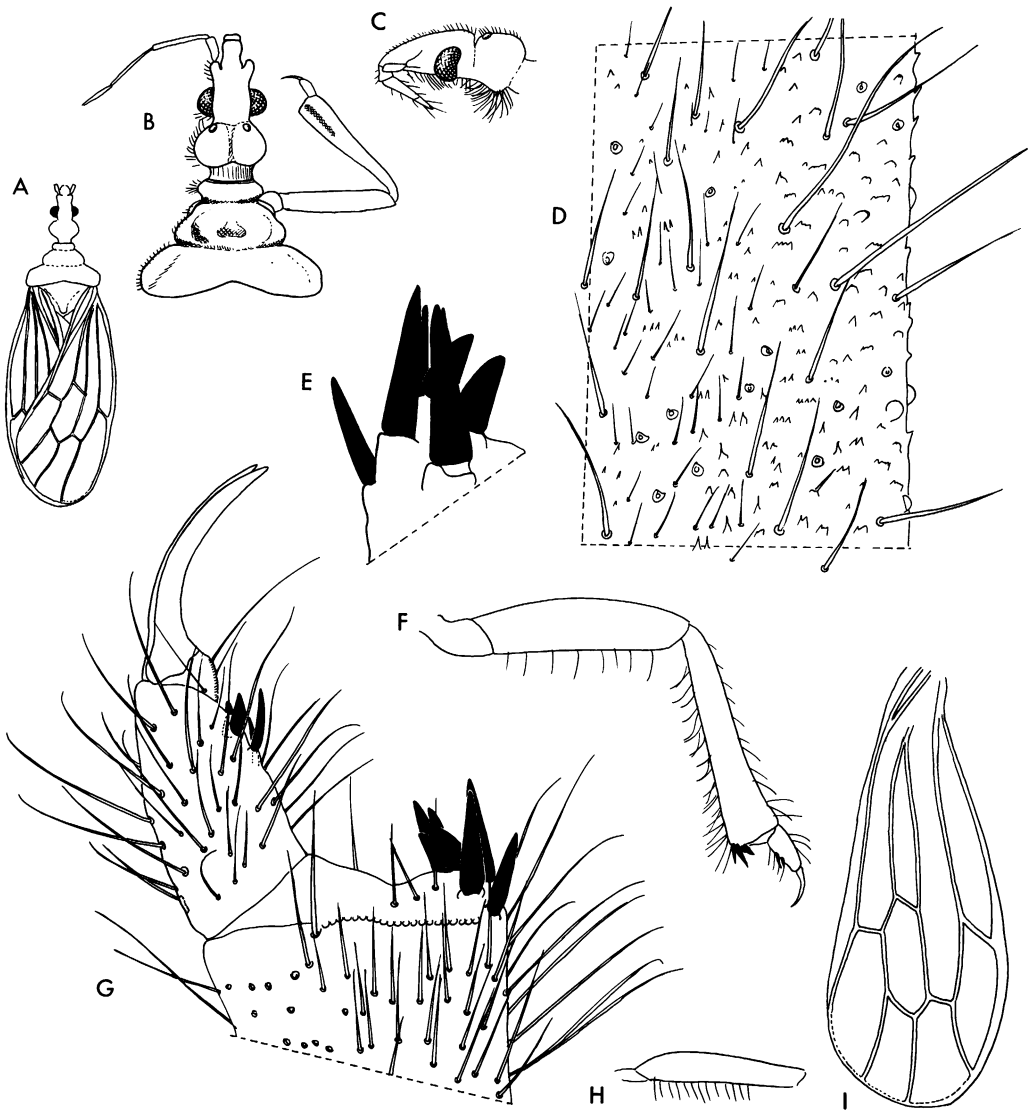


Fig. 133. *Neoncylocotis rhyparus*, ♂ (holotype). **A**. Dorsal. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Detail of forefemur, showing various size setae and cuticular structures. **E**. Foretibial spines, outer view. **F**. Foreleg, **G**. Apex of foreleg, inner surface. **H**. Hind femur. **I**. Forewing.

Head and pronotum equal in length (fig. 134B). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.5. Ratio length of eyes to anteocular portion 1:0.8; ratio width of eyes to synthlipsis 1:2.5. Posterior lobe of head conspicuously salient below, its height in side view 1.5 times the length from posterior edge of eye to limit between head and neck (fig. 134C).

Antennal segments I–IV 1:1.8:2:2.2 (fig. 134A), combined slightly shorter than head plus pronotum (1:1.4).

Pronotum as shown in figure 134B, with a moderate posterior incision. Proportional width of mid to hind lobes 1:1.6.

Forewings 2.5–2.8 mm long and often teratological in their venation (figs. 134K, L).

Abdomen bearing toothed microtrichiae interspersed among setae (figs. 134I, J). Setae on ventral surface of normal shaped but of two lengths (fig. 134J); setae on dorsal surface uniform in size but scale-shaped (fig. 134I).

Forelegs as shown in figure 134F. Ratio length to width of forefemur 1:0.24. Long

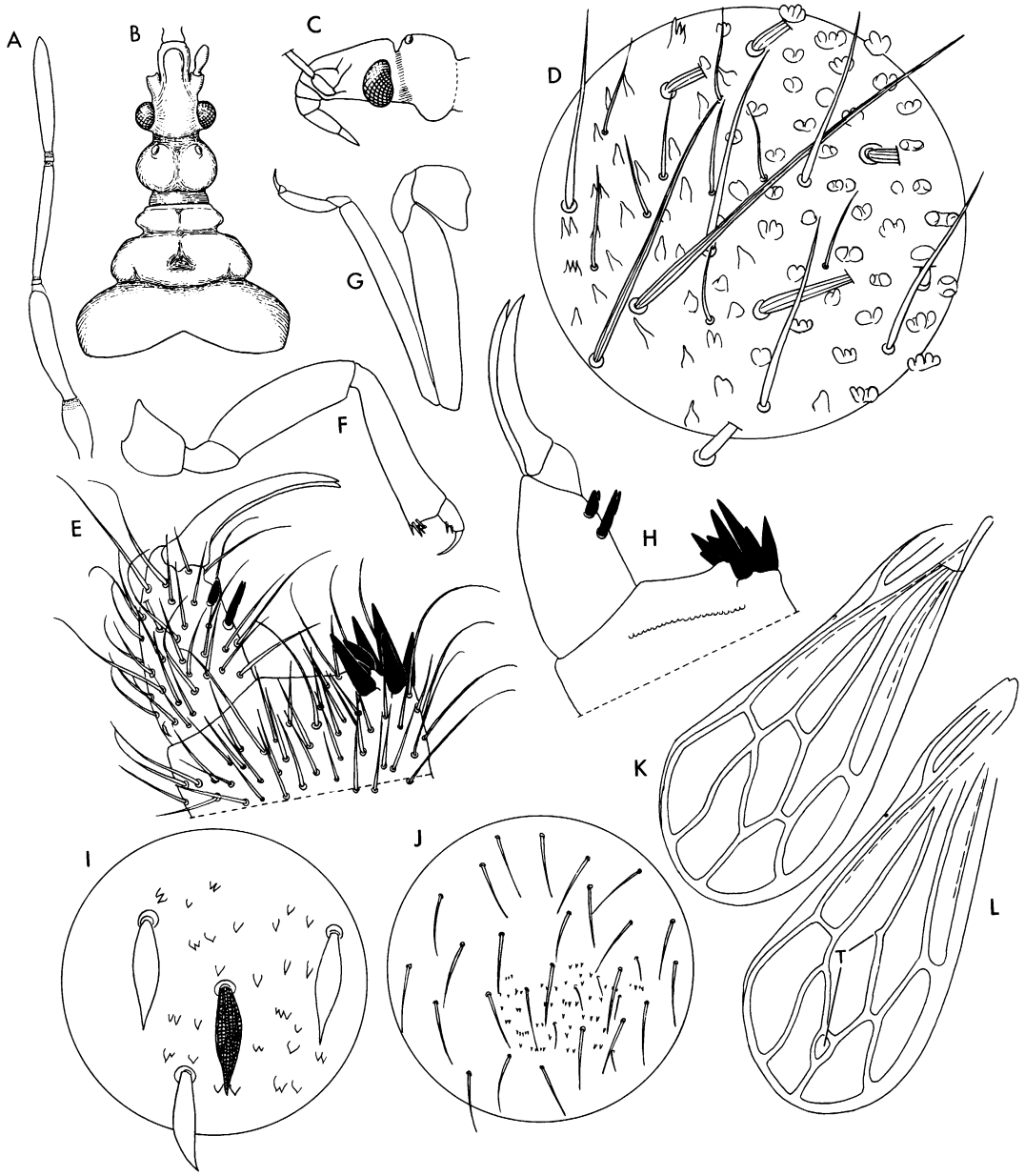


Fig. 134. *Neoncylocotis rubripes*, ♂. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Detail of inner (ventral) surface of forefemur, showing various size setae and cuticular structures. **E**. Apex of foreleg, outer surface. **F**. Foreleg. **G**. Hind leg. **H**. Apex of foreleg, inner surface. **I**, **J**. Setae and microtrichiae of abdomen (I) dorsal, and (J) ventral. **K**, **L**. Forewings, (L) teratological.

setae on forefemur interspersed with smaller ones (fig. 134D). Cuticular surface bearing microscopic granular structures (fig. 134D) each with one to four lobes or teeth. Ratio length to width of hind femur 1:0.18 (fig. 134G). Foretibia and tarsus bearing spines as shown in figures 134E, H. Longer setae, especially those on opposing surfaces of femur and tibia, curved at tips (fig. 134E). Ratio length to width of foretibia 1:0.27.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, PERU: Cerro Azul, 28 mi E of Tingo Maria, November 28, 1954 (Schlinger and Ross; CAS).

PARATYPES: PERU: **Huanuco**: Cerro Azul, 28 mi E of Tingo Maria, November 28, 1954 (E. I. Schlinger and E. S. Ross; CAS), 14♂; (E. I. Schlinger and E. S. Ross; AMNH), 3♂.

ETYMOLOGY: The specific name *rubripes* refers to the bright red legs of this species.

Neoncylocotis slateri, new species
Figures 118, 135

DISTRIBUTION: Peru.

DIAGNOSIS: This is a medium brown *Neoncylocotis* bearing scalelike hairs on most parts of its body and having two different colors of veins on the underside of its forewings: the Sc is whitish and the remainder of the veins are brown.

DESCRIPTION: Males unknown. Length of female 3.6–3.7 mm.

General body color medium brown. Head, pronotum, and scutellum uniform brown above, slightly lighter below. Antennae and rostrum light yellowish brown with terminal segments yellowish. Forewing membranes uniform translucent brown above, Sc whitish below, and all other veins on underside of wing brown. Abdomen bearing brown sclerotized plates and genital area and with rose tinted connexival membranes. Legs uniform light yellowish brown.

Head slightly longer than pronotum (1:0.9). Ratio head length to width across eyes 1:0.6 (fig. 135A). Ratio length to width of hind lobe of head 1:1.7. Ratio length of eyes to anteocular portion 1:1.2; ratio width of eyes to synthlipsis 1:3.1. Posterior lobe of head conspicuously salient below, its height in side view 1.44 times length from posterior edge of eye to limit between head and neck (fig. 135B).

Antennal segments I–IV 1:2.3:2.4:2.1, combined shorter than head plus pronotum (1:1.4).

Pronotum as shown in figure 135A, with a moderate posterior incision. Anterior lobe with 1 + 1 prominent tubercles dorsally. Midlobe of pronotum with deep central triangular depression and 1 + 1 deep lateral sulci accentuating height of lateral lobes. Ratio mid to hind lobe 1:1.4.

Forewings with scale-shaped setae (fig. 135I), and with many setae in lumens of cells (fig. 135K).

Dorsal surface of abdomen bearing scale-shaped setae interspersed with one- to three-toothed tubercles (fig. 135H). Ventral surface with normally shaped setae interspersed with both microthrichiae and cuticular granules (fig. 135J).

Forelegs as shown in figure 135C. Ratio length to width of forefemur 1:0.32. Setae on forefemur interspersed with microtrichiae (fig. 135G); anterior distal portion bearing cuticular tubercles resembling short wedge-shaped pegs. Ratio length to width of hind femur 1: 0.23 (fig. 135L). Foretibia and tarsus bearing spines as shown in figures 135D, E. Ratio length to width of foretibia 1:0.36; scale-shaped setae interspersed with microtrichiae as in figure 135F.

Most of the setae on head, pronotum, and forewings scale-shaped; some scale-shaped setae also on legs and antennae, especially on proximal portion of each segment.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, PERU: Junin: Pichita Caluga, San Ramon, Estancia Naranjal, 2000 m, August 8, 1957 (Weyrauch; AMNH).

PARATYPE: Same data as holotype (AMNH), 1♀.

ETYMOLOGY: This species is named for Dr. James A. Slater, who was largely responsible for the junior author's interest in entomology.

DISCUSSION: We also examined two similar specimens and two nymphs from San Ramon, Estancia Naranjal, and one specimen from Junin, San Ramon de Pangoa, 40 km SE of Satipo, which are very simlar to *N. slateri*. They all bear the scalelike setae over most of their bodies, but differ in subtleties of coloration, proportions, and setal length and arrangement.

Neoncylocotis stannardi (Kritsky), new combination
Figures 118, 136

Oncylocotis stannardi Kritsky, 1978c: 196.
Oncylocotis braziliensis Kritsky, 1978c: 196. NEW SYNONYMY.

DISTRIBUTION: Southern Brazil.

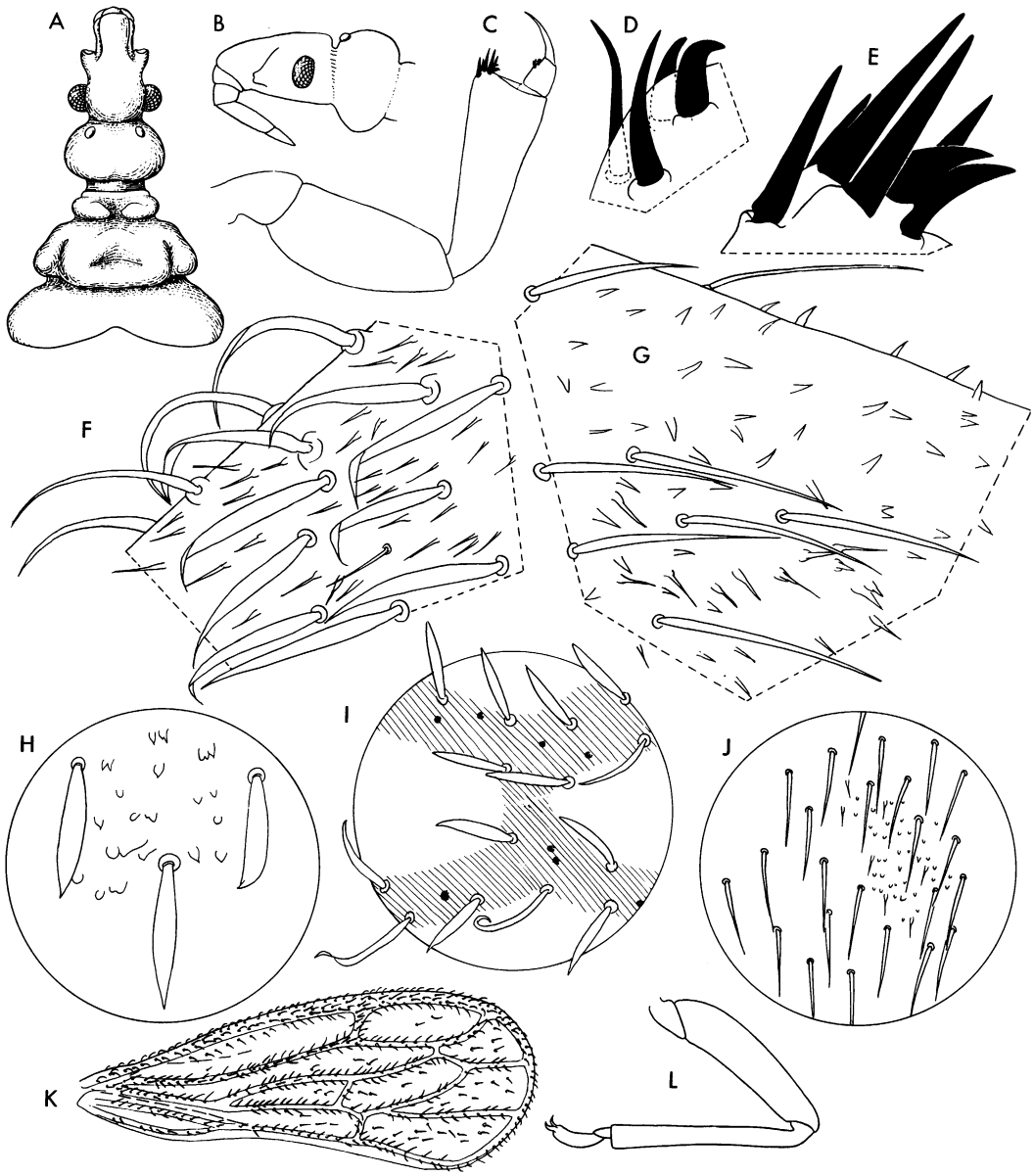


Fig. 135. *Neoncylocotis slateri*, ♀. **A**. Head and pronotum. **B**. Lateral view of head. **C**. Foreleg. **D**. Foretarsal spines. **E**. Foretibial spines, outer view. **F**. Detail of foretibia, showing scalelike setae and microtrichiae. **G**. Detail of forefemur. **H, J**. Details of abdomen, dorsal and ventral surfaces, respectively. **I**. Detail of forewing at r-m crossvein. **K**. Forewing. **L**. Hind leg.

DIAGNOSIS: This is a small uniformly brown *Neoncylocotis* similar to *mexicanus* in its expanded setal insertions on much of its body; however, they are not expanded on the forefemur of *mexicanus* as they are in *stannardi*.

ADDITION TO DESCRIPTION: We have seen the holotypes of *stannardi* and *braziliensis* and here synonymize the two under the name *stannardi* (see Discussion). We add to Kritsky's (1978c) original description of *stannar-*

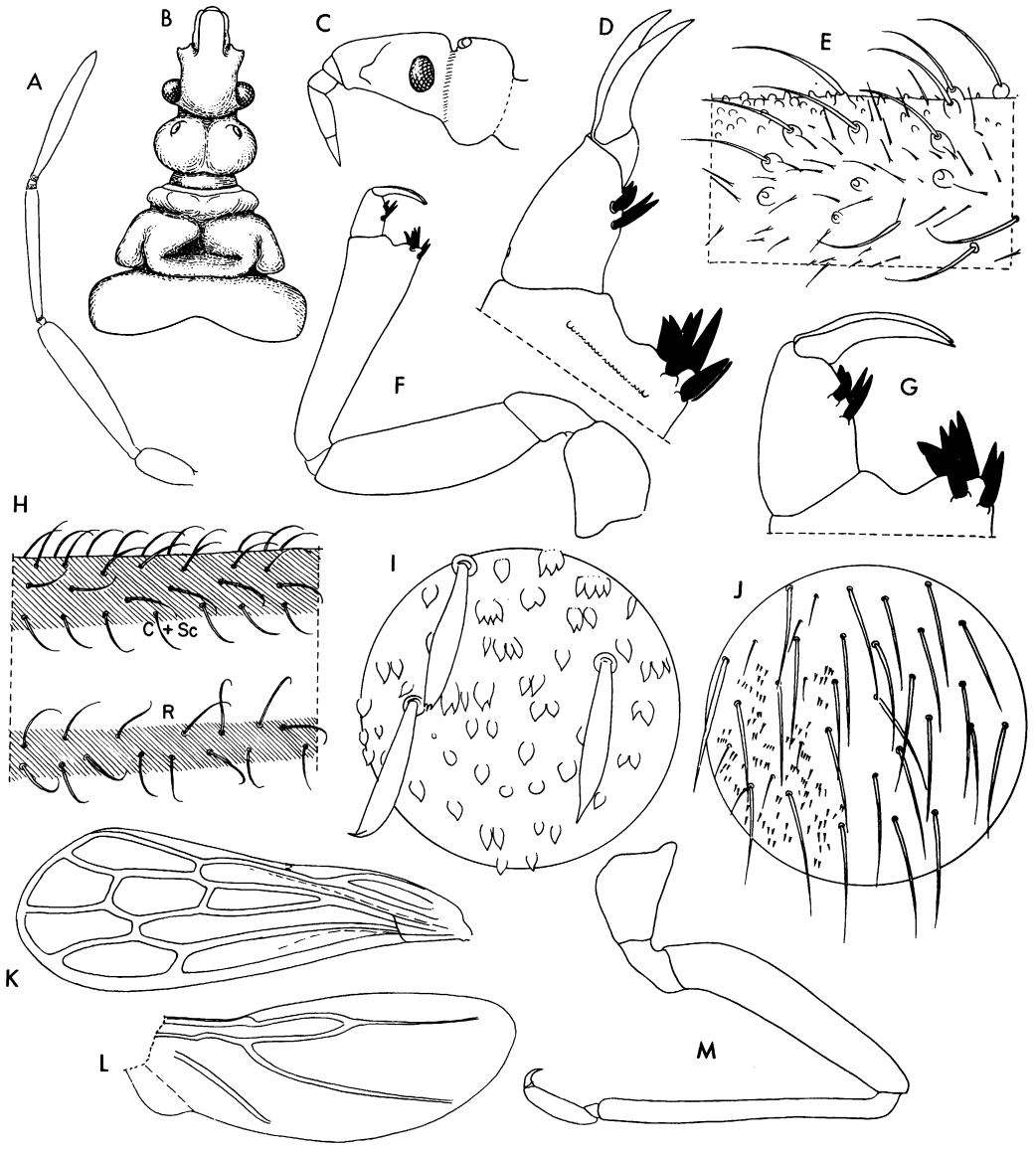


Fig. 136. *Neoncylocotis stannardi*. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Apex of foreleg, inner surface. **E**. Detail of inner (ventral) surface of forefemur, showing cuticular granules and expanded setal bases. **F**. Foreleg. **G**. Apex of foreleg, outer surface. **H**. Detail of forewing at level of basal cell. **I, J**. Details of abdomen showing setae and microtrichiae, (I) dorsal, (J) ventral. **K**. Forewing. **L**. Hind wing. **M**. Hind leg.

di the following information which is based on the holotype plus five additional specimens:

Males unknown.

General body color medium brown; appendages lighter. Area around ocelli usually red. Setae vary from short and sparse to longer, curved, and somewhat woolly. Insertions of most setae expanded to form quite obvious tubercles, including setae of forefemora (fig. 136E).

Ratio head length to pronotum length 1:

0.9 (fig. 136B). Ratio head length to width across eyes 1:0.5 to 1:0.6. Ratio length to width of hind lobe of head 1:1.7. Ratio length of eyes to anteocular portion 1:1.3; ratio width of eyes to synthlipsis 1:1.3. Posterior lobe of head conspicuously salient below, height in side view 1.5 times the length from posterior edge of eye to limit between head and neck (fig. 136C).

Antennal segments I–IV 1:2.1:1.9:2 (fig. 136A), combined shorter than head plus pronotum (1:1.3).

Pronotum as shown in figure 136B with a moderate posterior incision. Proportional width of mid to hind lobes 1:1.3.

Forewings as shown in figure 136K. Setae distinctly two-ranked on inner veins of disc (fig. 136H). Hind wings as in figure 136L.

Abdomen bearing toothed microtrichiae interspersed among setae (figs. 136I, J). Setae on ventral surface of abdomen normal shape but of two lengths (fig. 136J); those on dorsal surface uniform in size but scale-shaped (fig. 136I).

Forelegs as in figure 136F, their tarsal and tibial spines as in figures 136D, G. Setae of forefemora with expanded insertions (fig. 136E). Forefemora with minute tubercles in a narrow band along anterior edge, most numerous distally; microtrichiae of uniform size, or with at most a few smaller ones. Hind legs as in figure 136M.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRAZIL: Parana, Bocaiuva, 25°11′S (label text in error, saying 35°11′N), 49°04′W, May 1964 (Fritz Plaumann; USNM); examined.

MATERIAL EXAMINED: BRAZIL. – **Santa Catarina**: Nova Teutonia, June 30, 1955 (F. Plaumann; USNM), 1♀ (holotype of *N. braziliensis*); August, 1953 (Plaumann; Field Museum), 1♀; November 1, 1957 (F. Plaumann; AMNH), 2♀; July 6, 1959 (F. Plaumann; P. Ashlock collection), 1♀.

DISCUSSION: We have examined the types of *N. stannardi* and *N. braziliensis*, as well as five other specimens from Santa Catarina and can find no consistent differences between them. Kritsky, in his key (1978c), separated the two species on the basis of the depth of the groove between the mid and hind pronotal lobes, but we were not able to observe the difference. In addition, all specimens have quite characteristic expanded setal insertions over most of their bodies. There are subtle differences in color, head proportions, and coloration of the undersides of the forewing veins, but these do not fall into clearly separable groups.

With the small amount of material available to us, it is impossible to determine for certain whether these differences are due to intraspecific variation or whether there are several species involved.

Neoncylocotis weyrauchi, new species
Figures 118, 137

DISTRIBUTION: Peru.

DIAGNOSIS: This is a large, uniformly dark brown *Neoncylocotis* that has numerous setae in the lumens of the forewing cells, and no cuticular granules on the forefemora.

DESCRIPTION: Males unknown. Length of female 5.5–6.3 mm.

General body color uniform dark brown. Rostrum, antennal segments III and IV, tarsi, and trochanters vary from brown to light yellowish brown. Membranous areas of abdomen whitish, tinged with brown or rose. Dark brown sclerotized areas present on ventral surface of abdomen and arranged in two lateral rows on segments II-VII, and centrally on segments I–IV and VIII (fig. 137N). Dorsal surface of abdomen bearing single, broad, sclerotized areas on segments II–VIII (fig. 137I). Genital capsule heavily sclerotized.

Head very slightly longer than pronotum (1:0.9; fig 137B). Ratio head length to width across eyes 1:0.5. Ratio length to width of hind lobe of head 1:1.4. Ratio length of eyes to anteocular distance 1:1.5; ratio width of eyes to synthlipsis 1:2.7. Posterior lobe of head not especially salient below, its height in side view 1.1 times length from posterior edge of eye to limit between head and neck (fig. 137C).

Antennal segments I–IV 1:2.8:2.7:2.1 (fig. 137A), combined shorter than head plus pronotum (1:1.3).

Pronotum as shown in figure 137B, with a shallow to moderate posterior incision (not quite half of the total length of the hind lobe). Proportional width of mid to hind lobes 1:1.5.

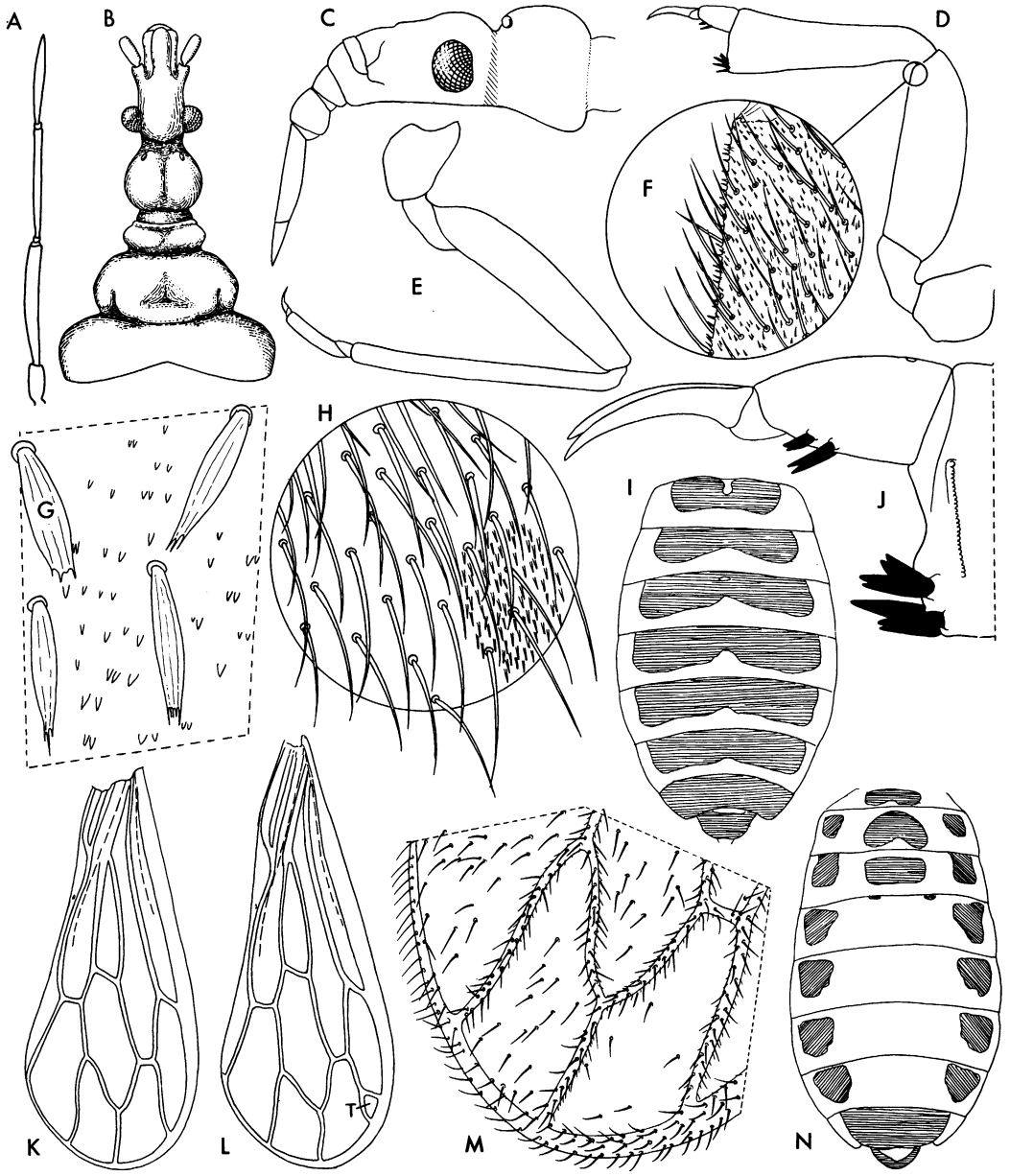


Fig. 137. *Neoncylocotis weyrauchi*, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head. **D**. Foreleg. **E**. Hind leg. **F**. Detail of inner (ventral) surface of forefemur. **G**. Setae and microtrichiae on dorsal surface of abdomen. **H**. Setae and microtrichiae on ventral surface of abdomen. **I**. Abdomen, dorsal. **J**. Apex of forefemur, inner surface. **K**, **L**. Forewings, the latter with extra cell. **M**. Detail of apex of forewing. **N**. Abdomen, ventral.

Forewings with setae roughly two-ranked on all inner veins of disc, and very numerous in lumens of cells (fig. 137M). Microtrichiae interspersed among setae on veins on wing.

Setae on both dorsal and ventral surfaces of abdomen of one length, but interspersed with microtrichiae. Setae on ventral surface of normal shape (fig. 137H); those on dorsal surface short and scale-shaped (fig. 137G).

Forelegs as shown in figure 137D. Ratio

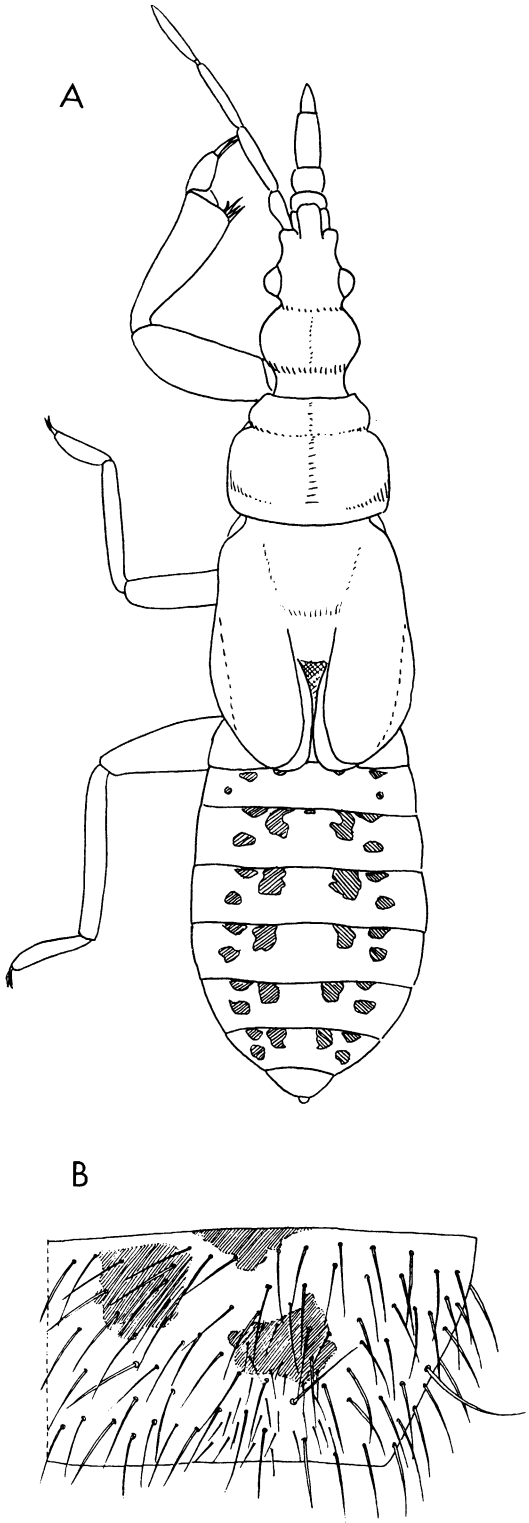


Fig. 138. *Neoncylocotis* sp. **A**. Fifth instar nymph. **B**. Detail of tergum VI.

length to width of forefemur 1:0.28. Setae on forefemur interspersed with short and long microtrichiae. No cuticular granules present on the anterior edge of the forefemur (fig. 137F). Ratio length to width of hind femur 1:0.21 (fig. 137E). Foretibia and tarsus bearing spines as in figure 137J; ratio length to width 1:0.29.

MEASUREMENTS: See Appendix.

HOLOTYPE: PERU: Cajamarca: Contumaza, 2850 m, under stones (W. Weyrauch; AMNH).

PARATYPES: Same data as holotype (AMNH), 4♀ (3 pinned specimens and 1 slide).

ETYMOLOGY: This species is named for W. Weyrauch, its collector.

Urnacephala, new genus

TYPE SPECIES: *Urnacephala californica*, new species.

DISTRIBUTION: Central and southern California (fig. 139).

DIAGNOSIS: *Urnacephala* males (females unknown) can be distinguished by the urn-shaped hind lobe of their heads (fig. 140A), the absence of a basal cell in the forewings (143H), the presence of a closed discal cell, the long and slender foretarsus with two subequal claws (fig. 140D), and the complete loss of tarsal spines (fig. 140E).

DESCRIPTION: Females unknown (see Discussion).

Male. Small size (length 2.9–4.1 mm). General color brown. Body surface shining; setiferous tubercles absent. All setae simple, slender. Macropterous.

Head with constriction behind eyes distinct (fig. 140A). Eyes large, but synthlipsis wide. Hind lobe of head urn-shaped with sides conspicuously convex, strongly converging posteriorly (fig. 140A). Ocelli medium size. Antennae with third and fourth segments subequal in length, second much longer (fig. 140A). Rostrum slender (fig. 140B).

Pronotum unarmed (fig. 140A). Median lobe with a simple median longitudinal impression; disc of lateral portions of midlobe lacking sculptural elements. Hind lobe of pronotum very short, almost ribbon-shaped, its posterior border emarginate. Anterior acetabula open behind.

Scutellum broadly triangular (fig. 140A), widely exposed. Meso- and metanotum (fig. 141D) with wing-body coupling groove

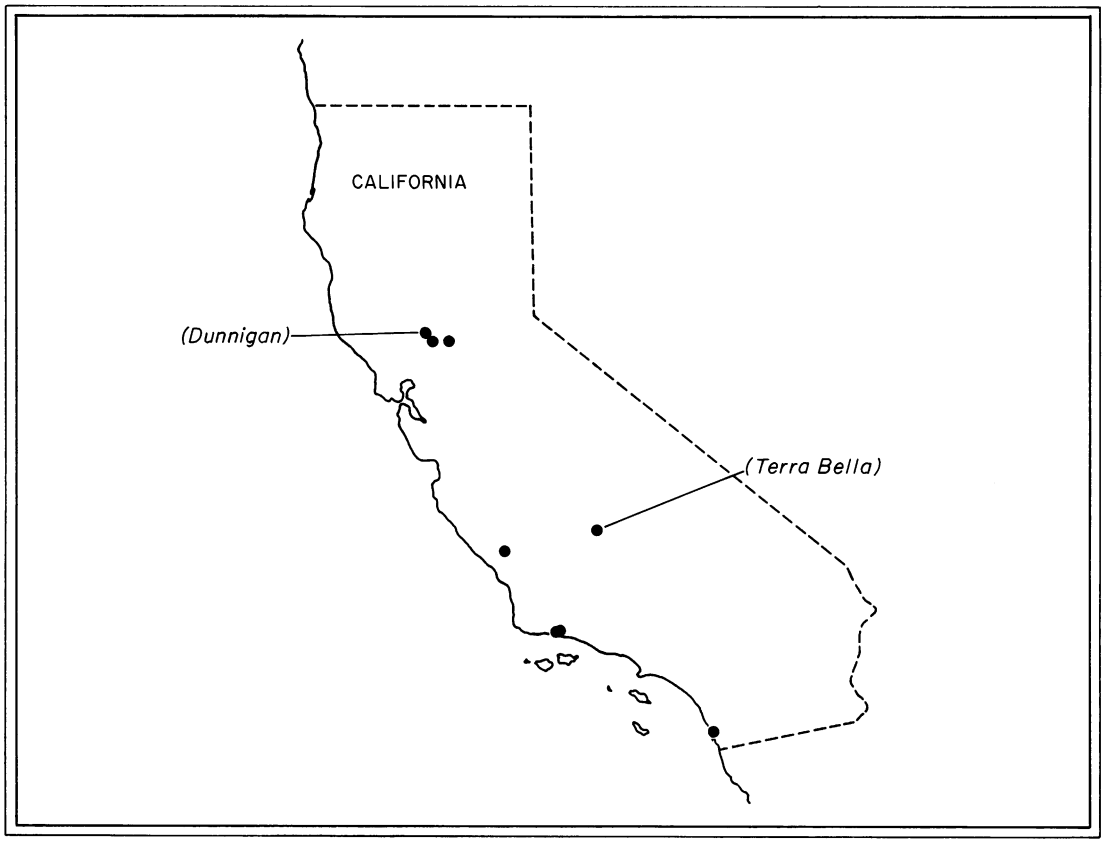


Fig. 139. Distribution of *Urnacephala. U. californica* (●).

(above metathoracic synpleuron) shallow, not well developed. Saucer-shaped evaporatory structures on posteroventral corners of thorax and on abdominal sterna (figs. 142A, D).

Forewings without basal cell; discal cell closed (fig. 143H). Stigmal cell over half as long as discal cell. Apex of Cu attaining wing margin. PCu extending beyond Cu-PCu crossvein. Both anal veins developed. Setae arranged in two irregular rows on most veins, but mostly in a single row on R+M, and much more numerous on costal margin. Lumens of cells with a few setae (fig. 145H). Wing coupling device C-shaped, with arm of "C" closest to wing edge bearing short microtrichialike processes, other arm with longer ones (fig. 141B, C).

Hind wings with a few setae along anterior margin and on membrane. Wing edge slightly rolled inward at level of wing coupling device but lacking foliaceous structures (fig. 141E, F).

Abdomen with ventral connexival plates separate from sternites; spiracles on ventral connexival plates II-VIII (fig. 142A). Divisions between dorsal connexival plates and tergites barely discernible, if present. Sterna II and III (at least) with 1 + 1 lateral patches of saucer-shaped evaporatory structures (fig. 142A, D; under compound microscope, these can be seen as faint open circles that are larger than setal insertions).

Front legs slender. Trochanter lacking process. Inner apical angle of tibia with two long spines and one or two slender short spines (figs. 140D, 143F, 144G). Tarsus much longer (1½ to 2 times) than proximal width of apical portion of tibia; tarsal spines absent (fig. 140E). Tarsal organ dorsally situated. Claws practically identical in length, not over one-third as long as tarsus (fig. 140D). Mid and hind legs without special characters; apex of tibiae with two bristle combs and two large spines (fig. 141A).

Guide truncate to slightly rounded at tip (figs. 142E, 143I, 145I). Tenth tergum sub-

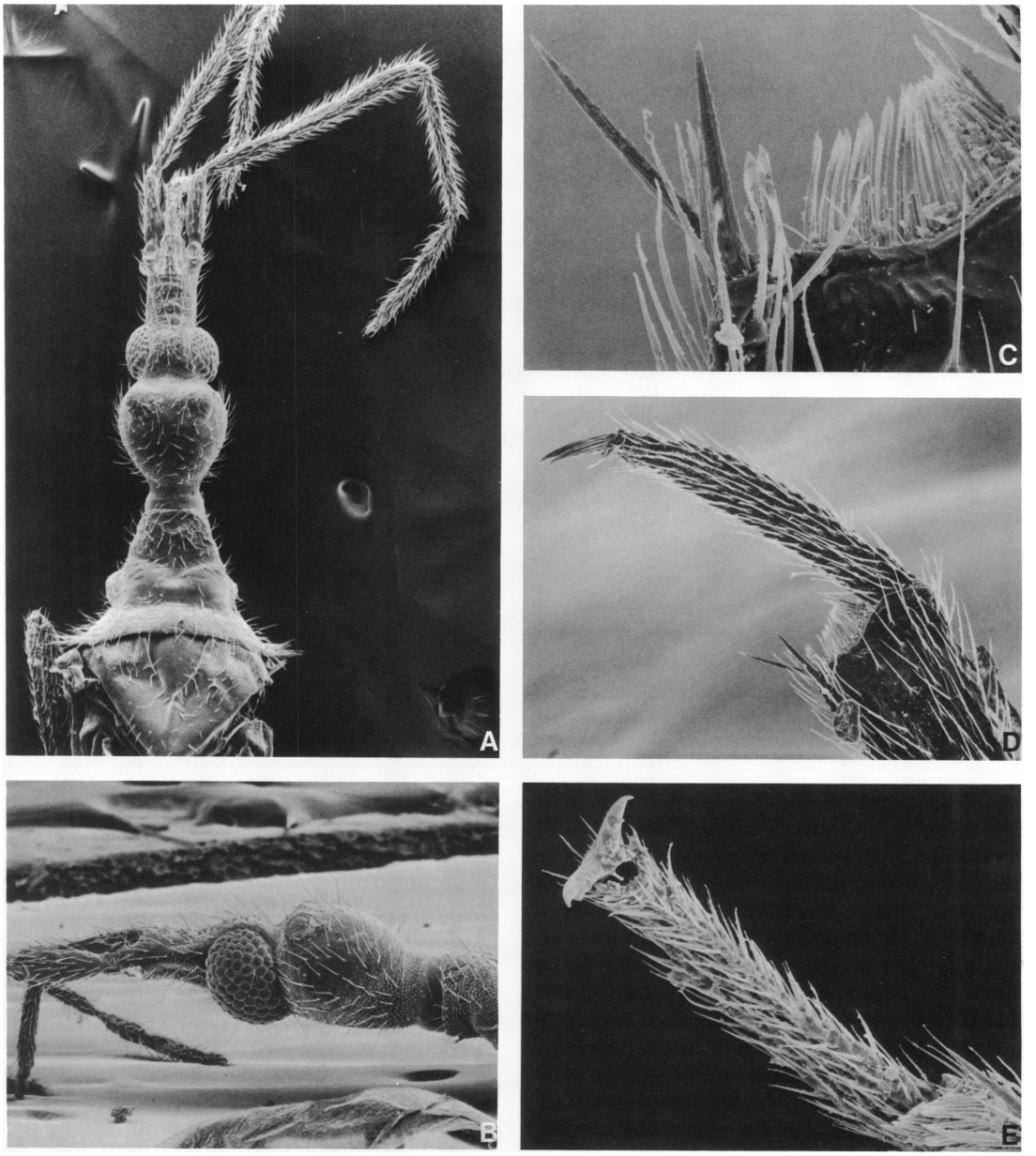


Fig. 140. *Urnacephala californica*, ♂. **A**. Head, pronotum, and scutellum, dorsal. **B**. Head, lateral. **C**. Foretibial spines. **D**. Foretarsus. **E**. Detail of foretarsus, showing absense of spines.

semicircular with median posterior tab probably the reduced 11th tergum (figs. 142F, 143J, 145J).

ETYMOLOGY: *Urnacephala* is from the Latin *urna*, f., meaning urn, plus the latinized Greek word *kephale*, f., meaning head.

DISCUSSION: Females of *Urnacephala* are unknown, as are those of *Brevidorsus* and *Lysenicocephalus*. We suspect that females of these three genera may be similar to those of *Hymenocoris* and live in much the same habitats; i.e., they may be apterous, have small eyes, and live deep in the ground.

We have one specimen of a small *Hymen-*

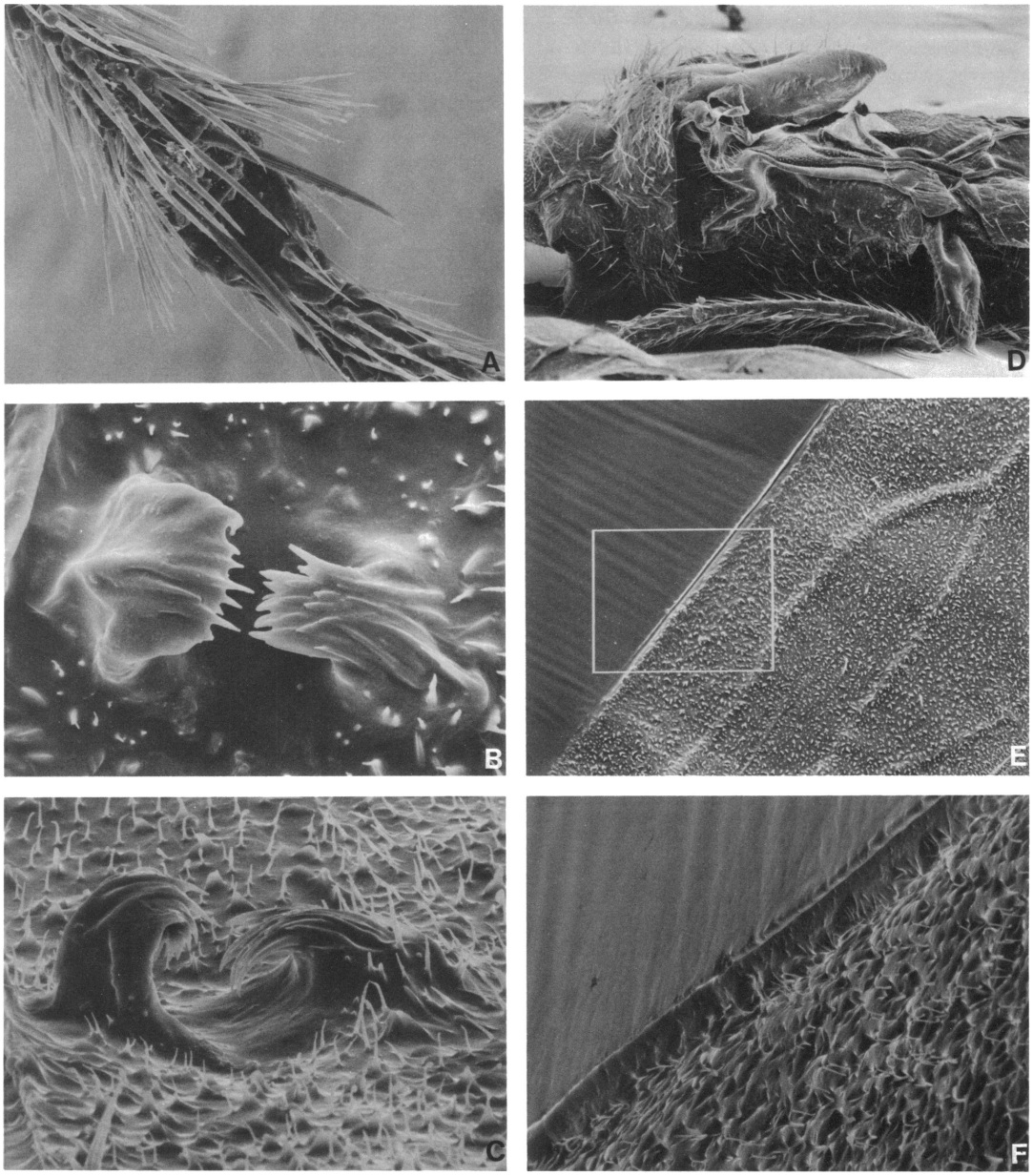


Fig. 141. *Urnacephala californica*, ♂. **A**. Apex of hind tibia. **B**, **C**. Wing coupling mechanism beneath hind edge of forewing, ventral and lateral views, respectively. **D**. Thorax, lateral. **E**, **F**. Hind wing edge at level of wing coupling mechanism.

ocoris-like female from Russelman's Park, Contra Costa County, California (fig. 146). It has foretarsal and tibial spines, forefemoral spur, and general shape similar to *Hymenocoris*. However, the shape of the hind lobe of its head is different, and it is quite a bit smaller. This could be a female of a small *Hymenocoris*-like species, which we have not seen yet, or it could be a female of one of the smaller genera. From a distributional point of view, *Urnacephala* would be most probable. However, *Lysenicocephalus* and *Brevi-*

dorsus are possibilities as well, since there is no reason to believe that we know the total range of these genera.

Urnacephala californica, new species
Figures 139–145

DISTRIBUTION: Central and southern California.

DIAGNOSIS: *Urnacephala californica* can be distinguished by the proportions listed below.

DESCRIPTION: Females unknown.

Length of males 3.7 (2.9–4.1) mm. (All measurements and proportions from the holotype are first; the range from other specimens follows in parentheses.)

General body color brown. Head dark reddish brown, eyes and ocelli reddish. Rostrum, antennae, pronotum, scutellum, and legs medium brown, lighter than head and not tinged with red. Entire body, legs, and wings somewhat shiny, sparsely clothed in medium length setae. Wings delicate, shiny, translucent, and very sparsely clothed with short setae. Abdomen light straw color with slightly darker genital area.

Head longer than pronotum 1:0.7 (0.5–0.6). Ratio head length to width across eyes 1:0.5 (0.4–0.5). Ratio length of eyes to anteocular distance 1:1.3 (0.8–1.2); ratio anteocular length to (narrowest) width in front of eyes 1:0.6 (1:1.1; only specimens from Rio Linda and holotype measured for this proportion; see Discussion). Ratio width of hind lobe of head to head width across eyes 1:0.9 (0.9–1.1). Ratio length to width of hind lobe of head 1:1.1 (1.1–1.3). Ocelli medium size (fig. 143A). Rostrum as in figure 143C.

Antennal segments I–IV 1:2.9(2.8–3.4): 1.9(1.9–2.3): 1.8(2.0–2.2), combined length greater than head plus pronotum 1:0.6 (0.6–0.8).

Pronotum as shown in figure 140A. Ratio length to width of pronotum 1:1.4 (1.4–1.5). Scutellum as in figure 140A.

Abdomen lightly sclerotized; genital area as in figures 142E, F; 143I, J.

Forewings poorly sclerotized, veins difficult to see (fig. 143H). Venation as in generic description. Setae short and sparse, more numerous along costal margin and veins of disk, and extremely sparse proximally. A few setae contained in lumens of cells.

Forelegs as in figures 143E, 144H. Forefemora bearing setae of one length (fig. 144I); cuticular surface with poorly to well-developed microtrichiae. Ratio length to width of forefemur 1:0.19 (1:0.17–0.23). Ratio length to width of hind femur 1:0.17 (1:0.14–0.20). Ratio length to width of foretibia 1:0.17 (1:0.17–0.24), the apex bearing two to four spines as in figures 143F and 144G. Foretarsus long and slender (fig. 143F), approximately 1.7 times the width of apex of foretibia and bearing no spines.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, USA: CALIFORNIA: *Tulare Co.*: Terra Bella, light trap, May 31 1968 (H. Robinson; AMNH).

PARATYPES: USA: **California:** *Tulare Co.*: Terra Bella, light trap, May 28, 1968 (H. Robinson; AMNH), 1♂, paratype (part on slide; part used for SEM), 1 other male; June 25, 1968 (H. Robinson; AMNH), 1♂; June 27, 1968 (H. Robinson; AMNH), 1♂.

OTHER SPECIMENS EXAMINED: USA. – **California**: *Sacramento Co.*: Rio Linda, light trap, August 5, 1960 (J. Fowler; UCD), 4♂ (1 on slide). *San Diego Co.* La Jolla, UV light, June 25, 1963 (J. Powell; AMNH), 2♂. *San Luis Obispo Co.*: Paso Robles, July 19, 1931 (C. H. Hicks; AMNH), 1♂ (2 legs on slide, also 2 extra wings on another slide). *Santa Barbara Co.*: Santa Barbara, San Roque Canyon, light trap, Sept. 5., 1967 (R. F. Denno; AMNH), 1♂. *Yolo Co.*: 9 mi W Zamora, light trap, August 14, 1959 (J. Fowler; UCD), 1♂; 4 mi SW Dunnigan, light trap, July 14 and 27, 1959 (J. Fowler; UCD), 2♂.

ETYMOLOGY: Named for its occurrence in California.

DISCUSSION: We consider *Urnacephala californica* to be a complex of populations or species that cannot be resolved on the basis of the small number of specimens we have seen. For the most part, there seem to be two easily recognizable groups, one with long, slender proportions (figs. 140–144) and another of shorter fatter form (fig. 145). The holotype from Terra Bella is of the former type. All of the SEMs are of the slender variety from the type locality as well.

The problems with this complex are twofold. Both forms occur sympatrically in Terra Bella. It is not known whether they inhabit different microhabitats, since all specimens were caught at lights. In general, the short,

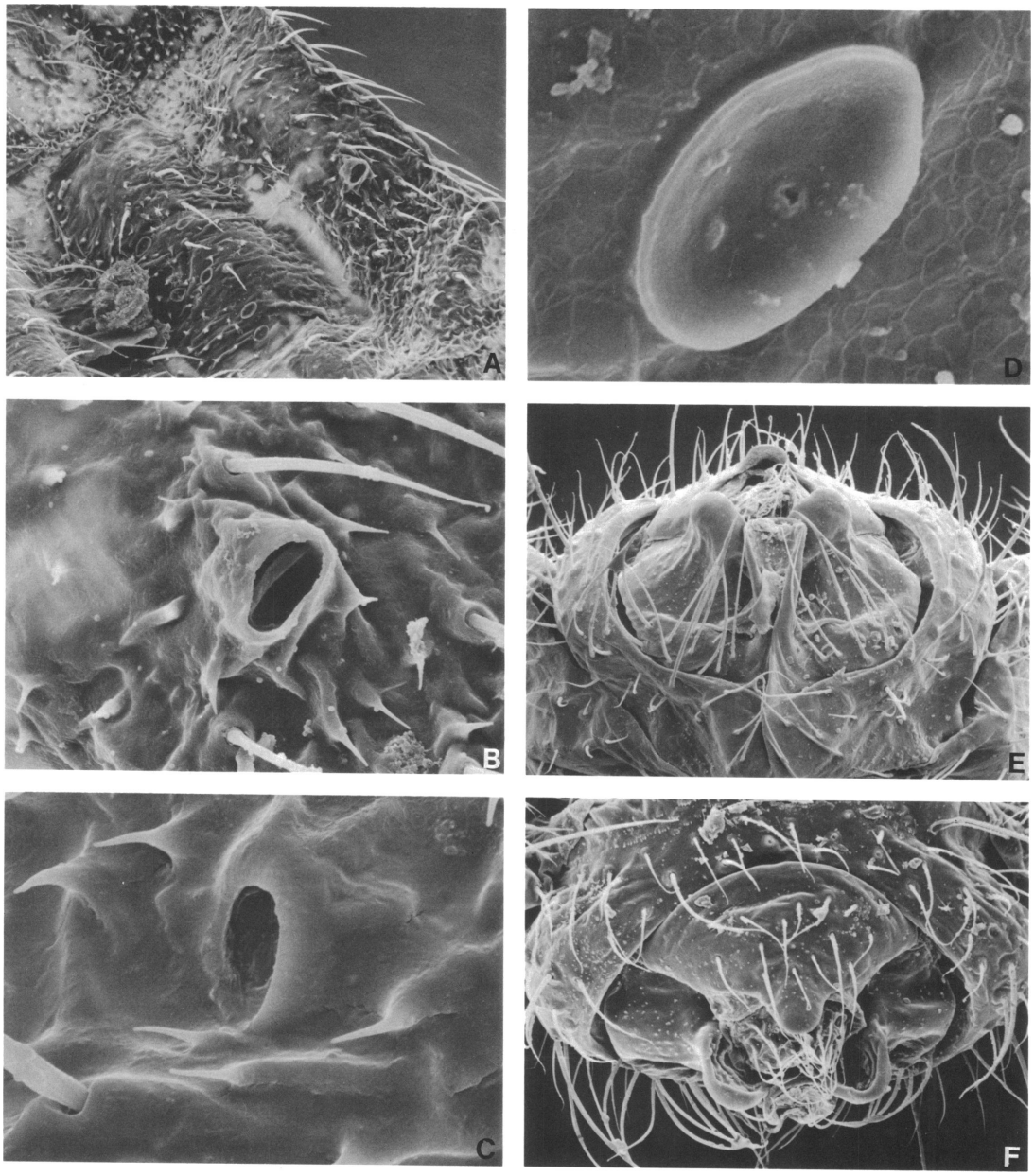


Fig. 142. *Urnacephala californica*, ♂. **A**. Sternum IV and ventral connexival plate. **B**. Detail of photo A showing spiracle. **C**. Spiracle of ventral connexival plate II. **D**. Detail of disk-shaped cuticular structure in photo A. **E**, **F**. Genital capsule, posteroventral and dorsal views, respectively.

fat forms are found farther north than the others (in central California), while the slender ones occur farther south. This may reflect a natural distribution or may be a coincidence of collecting.

The other problem arises with the Dunnigan specimens, which are intermediate in length and proportions. It may be that we are dealing with two fairly well-defined species that have interbred (Dunnigan material). Or, the situation may be more like that of *Hymenocoris formicinus* in which many, somewhat differing, populations seem to exist with varying degrees of overlap in their characters.

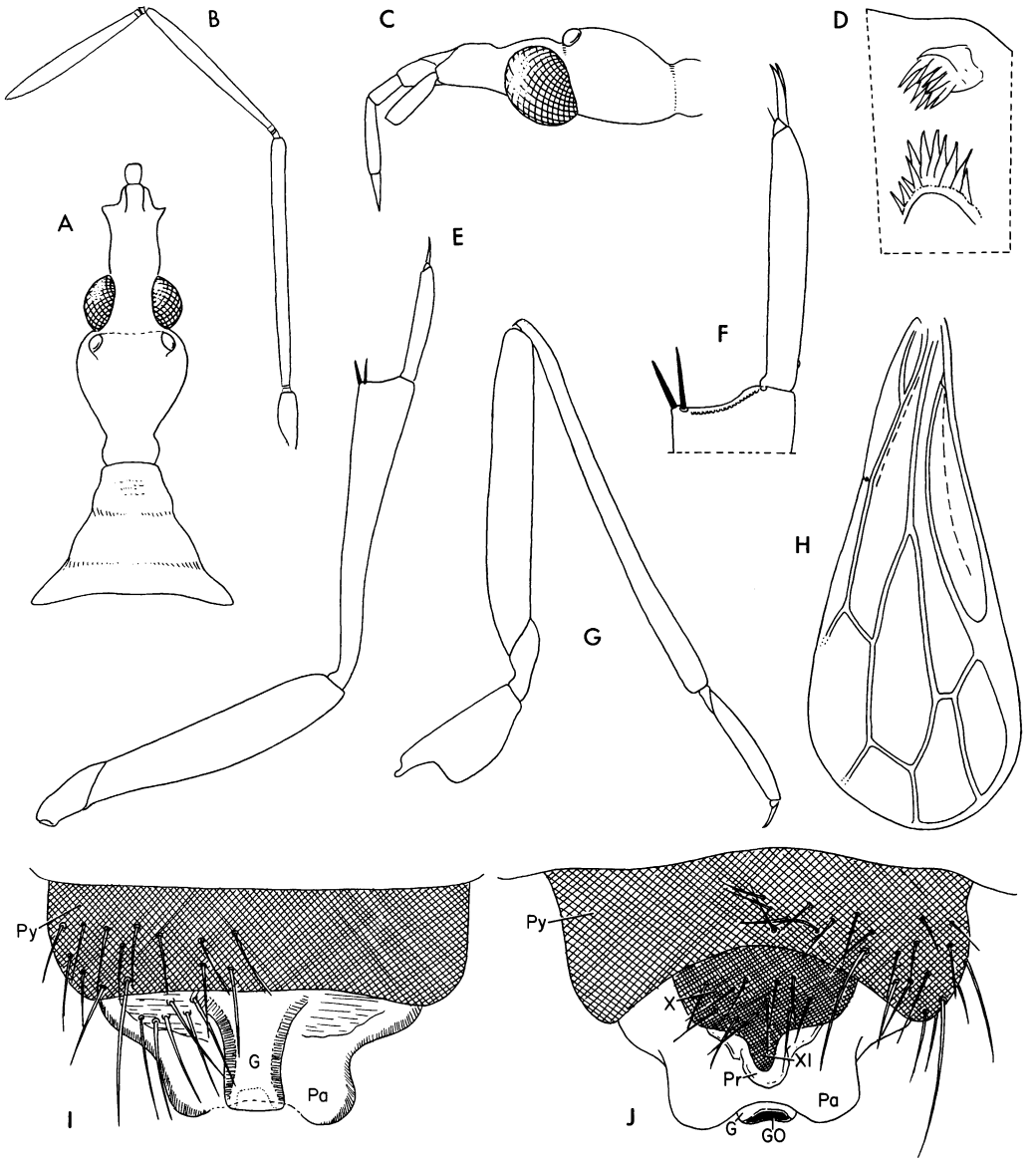


Fig. 143. *Urnacephala californica*, ♂. Holotype, slender form from Terra Bella, California. **A**. Head and pronotum, dorsal. **B**. Antenna. **C**. Head, lateral. **D**. Wing coupling mechanism under hind edge of forewing. **E**. Foreleg. **F**. Apex of foreleg, inner surface. **G**. Hind leg. **H**. Forewing. **I**. Genital region, ventral view. **J**. Genital region, dorsal view.

Xenicocephalus, new genus
Figures 147–150

TYPE SPECIES: *Xenicocephalus giganticus*, new species.

DISTRIBUTION: Southern Central America and northern South America.

DIAGNOSIS: Adults large, at least 8 mm in length. Most of cuticular surface covered with dense tubercles (fig. 148I). Forelegs distinctive as follows: trochanter ventrally with a heavily sclerotized, ridgelike projection (fig. 149E); inner apical angle of tibia in shape of pointed, strongly sclerotized projection bearing 3–5 straight, slender spines inserted sub-

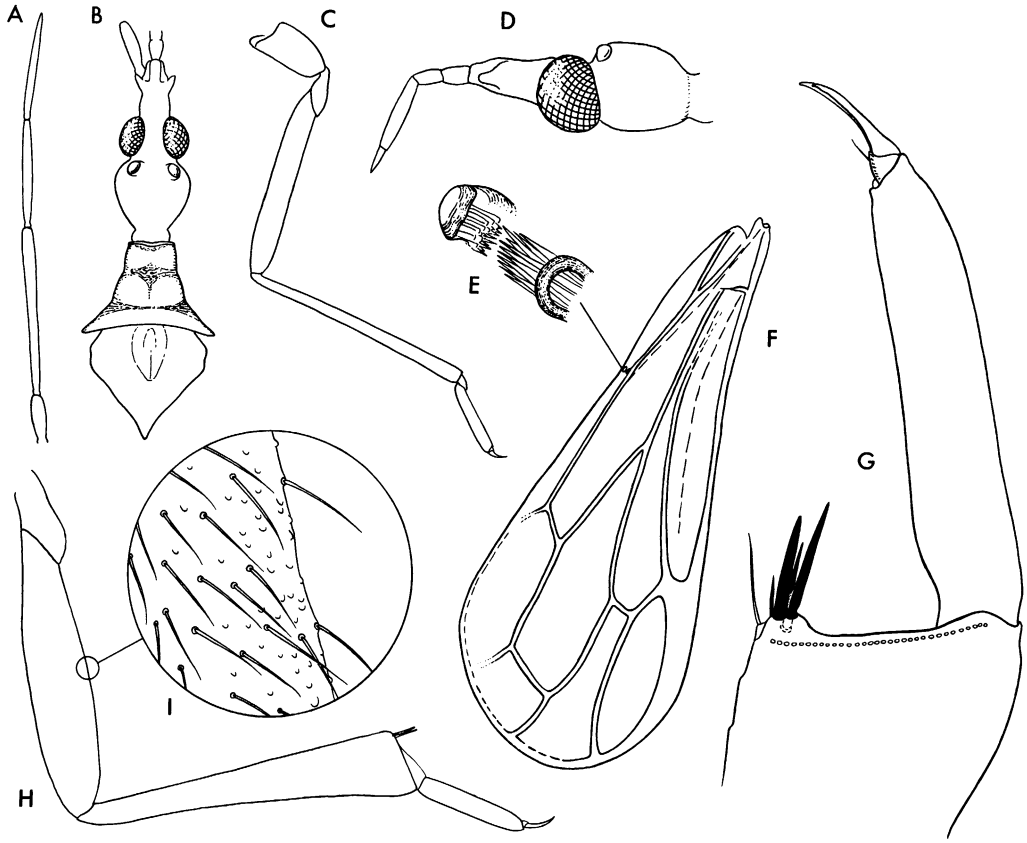


Fig. 144. *Urnacephala californica*, ♂. Slender form from Paso Robles, California. **A**. Antenna. **B**. Head, pronotum and scutellum, dorsal. **C**. Hind leg. **D**. Head, lateral view. **E**. Wing coupling mechanism **F**. Forewing. **G**. Apex of foreleg, inner surface. **H**. Foreleg. **I**. Detail of inner (ventral) surface of forefemur.

apically (figs. 149C, D); and foretarsus bearing one stout claw (figs. 149C, D).

DESCRIPTION: (The adult female holotype is missing the head, pronotum, and forelegs; see description of fifth instar nymph and discussion.) Males unknown.

Adult female. Very large and robust, macropterous. Setae simple, slender. Setiferous tubercles absent. Most areas of body covered with dense cuticular tubercles.

Scutellum broadly triangular with a small apical knob (fig. 148A). Scent gland auricle in shape of a small arched flap on sunken posterolateral ridge behind scutellum.

Forewings macropterous but short, not extending to apex of abdomen (fig. 148A). Basal and discal cells present and closed, the latter pointed apically. Setae arranged randomly on proximal veins (fig. 148C) and two ranked on veins of disc (fig. 148F). A few setae in lumens of cells. Wing coupling mechanism not quite halfway to wing apex. Hind wing as in figure 148B; veins not extending to wing edge. Apex not setose. Costal edge rolled in at level of forewing-coupling mechanism and bearing foliaceous structures. Forewing pads of nymph stout, rounded apically, and meeting medially along posterior half.

Hind legs (fig. 148G) without setiferous tubercles, but with numerous cuticular granules. Hind femur with granules both dorsally and ventrally, but not along center of segment. Setae present and interspersed with smaller microtrichiae of one length. Hind tibiae with two apical bristle combs separated by two spines. Spines even with arc (i.e., neither within arc, nor outside of it) formed by bristle combs. Hind tarsi two-segmented and with two claws.

Abdomen broadly ovate, wider than folded

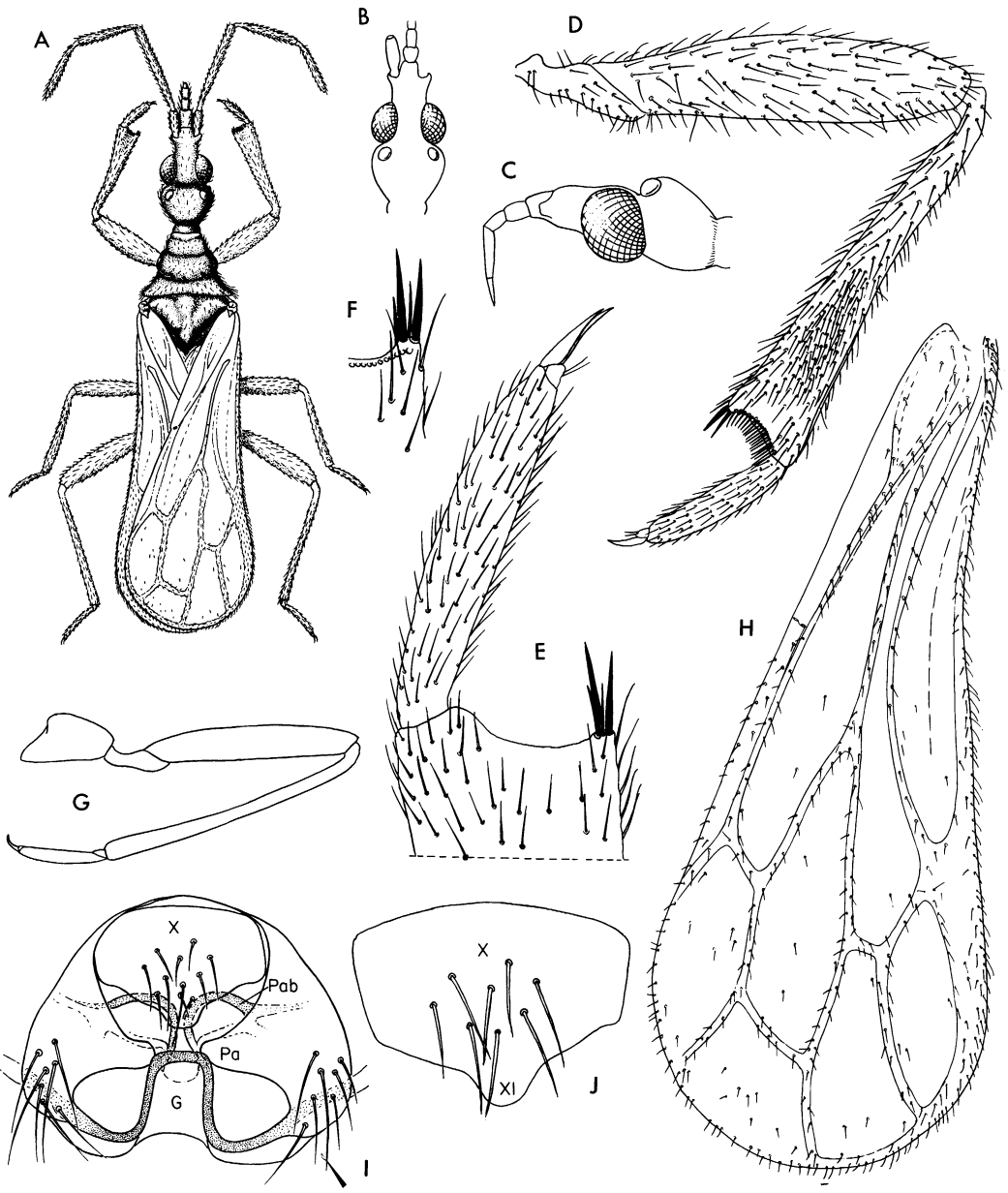


Fig. 145. *Urnacephala californica*, ♂. Stockier form from Rio Linda, California. **A**. Dorsal view. **B**. Head, dorsal. **C**. Head, lateral. **D**. Foreleg, inner surface. **E**. Apex of foreleg, outer surface. **F**. Detail of foretibial spines, inner view. **G**. Hind leg. **H**. Forewing. **I**. Genital region, posterior view. **J**. Fused terga X and XI.

wings, and well sclerotized (fig. 148A). Dorsal and ventral connexival plates separate from one another and also from tergites and sternites. Sternite VIII with a small median, posteriorly projecting tab.

Fifth instar nymph. Head with conspicuous constriction behind eyes (fig. 149A). Posterior lobe globular, slightly wider than long, with a shallow median furrow dorsally. Antennae slender, segments II, III, and IV sub-

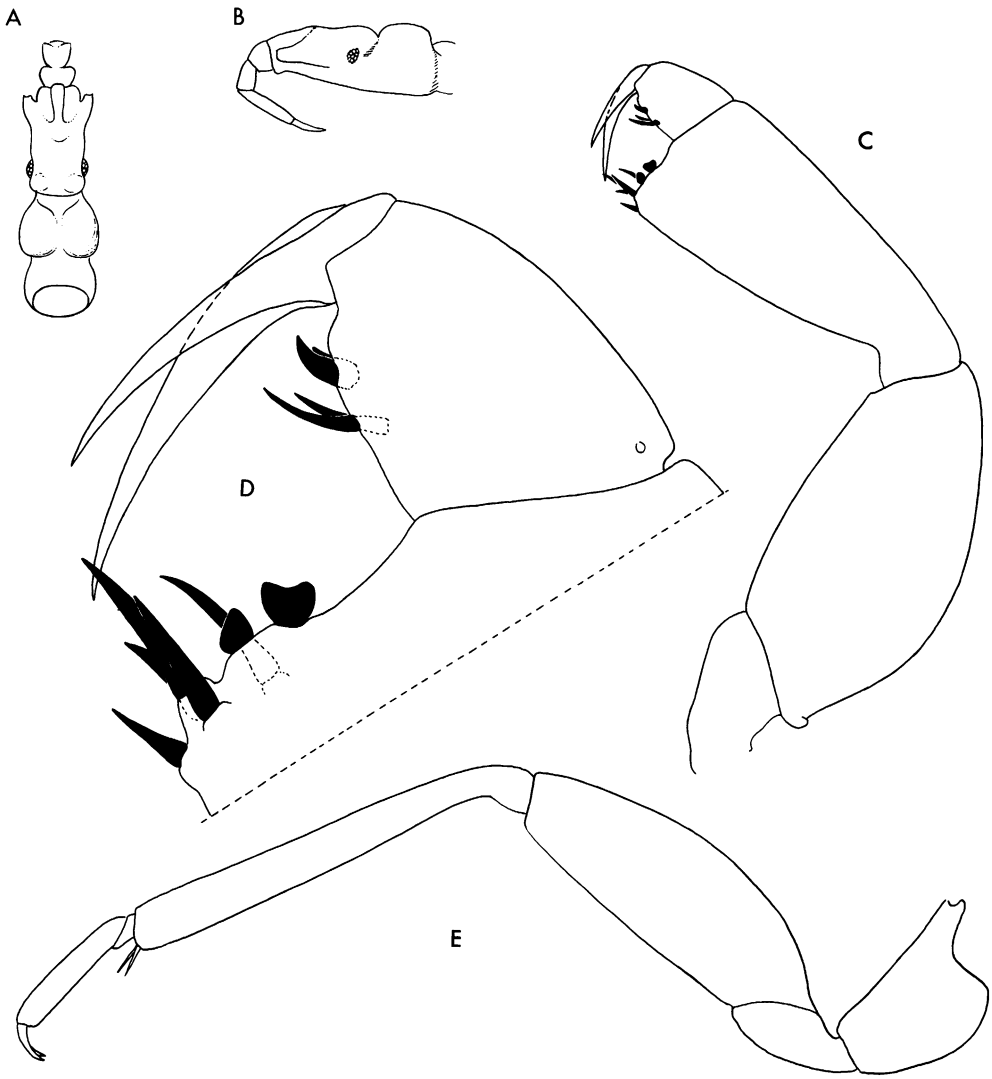


Fig. 146. Very small *Hymenocoris*like female of unknown genus (See discussion under *Urnacephala*). **A**. Head, dorsal. **B**. Head, lateral. **C**. Foreleg, **D**. Apex of foreleg. **E**. Hind leg.

equal in length. Eyes in side view remote from both upper and lower surfaces of head (fig. 149B). Rostrum stout.

Pronotum two-lobed (most likely three-lobed in adults, as in other genera; fig. 149A). Forelobe in shape of wide collar. Hindlobe relatively unsculptured, but with a slight median impression; lateral outline sinuous.

Wingpads apically rounded, meeting at midline along posterior half.

Forelegs, especially femora, moderately stout (fig. 149 E). Trochanter with ventral, heavily sclerotized, ridgelike projection. Forefemur conspicuously curved, bearing dense cuticular granules ventrally and dorsally. Foretibia not as stout; inner apical angle in form of pointed, strongly sclerotized projection bearing 3–5 straight, slender spines inserted below apex. Apex of central portion of inner surface of foretibia with a field of short, stout setae. Foretarsus bearing 1 claw and 4 spines, spines I, II, and IV straight and slender, III short.

Abdomen membranous, but bearing reg-

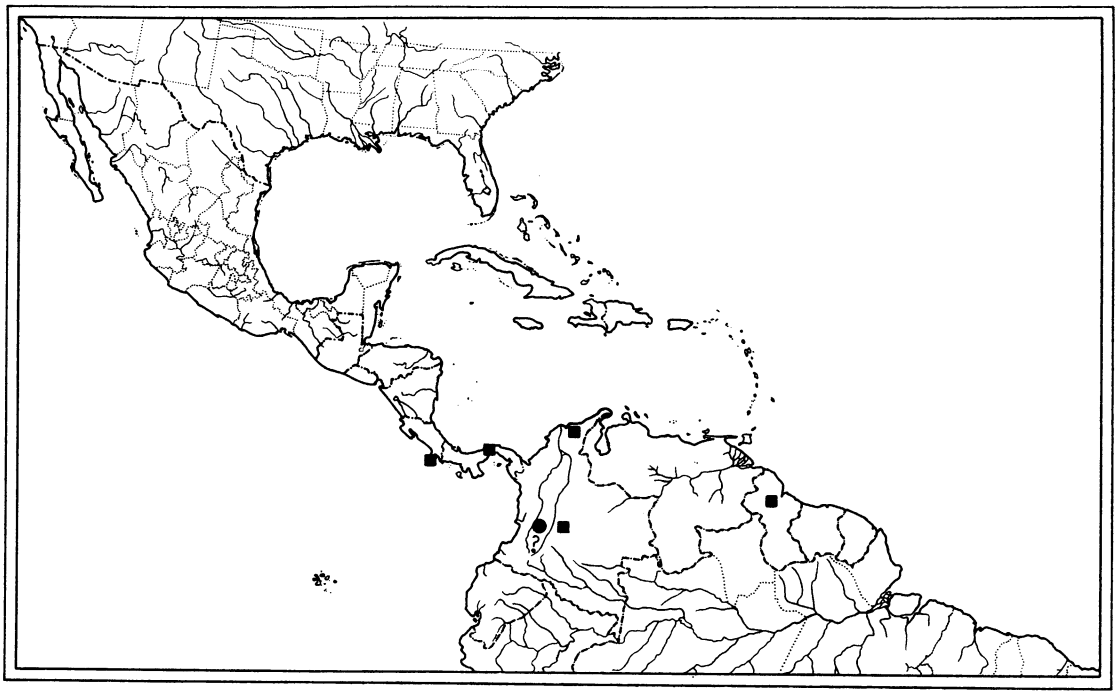


Fig. 147. Distribution of the *Xenicocephalus*. *X. giganticus* (●); *Xenicocephalus* nymphs (■).

ularly arranged sclerotized patches (fig. 149A). Tergites III–VII with 1 + 1 submedian sclerotized patches and an anteriolateral and posterolateral patch on each side (2 + 2). Tergite VIII lacking the 2 + 2 lateral patches. Tergites I and II largely membranous. Sternites III–VII with 1 + 1 submedian and 1 + 1 lateral sclerotized patches. Dorsal and ventral connexival plates separate from one another and delimited, although not separate from lateral sclerotized patches of sternites and tergites. Macrochetae absent.

ETYMOLOGY: *Xenicocephalus* is a contraction of the Greek *xenos*, meaning foreigner or stranger, and *Enicocephalus*.

DISCUSSION: The only known adult of this genus is a female missing its head, pronotum, and forelegs. Descriptions of those parts are taken from a fifth instar nymph, which is clearly congeneric, but may or may not be of the same species. Although this makes for less than an ideal situation, we describe the genus here because it is so distinctive. The extremely large size of the adult and nymphs, and the unique foreleg features make it extremely unlikely that *Xenicocephalus* will be confused with any other taxon.

In most other genera adult females have foretibial spination similar to fifth instar nymphs, so we are assuming that the adult condition in *Xenicocephalus* would be similar as well. The pronotal shape illustrated in figure 149A is neotenous and resembles the shape of the fifth instar nymphs of other Enicocephalinae. The shape of the adult pronotum would probably be more or less like that of *Enicocephalus*.

Affinities of *Xenicocephalus* cannot be established here because of the paucity of material and the absence of a male. The nymphs share with *Enicocephalus* the reduced (or nonexistent) condition of the foretarsal claw. The single foretarsal claw in *Xenicocephalus* is most likely the result of a loss of the outer claw, rather than a fusion of the two claws into one. Microscopic examination of the outer basal area of the remaining claw reveals a small tubercle that is probably a vestige of the outer tarsal claw (fig. 149D). It thus exhibits the ultimate condition of extreme reduction found in *Enicocephalus*. *Xenicocephalus* also shares with the oriental *Megenicocephalus* the extremely large size, the sclerotized projection of the underside of

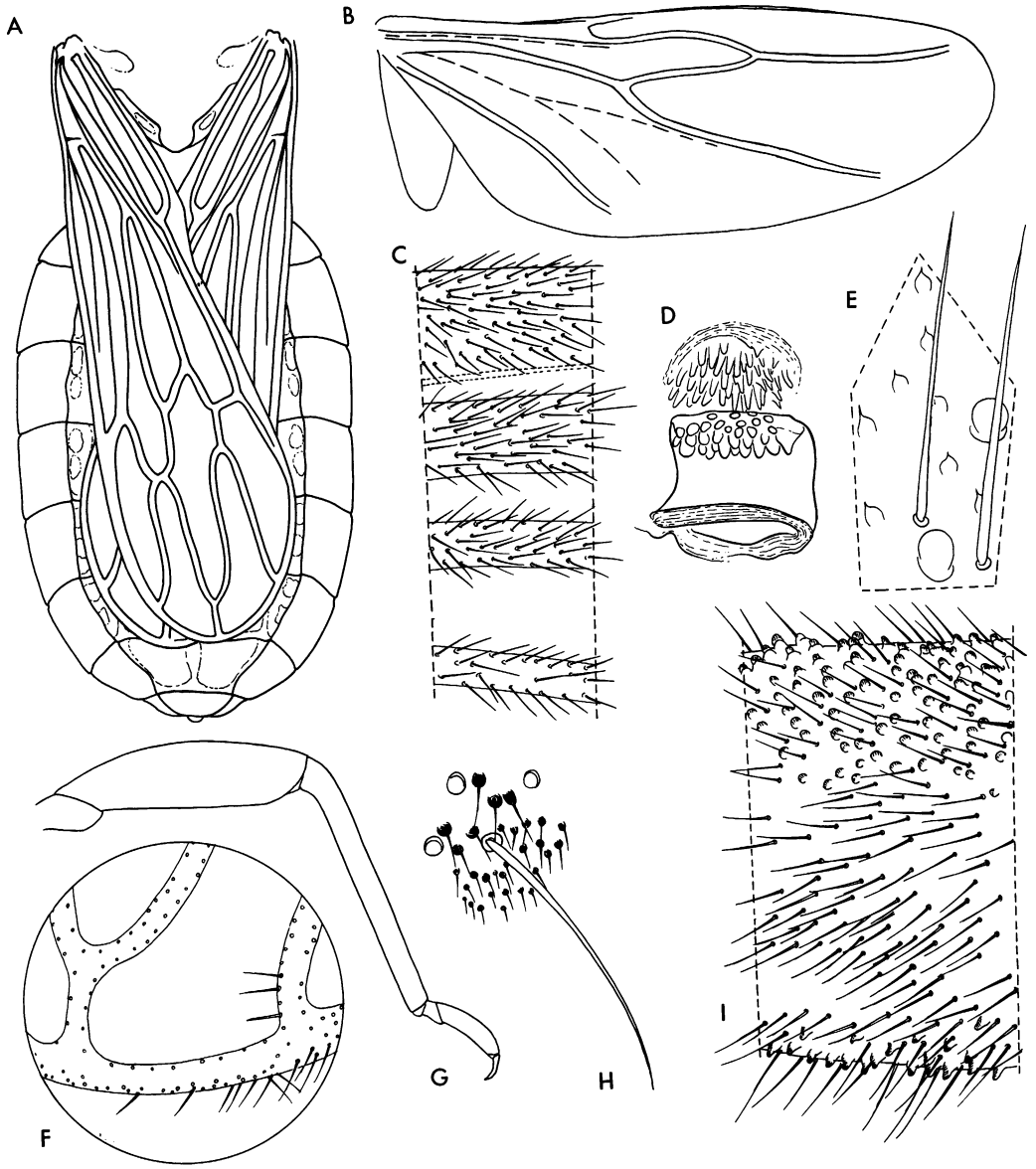


Fig. 148. Adult ♀ of *Xenicocephalus* from Sevilla, Colombia (missing head, pronotum, and forelegs). **A**. Dorsal view. **B**. Hind wing. **C**. Transverse detail of right forewing veins at level of center of basal cell. **D**. Wing coupling mechanism. **E**. Detail of hind femur. **F**. Apex of forewing. **G**. Hind leg. **H**. Detail of forewing. **I**. Detail of hind femur.

the foretrochanter, and the weak and straight foretibial spines, although in other characters the two genera are not very closely related.

Xenicocephalus giganticus,
new species

DISTRIBUTION: Known from only locality in Colombia.

DESCRIPTION: (The holotype of *Xenicocephalus giganticus* is a female missing the head, pronotum, and forelegs.) We add the following details to the generic description.

Length from wing base to apex of abdomen 5.4 mm; length forewing 4.8 mm; length abdomen 3.9 mm.

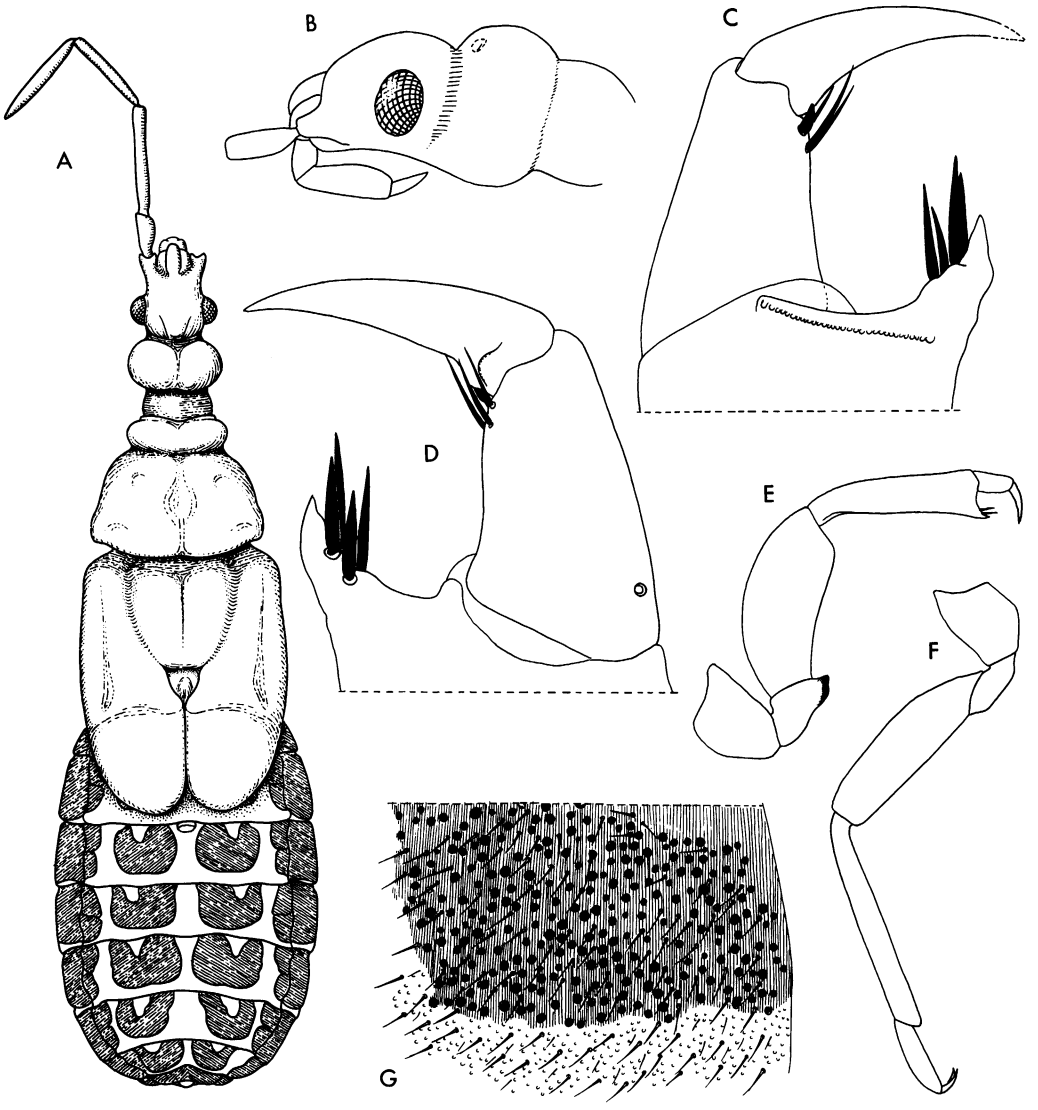


Fig. 149. Fifth instar nymph (probably ♀) of *Xenicocephalus* sp. from San Sebastian de Rabago, Colombia. **A**. Dorsal view. **B**. Lateral view of head. **C**, **D**. Apex of foreleg, inner and outer surfaces, respectively. **E**. Foreleg. **F**. Hind leg. **G**. Detail of sclerotized patch on abdomen.

General body color uniform light yellow brown; forewings slightly darker.

Ratio length to width of hind femur 1:0.29.

HOLOTYPE: Female (missing head, prothorax, and forelegs), COLOMBIA: **Magdalena**: Sevilla [no date] (Darlington; AMNH).

ADDITIONAL MATERIAL EXAMINED: COLOMBIA. – **Santa Marta**: Sierra Nevada de Santa Marta, San Sebastian de Rabago, 2000 m, April 1–10, 1968 (Malkin; AMNH), 1 female nymph, fifth instar (specimen used for description of fifth nymph). **Cundinamarca**: Monteredondo, E slope of the E Cordillera, mountain forest between Bogota and Villavicencio, 1700 m, December 2, 1955 (H. Sturm; AMNH), 1 nymph. PANAMA. – **Canal Zone**: Barro Colorado Island, October–November, 1941 (Jas. Zetek; AMHN), 1 nymph, early instar. COSTA RICA. – Rincon de Osa Pensinsula, July 14–26, 1969 (R. T.

Fig. 150. Early instar nymph of *Xenicocephalus* sp. from Barro Colorado Island, Panama. **A**. Lateral view. **B**. Apex of foretrochanter. **C**. Foreleg, outer surface. **D**. Detail of spicules of inner surface of foretibia. **E**. Claw of hind tarsus. **F**. Hind leg.

Schuh and J. Crane; AMNH), 1 nymph, early instar. GUYANA. – **Mazaruni-Potaro District**: 0.5 mi up Awhyape Creek on Cuyuni River, June 19–28, 1986, ex pitfall trap in lowland riverine forest (K. and R. Schmidt; AMNH), 1 nymph, 3rd or 4th instar.

DISCUSSION: We have not been able to locate "Sevilla" in Magdalena Province, and therefore consider the exact position of the type locality to be uncertain.

ALIENATINAE

Alienates Barber

Alienates Barber, 1953: 2. — Štys, 1978: 243. — Kritsky, 1981: 130. — Vasarhelyi, 1982: 158.

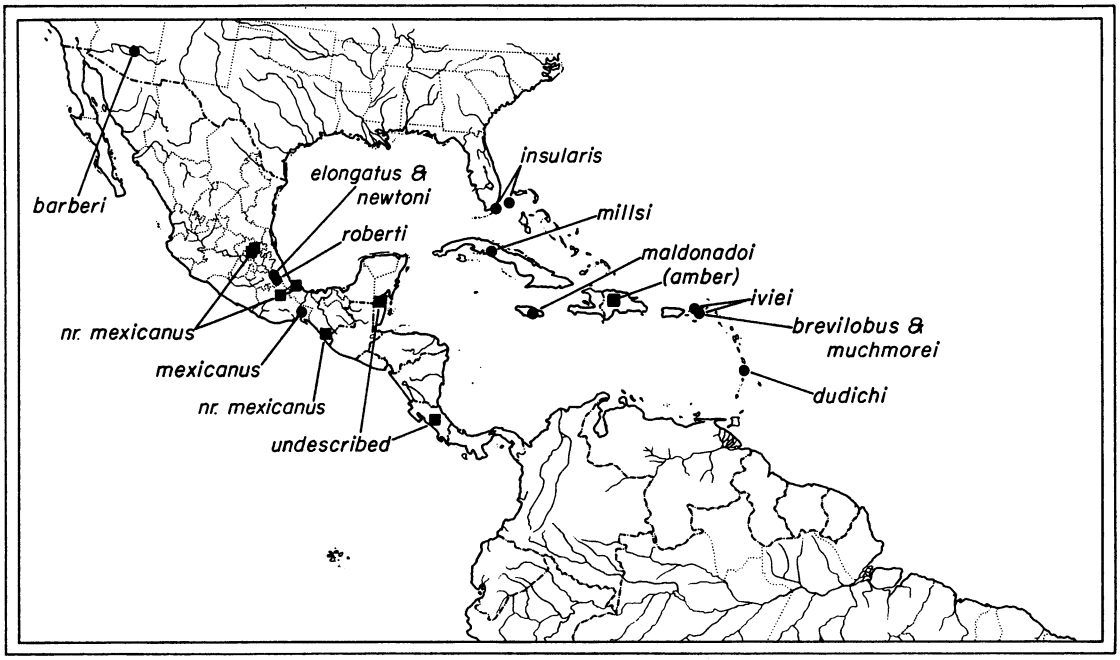


Fig. 151. Distribution of *Alienates*. Described species (●); undescribed, (■).

— Wygodzinsky and Štys, 1982: 127–128, 130, 134–135, 141.

TYPE SPECIES: *Alienates insularis* Barber. Fixation by monotypy.

DISTRIBUTION (fig. 151): Central America and Caribbean. The Central American component occurs predominantly in southern Mexico, with an undescribed species from Belize. The Caribbean component extends from the Florida Keys and Bahama Islands (type locality) through the Greater and Lesser Antilles, where the southernmost record is the Island of St. Lucia. In addition, one species has been described from an arboretum in Arizona. There are also two specimens in Dominican amber (not described here).

REDESCRIPTION: Very small species (2.1 mm or less). Strongly sexually dimorphic; males macropterous, with normal eyes and ocelli; females apterous, and lacking eyes and ocelli, with many associated morphological differences. Body slightly polished, on various areas with groups of minute cuticular granules, varying from globose to toothed (fig. 155F). Setiferous tubercles present in some species, especially on legs of males (fig. 152D–F). Setae simple, slender in females, those of legs of males sometimes barbed, with an auxiliary spine on basal tubercle.

Macropterous male. Head short; constriction behind eyes distinct (fig. 152A). Eyes well developed, closely approaching on under surface of head. Ocelli large. Antennae incrassate, equal to or slightly longer than head and pronotum combined; third segment shorter, fourth longer than second, fusiform (fig. 152B). Rostrum short and stout.

Pronotum unarmed, trapezoidal, with shallow transverse depression on anterior third (fig. 153A). Scutellum subtriangular, much wider than long. Anterior acetabula open behind.

Forelegs moderately thickened. Tarsi of all pairs of legs one-segmented. Foretarsus three-fourths as wide as long; tarsal organ situated on outer surface close to dorsal surface of article. Tarsal spines absent (fig. 152D–F). Foretarsus with two claws, the inner one distinctly longer than the outer (fig. 152D). Inner apical angle of foretibia with two, or sometimes three, straight spines (fig. 152D, E). Foretibia and sometimes femur with expanded setal insertions, often produced into spines (fig. 152F). Apex of mid and hind tibiae with two spines and two bristle combs

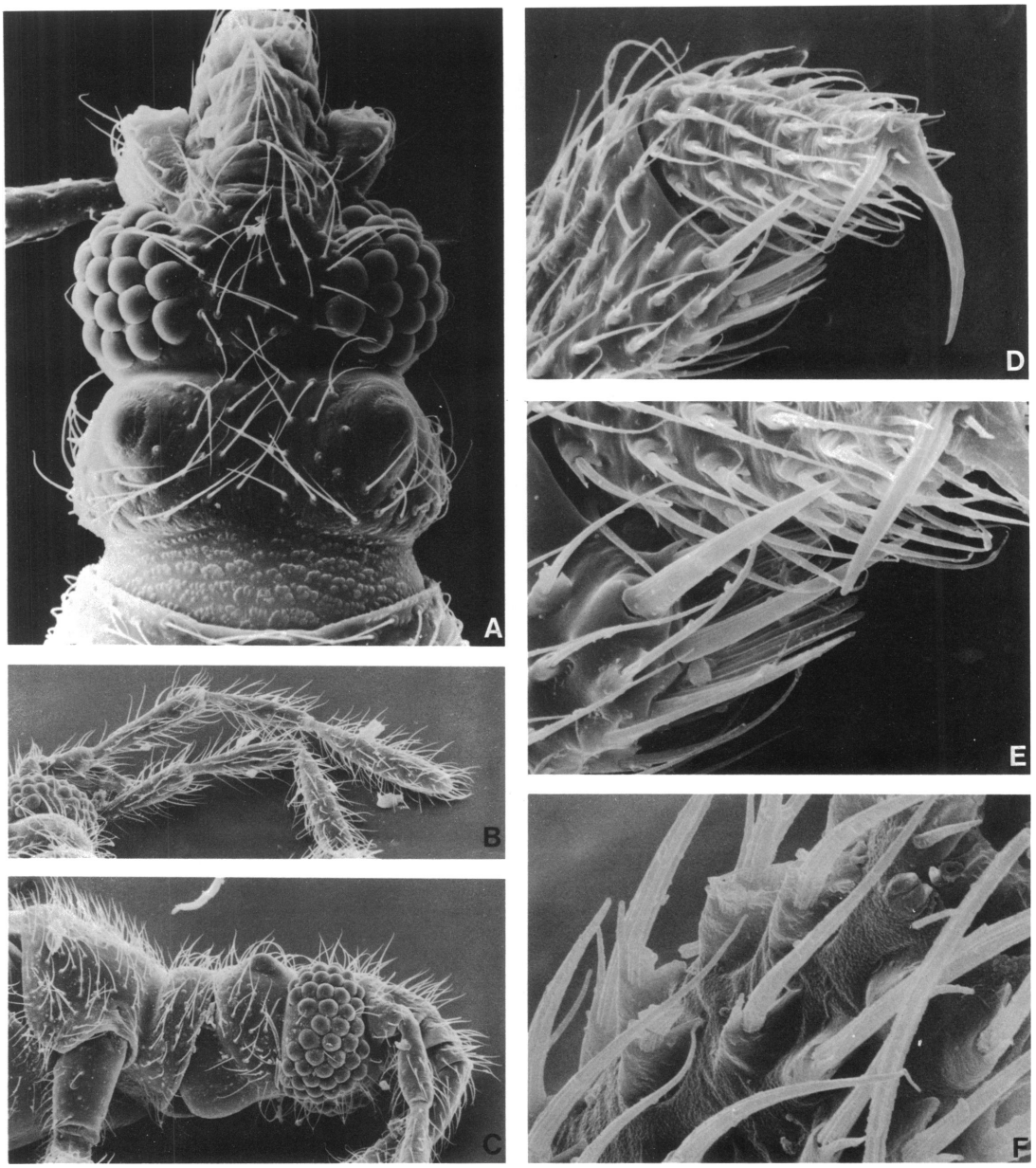


Fig. 152. *Alienates millsi*, ♂. **A**. Head, dorsal. **B**. Antennae. **C**. Head and pronotum, lateral. **D**. Apex of foreleg. **E**. Foretibial spines. **F**. Detail of inner surface of foretarsus, showing setae with basal spines and lack of foretarsal spines.

(fig. 154A). Tarsi of mid and hind legs subconical, much wider at base than at apex. Claws slightly dissimilar in size.

Forewings fully developed but with venation reduced, consisting of one marginal (C+Sc of Štys, 1980) and one submedian (M + Cu) longitudinal vein, connected or not by a transverse vein (r-m) shortly beyond middle of forewing (fig. 6C). Setae numerous on marginal vein, arranged in two series on submedian vein; shorter setae also present on membrane between submedian vein and hind

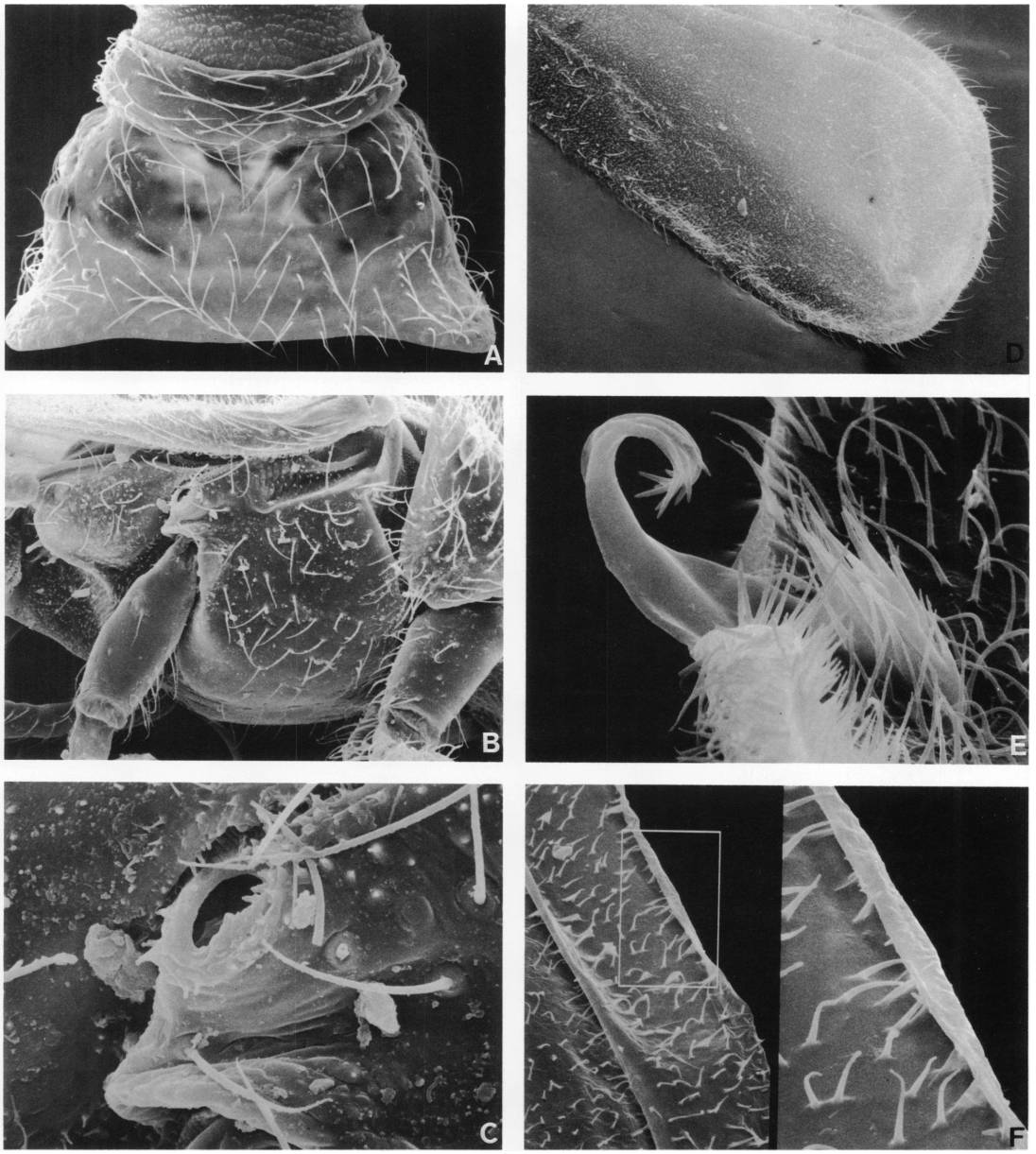


Fig. 153. *Alienates millsi*, ♂. **A**. Pronotum, dorsal. **B**. Meso- and metathorax, lateral (anterior to right). **C**. Detail of above, showing spiracle. **D**. Forewing. **E**. Wing coupling mechanism on hind edge of forewing. **F**. Edge of hind wing at level of wing coupling mechanism.

margin of forewing. Coupling mechanism of forewings (fig. 153E) situated on basal fourth of hind margin of wing, much closer to base than usual for the family. Hind wing of normal size, but lacking veins except for some longitudinal thickenings near base. Membrane of hind wing with scattered short setae; longer setae along margin, especially on apical portion of wing. Anal lobe not developed. Costal edge of hind wing rolled inward at level of wing coupling mechanism (fig. 153F), presumably catching hook from forewing.

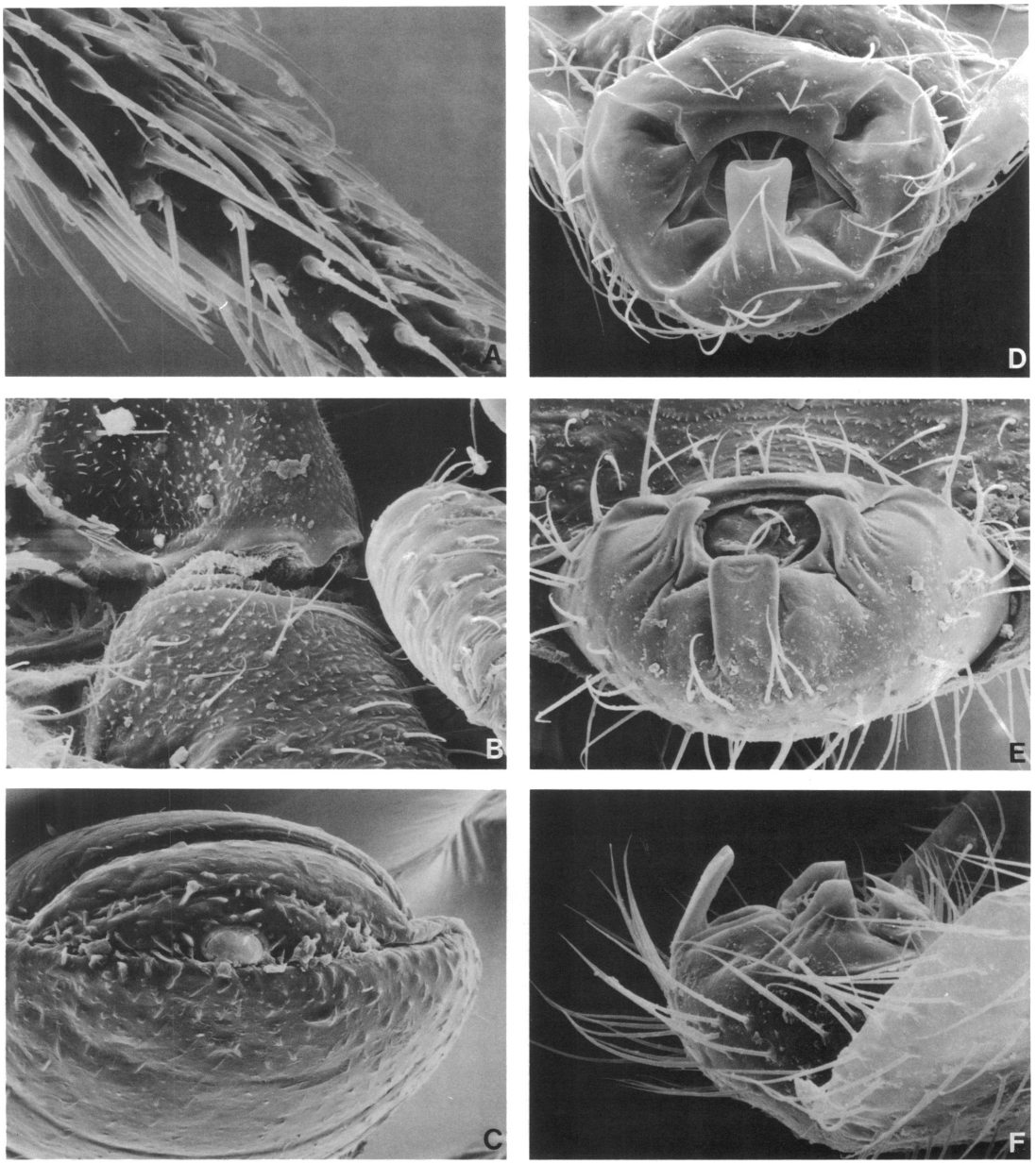


Fig. 154. *Alienates* spp. **A**, **B**. *A. millsi*, ♂. **A**. Apex of hind tibia, showing bristle comb and two spines. **B**. Thoracicoabdominal junction, ventral. **C**. *A. insularis*, ♀, apex of abdomen. **D–F**. *A. millsi*, ♂, genitalia. **D**, **E**. Posterior view of two different specimens. **F**. Lateral.

Abdomen relatively wide and short, ovoid (except in *A. elongatus*) equally sclerotized dorsally and ventrally; connexivum developed dorsally and ventrally.

Pygophore small, subtrapezoidal as seen from behind (fig. 154D). Guide small, pointed, truncate, or rounded apically, with opening variously placed on posterior surface (fig. 154D–F).

Apterous female. Head short, with two transverse constrictions (fig. 155A). Eyes absent, or occasionally represented by a few pig-

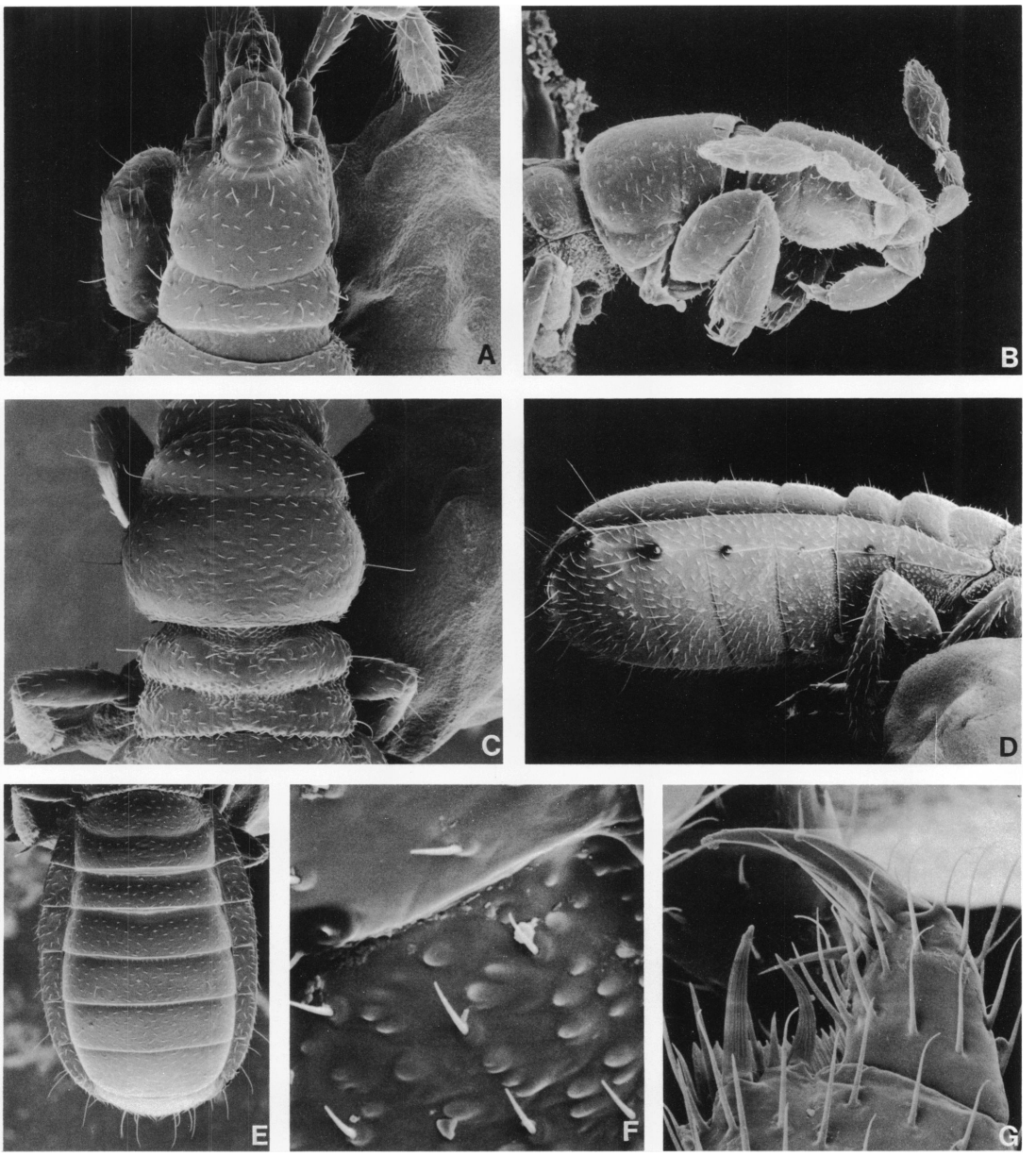


Fig. 155. **A, C–G.** *Alienates brevilobus*. **B.** *Alienates insularis*. **A.** Head, dorsal. **B.** Head and pronotum, lateral. **C.** Thorax, dorsal. **D.** Abdomen, lateral. **E.** Abdomen, dorsal. **F.** Detail of sternum IV and ventral connexival plate. **G.** Apex of foreleg.

mented spots or ommatidia. Ocelli absent. Antennae incrassate, shorter than, or equal to length of head and prothorax combined (fig. 155B), their general structure as in male. Rostrum as in male.

Pronotum divided into two lobes by a transverse constriction on anterior third (fig. 155C); hind lobe of pronotum with sides angularly salient, widest shortly behind middle. Mesonotum and metanotum short, transverse; combined length shorter than pronotum. Anterior coxal cavities open behind.

Tarsi of all legs one-segmented. Forelegs similar to those of male, but slightly stouter. Inner surface of forefemur granulose. Inner apical angle of foretibia with five spines (figs. 10C, 155G), possibly homologous with spines III, IV, V, VI and VII of the generalized type. III long and slender, straight; IV elongate-conical, stout; V very slender, slightly curved; VI stout, but narrowly pointed at apex, strongly curved, almost sickle-shaped; VII much shorter than the remaining, wide at base, tapering to a narrowly pointed apex. Tarsus very short, about as long as wide; tarsal organ situated on dorsal surface close to dorsum of article. Four or five tarsal spines present (fig. 155G), all slender and of varying lengths, with the exception of one (possibly III of generalized type) which is much stouter than the remaining, almost as long as large claw. Claws of forelegs and general structure of mid and hind legs as in male, but under surface of femora with a few cuticular granules.

Abdomen much wider than thorax, heavily sclerotized (fig. 155E). Connexival plates developed dorsally and ventrally (figs. 155D, E). Spiracles usually on ventral connexival plates III–VII, although occasionally on sternites or in intersegmental membranes (fig. 155D). Anterior third of terga and sterna with minute tubercles, more or less numerous depending on species. Posterior two-thirds of sclerites with scattered short setae. External genitalia not developed.

Fifth instar nymph, male (fig. 170A). General shape stout. Eyes obsolescent. Antennae stout. Neck short but distinct. Mesothoracic wing pads meeting medially, longer than wide, truncate or slightly rounded posteriorly. Armature of foretibia and tarsus as in adult female (fig. 170B). Abdomen strongly sclerotized, terga with short setae of uniform size. Macrochaetae arranged as in adult and nymphal females.

Fifth instar nymph, female (fig. 170D). General shape stout, very similar to that of adult. Eyes obsolete. Antennae stout. Neck short but distinct. Meso- and metanotum in shape of transverse bands. Wing pads absent. Forelegs as in adult female (fig. 170E). Abdomen heavily sclerotized, but membrane distinct between second and third, and third and fourth segments. Sternum of second segment not fused to ventral connexival plates. Spiracles situated on ventral connexival plates of third to seventh segments. Terga with short setae of uniform size, or, in some species, with 2 + 2 macrochaetae near posterior border.

DISCUSSION: This genus is very distinctive; Barber (1953) erected for it a separate subfamily, the Alienatinae. Among the most striking characters are the small body size, the one-segmented tarsi of the adult, the apterous and (nearly) eyeless condition of the females and the reduced venation of the forewing in the males. (For a discussion of the phylogenetic affinities of the Alienatinae, see under Genitalia, Homologies, and Phylogeny of New World Taxa.)

It seems appropriate to discuss the subject of intraspecific variation here, since we have incurred difficulties with such variation throughout this genus. We have done several small studies with the females of *Alienates insularis*, *A. maldonadoi*, and *A. muchmorei* using the characters of gular shape, shape of the posterior border of the head, thoracic keel shape, spiracle placement, and abdominal segmentation.

The variation in the shape of the gula and the posterior border of the head were studied using *A. insularis* and supported with additional information from *A. maldonadoi* (see Discussion and figures under *A. insularis*; figs. 164A–L). The *insularis* specimens were all from South Bimini Island, collected in two separate months; the *maldonadoi* specimens were from three different localities in Jamaica. Although we had too few specimens for a numerically sound conclusion, we could see that the gular shape varied substantially, and could not be correlated with collection locality, date, or any other observable parameter. Variation existed, but was less conclusive, in the shape of the posterior lobe of the head (figs. 164M–X). The above two characters should probably not be used as specific characters, or if so only with the greatest of caution, since overlap between specimens of otherwise distinguishable species does occur.

We also looked at thoracic keel shape of our specimens of *A. mexicanus* (fig. 169) and specimens we labeled "near *mexicanus*" from five other localities in southern Mexico. The shapes in the *mexicanus* specimens were sim-

ilar, but the near *mexicanus* specimens varied considerably and failed to fit into clearly separable categories. We could reach no conclusion on the validity of this structure as a character and feel that further study is required.

Spiracle placement and abdominal segmentation are also highly variable in females of *A. insularis* and *A. maldonadoi* (see also discussions under individual species). *Alienates insularis* exhibits the most common condition for *Alienates*, i.e., spiracles on ventral connexival plates III–VII, and nonfusion of sternum II and its corresponding ventral connexival plates. Many *insularis* specimens vary considerably from this pattern (fig. 163). Some spiracles were found in the intersegmental membranes, and one specimen had an extra spiracle on ventral connexival plate II (not ordinarily present). They are not always bilaterally symmetrical either: *A. maldonadoi* shows extreme plasticity in these two characters as well (figs. 166H–M); *A. dudichi*, on the other hand, has all spiracles on its sterna.

The most striking example of inconsistent spiracle placement is of two specimens, collected together in the same lot, which show tremendous extremes. The holotype of *A. maldonadoi* (fig. 166H) has a nearly normal arrangement of spiracles and segmentation, but the other specimen (fig. 167I) has spiracles on sterna III–VII with one spiracle on segment III in the intersegmental membrane, spiracles on segment II, and no division between ventral connexival plate and sternite II. Five specimens from other localities in Jamaica have various conditions that fall between the two. On the whole they are most similar to the holotype.

The plasticity in the characters discussed above, and many others, is a problem when delineating species of *Alienates*. Add to this the reduction and fusion of sclerites, and the generally uninformative condition of the genitalia, and it becomes even more difficult to distinguish between superficially similar groups of specimens. It may well be that many isolated populations are somewhere in the midst of the speciation process and are not yet well differentiated from one another. These are small insects with limited mobility and could possibly achieve isolation from one another in rather short geographical distances.

Ideally, future collections should include many specimens from closely spaced localities. These should be carefully analyzed for their limits of variation before naming species. In general we have named only species that have some striking character, such as color pattern, extraordinary proportions, or very different wing venation.

Note: Since females of this genus are so different from most other enicocephalids, we have made a different set of measurements for them. See figures 4C and G for an explanation of the measurements.

UNDESCRIBED MATERIAL: We have seen a male from Belize which is missing its forewings. It has a long slender guide. In addition, we have examined two male specimens in amber from the Dominican Republic.

KEY TO MALES OF *ALIENATES*

1. Length less than 1.50 mm. Forewings with four veins (fig. 156E). Guide spoon-shaped, rounded at tip (fig. 156B) .. *barberi* Kritsky
   Length 1.50–1.70 mm. Forewings with two or three veins (figs. 160F, 171G). Guide either truncate or pointed at tip (figs. 154E, 160D) 2
2. Forewings with three veins (fig. 160F). Guide pointed at tip (fig. 160D). Tergum X convex behind. Eyes slighly narrower than in *millsi*; ratio eye width to synthlipsis 1:1.8. Eyes only slightly excavated behind in side view .... *insularis* Barber
   Forewings with two veins (fig. 171G). Guide truncate at tip (figs. 171J, K). Tergum X concave behind. Eyes wider than in *insularis*; ratio eye width to synthlipsis 1:1.4. Eyes deeply emarginate behind ..... *millsi* Kritsky

KEY TO FEMALES OF *ALIENATES*

1. Body distinctly bicolorous. Meso- and metathorax and band on segments IV–VI dark brown, sharply contrasting with lighter brown of rest of body ..... *muchmorei*, n. sp.
   Body unicolorous, or nearly so. Appendages usually slightly lighter than rest of body, but no area sharply contrasting with any other 2
2. Length 1.20 mm or less 3
   Length 1.28 mm or more 5
3. Spiracles on ventral connexival plates (fig.

165E). Color light chestnut brown (a warm brown with no grayish tint) 4

Spiracles on sterna III–VII (fig. 158C). Pale straw colored with a distinct grayish-brown tinge. Length (average) 1.16 mm. Ventral connexival plate II fused with sternite II (fig. 158C). Dorsal connexival plate VIII twice as long as wide, and half the length of tergum VIII ..... *dudichi* Vasarhelyi

4. Length 1.00–1.10 mm. Abdomen slender; ratio length to width 1:0.4. Hind lobe of head of normal length (fig. 165A); ratio length to width 1:2.7. Meso- and metanotum (taken together) 1.6 times wider than long, more square than in *newtoni*; foretibial spines typical for genus (figs. 165B, C) ... *iviei*, n. sp.

Length 1.17–1.20 mm. Abdomen more ovate; ratio length to width 1:0.7. Hind lobe of head extremely short and transverse (fig. 173E); ratio length to width 1:6. Meso and metanotum (taken together) 2.8 times wider than long, more transverse than above. Spine on foretibia closest to tarsus, elevated slightly on a pedestal, and spoon-shaped (figs. 173B, D) ..... *newtoni*, n. sp.

5. Hind lobe of head very short; ratio length to width 1:4.3 (fig. 157A). Length 1.5–1.6 mm ..... *brevilobus*, n. sp.

Hind lobe of head longer; ratio length to width varies from 1:2.2 to 1:3.3 (fig. 159A). Length variable 6

6. Length 1.65 mm. Body very elongate. Abdomen long and narrow; ratio length to width 1:3.1 (figs. 159A, D, F). Fused meso- and metanotum nearly square (dorsal view); ratio length to width 1:1.3. Basal two-thirds of abdomen covered with large cuticular granules. No pigmented eye spots .... *elongatus*, n. sp.

Length variable, from 1.30–1.80 mm. Body not elongate; abdomen ovoid. Fused meso- and metanotum more transverse; ratio length to width 1:1.9 or more. Abdomen not densely covered with cuticular granules, but some may be present, especially on intersegmental membranes. Eye pigments variable 7

7. Large species, 1.80–2.10 mm. Foretibia extremely stout; ratio length to width 1:0.56; apical end flared, bearing a stout spine on a pedestal (figs. 174C, D). Outer claw small, about one-third length of inner claw (fig. 174D). Ratio length to width of fused meso- and metanotum 1:1.9. Sterna II–VI faintly divided centrally. Dorsal connexival plate VIII more than twice as long as wide, as long as tergum VIII ..... *roberti*, n. sp.

Medium-size species, 1.60 mm or less. Foretibia less stout; ratio length to width 1:0.38 to 1:0.43. Foretibial and tarsal spines unremarkable, as in generic description. Outer claws of foretarsus at least half as long as inner claws (fig. 166E). Shape of dorsal connexival plate VIII variable 8

8. Color medium brown to darker chestnut brown. Eye spots absent. Lateral outline of pronotum gradually expanding, not abruptly steplike (fig. 167B). Abdomen stout, broadly ovate, ratio length to width 1:0.63 or stouter (figs. 167I, J). Apodemes on abdominal sternum III straight and flat, widely divided centrally (fig. 167J) ..... *maldonadoi*, n. sp.

Color yellowish brown. Eye spots present or absent. Lateral outline of pronotum either gradually expanding or steplike. Abdomen ovate, ratio length to width 1:0.59 or narrower. Apodemes on sternum III distinctly wavy or rectangular, narrowly divided centrally (figs. 162F, 168H) 9

9. Eye spots present (fig. 168A). Lateral outline of pronotum abruptly steplike (fig. 168A). Apodemes on abdominal sternum III wavy (fig. 168H) ..... *mexicanus*, n. sp.

Eye spots absent (fig. 162A). Lateral outline of pronotum gradually widening. Apodemes large, distinctly rectangular, narrowly divided centrally (fig. 162F) ... *insularis* Barber

Alienates barberi Kritsky

Figures 151, 156

Alienates barberi Kritsky, 1981: 130–132.

DIAGNOSIS: Males of *Alienates barberi* can be distinguished by the spoon-shaped (rounded) tip of the guide (fig. 156B), and by the unique wing venation (fig. 156E).

ADDITION TO ORIGINAL DESCRIPTION: Females unknown. Male: Cuticular granules present on gula, antenniferous tubercles, and undersides of prothorax. Eyes large in side view, with ommatidia missing along middle of posterior border, but with pigmented area present, making hind border of eye appear normally convex (fig. 156A). Foretibia with three major spines and approximately 15 bristles in bristle comb. Foretarsus with spines thin and nearly indistinguishable from setae (figs. 156C, D). Outer claw relatively long, about two-thirds length of inner claw (fig. 156C). Guide rounded apically, spoon-shaped (fig. 156B). Setae sparse on wing veins, more numerous on distal portion of wing, and absent from membranes (fig. 156E).

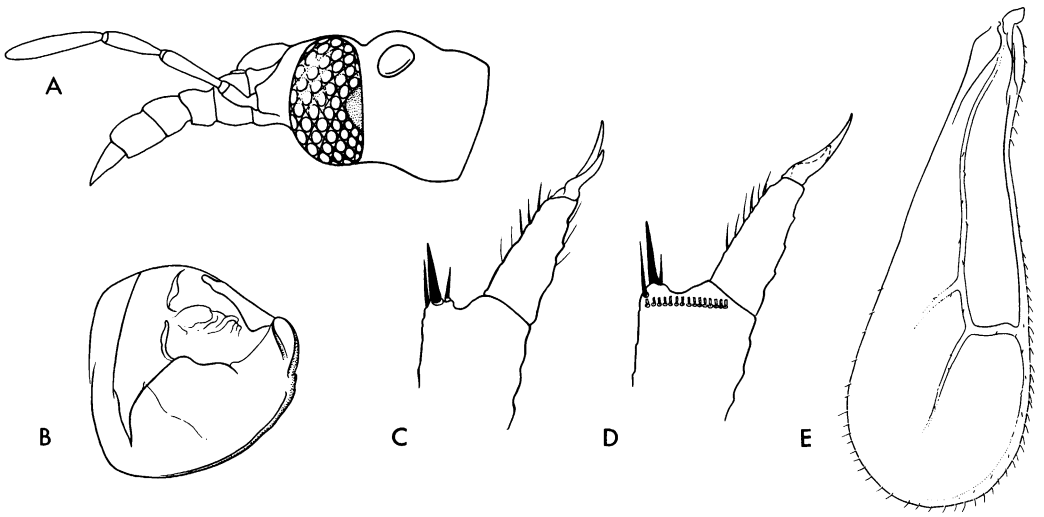


Fig. 156. *Alienates barberi*, ♂. **A**. Head, lateral. **B**. Genital capsule, dorsolateral view. **C**, **D**. Apex of foreleg, outer and inner views, respectively. **E**. Forewing.

Ratio head length to pronotum length 1:0.8. Ratio length of eyes to anteocular distance 1:0.6. Antennae longer than head plus pronotum (1:0.8); ratio segments I–IV 1:1.5:1.5:2.7.

Ratio length of forelobe of pronotum to length of hind lobe 1:2.3.

Ratio length to width of forefemur 1:0.25; ratio length to width of foretibia 1:0.26. Ratio length to width of hind femur 1:0.23.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, USA: Arizona; Pinal County, Boyce Thompson Arboretum near Superior, at light, October 3, 1949 (B. W. Benson; INHS); examined.

MATERIAL EXAMINED: Holotype, above.

DISCUSSION: This species occurs in a locality quite far removed from the remainder of the genus, giving rise to questions about its area of natural occurrence. On one hand, its presence in Arizona may reflect the natural distribution of the genus and the possibility that northern Mexico has been very poorly collected. This is a likely possibility, since the specialized techniques of leaf litter collecting (for females) are infrequently employed. However, in this case, it would be odd that more males have not been caught at lights.

On the other hand, we could also speculate that this species has been introduced into Arizona, since it was found in an arboretum. Other members of the genus regularly inhabit lower leaf sheaths of plants such as agave and palms, and also live in stumps, soil, and rocks, which would undoubtedly be transported along with plant specimens.

Alienates brevilobus, new species

Figures 151, 155, 157

DISTRIBUTION: U.S. Virgin Islands: St. John.

DIAGNOSIS: *Alienates brevilobus* can be distinguished from its congeners by the extremely short hind lobe of the head (ratio length to width 1:4.3; fig. 157A), its lack of eye spots (thus differing from *A. newtoni*), and the proportions below.

DESCRIPTION: Males unknown. Length of females 1.5–1.6 mm. General body color medium to dark chestnut brown. Legs, antennae, and rostrum slightly lighter than rest of body. Setae extremely short and sparse. Cuticular granules present on several areas of body, including gula and sides of head, ventral keel and sides of pronotum, all surfaces of meso- and metanotum, scattered areas on abdominal segments I–III and their intersegmental membranes, and very sparse on inner surfaces of forefemora (fig. 157E, F).

Head as in figures 157A, B. Eye spots absent. Hind lobe of head very short (fig. 157A);

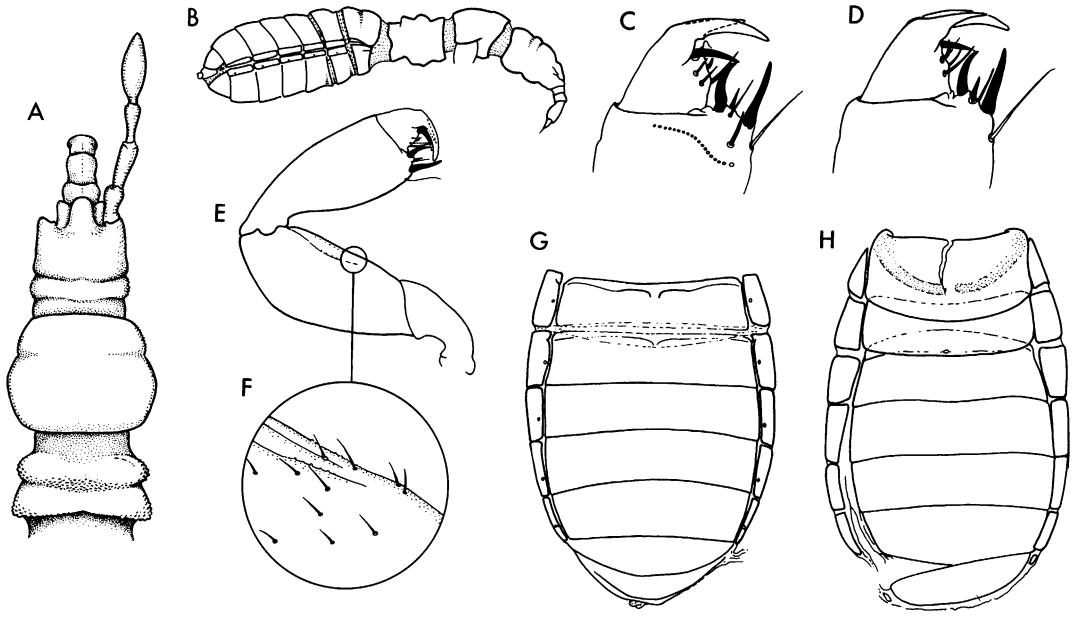


Fig. 157. *Alienates brevilobus*, ♀. **A**. Head and thorax, dorsal. **B**. Lateral view, legs removed. **C**, **D**. Apex of foreleg, inner and outer surfaces, repectively. **E**. Foreleg. **F**. Detail of inner (ventral) surface of forefemur. **G**. Abdomen, ventral. **H**. Abdomen, dorsal.

ratio length to width 1:4.3. Ratio head length to pronotum length 1:1.4. Ratio head length to width 1:1.

Antennae shorter than head plus pronotum (1:1.3). Ratio segments I–IV 1:1.4:1.2:2.6.

Pronotum as in figure 157A; ratio length to width 1:1.2. Ratio width of fore to hind lobe 1:1.2. Combined meso- and metanotum of average proportions; ratio length to width 1:2.1.

Abdomen, as in figure 157G, H, of standard proportions and segmentation; ratio length to width 1:0.6. Spiracles on ventral connexival plates III–VII.

Forelegs of average proportions (fig. 157E), with tarsal and tibial spination as in generic description. Ratio length to width of foretibia 1:0.42, of forefemur 1:0.43, and of hind femur 1:0.30. Forefemur with very sparse granules on its inner surface.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, U.S. VIRGIN ISLANDS: St. John, Trunk Bay, from leaf litter, October 6, 1979 (W. B. Muchmore; AMNH) (in glycerine).

PARATYPES AND NYMPHS: Same data as holotype (AMNH), 1♀ (in glycerin). U.S. VIRGIN ISLANDS: **St. John**: Lameshur Bay, VIERS, under large tamarind tree, May 24, 1979 (W. B. Muchmore; AMNH), 1♀ (on slide); Europa Bay, from litter alongside boulders, March 17, 1984 (W. B. Muchmore; AMNH), 1♀, 1 nymph.

ETYMOLOGY: From Latin, meaning short lobed, in reference to the extremely short hind lobe of its head.

Alienates dudichi Vasarhelyi
Figures 151, 158

Alienates dudichi Vasarhelyi, 1982: 157–170.

DISTRIBUTION: Lesser Antilles: St. Lucia.

DIAGNOSIS: *Alienates dudichi* (adult female) can be distinguished from its congeners by its pale straw or light dusky brown color, its extremely small size (average 1.16 mm), the presence of spiracles on the sterna (fig. 158C), and the small number of bristles in the bristle comb of the foretibia (±15; figs. 158D, E). It differs from the similar *A. iviei* by its larger size, different spiracle placement, and slightly shorter and thinner fourth antennal segment.

ADDITION TO DESCRIPTION: We add the fol-

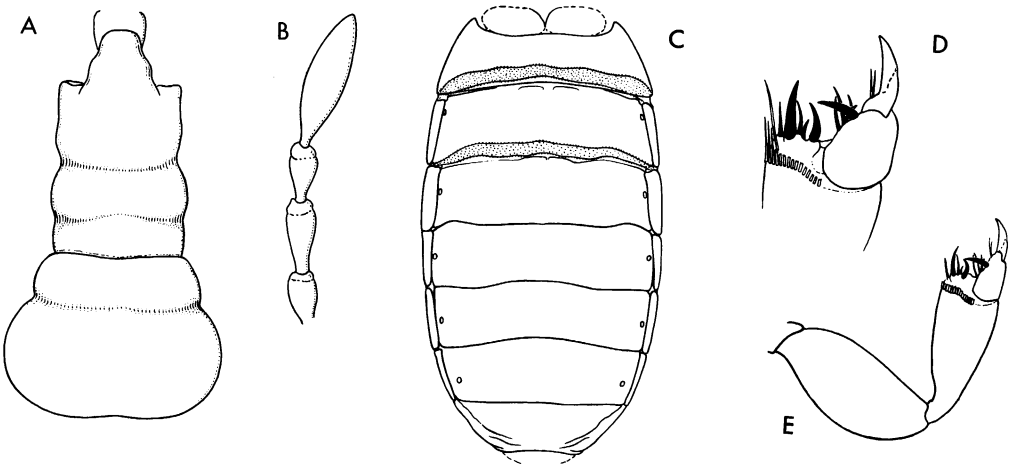


Fig. 158. *Alienates dudichi*, ♀ (paratype). **A**. Head and pronotum. **B**. Antenna. **C**. Abdomen, ventral. **D**. Apex of foreleg, inner view. **E**. Foreleg.

lowing proportions to Vasarhelyi's excellent description of this species. Because our methods of measurement differed from those of Vasarhelyi (1982), we have included our measurements from a paratype rather than using his data.

Male unknown.

Length of female 1.16 mm.

Head shorter than pronotum (1:1.2). Ratio head length to width across hind lobe 1:1. Ratio length of antenna to length of head plus pronotum 1:1. Antennal segments I–IV 1:1:0.8:2. Ratio length to width of pronotum 1:1.4. Ratio width of fore to hind lobe of pronotum 1:1.4; length of fore to hind lobes 1:2. Ratio length to width of metanotum 1:2. Ratio length to width of forefemur 1:0.45. Ratio length to width of foretibia 1:0.50. Ratio length to width of hind femur 1:0.33.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, LESSER ANTILLES: Isl. St. Lucia, No. 27, Castries, Vigie Point, November 7, 1981 (S. Mahunka and L. Mahunka-Papp; HNHM); not examined.

MATERIAL EXAMINED: LESSER ANTILLES. – Isl. St. Lucia, No. 27, Castries, Vigie Point, Nov. 7, 1981 (S. Mahunka and L. Mahunka-Papp; AMNH), 1♀, paratype.

Alienates elongatus, new species
Figures 151, 159

DISTRIBUTION: Southern Mexico.

DIAGNOSIS: This is the only known long and slender *Alienates*. Its abdominal sclerites, both dorsal and ventral, are densely covered with cuticular granules (fig. 159A).

DESCRIPTION: Males unknown. Length of female 1.65 mm (somewhat expanded in alcohol).

General body color uniform light brown. Body sparsely covered with medium-length setae. Cuticular granules present on gula, sides of antenniferous tubercles, undersides of thorax, surface of meso- and metanotum, dorsal and ventral surfaces of abdominal segments I–VII (less evident posteriorly), and on inner edges of all femora (figs. 159C, E). Intersegmental membranes of abdomen textured, but generally not with large cuticular granules as on sclerites.

Head as in figure 159A. Head and pronotum equal in length. Ratio head length to width across eye lobe 1:0.7; ratio head length to width across hind lobe 1:0.8. Ratio length to width of hind lobe of head 1:2.2. Eye lobe small, but jutting out sharply laterally. Eye pigmentation and ommatidia lacking.

Antennae very slightly shorter that head plus pronotum (1:1.1). Ratio segments I–IV 1:1.2:1:1.6.

Pronotum as in figure 159A, with lateral outline widening steplike, not gradually. Ratio length to width 1:1.3. Ratio width of fore to hind lobe 1:1.4; ratio length of fore to hind lobe 1:2.5. Meso- and metanotum, taken together, nearly square rather than transverse; ratio length to width 1:1.3 (fig. 159A).

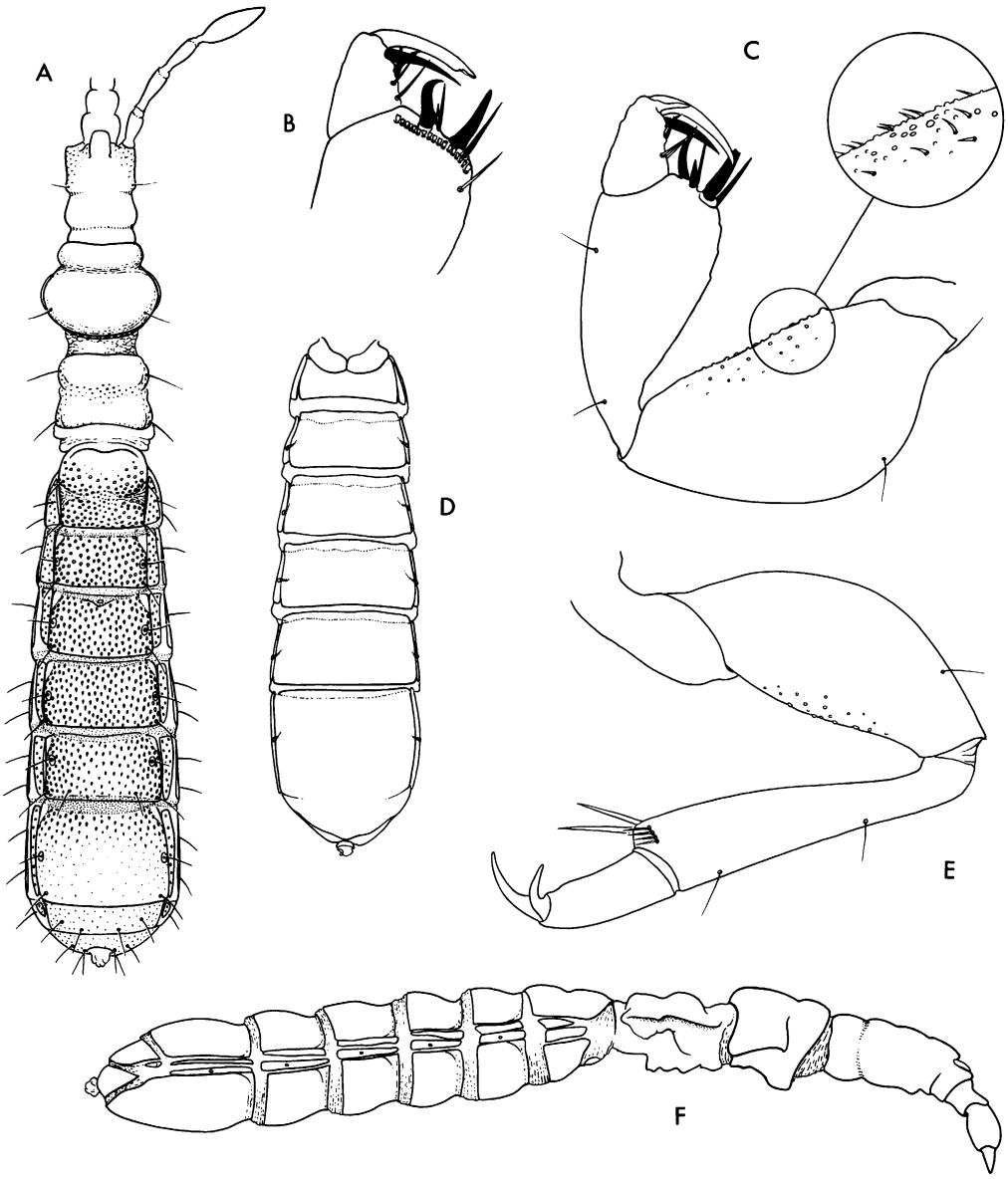


Fig. 159. *Alienates elongatus*, ♀. **A**. Dorsal view, legs missing. **B**. Apex of foreleg, inner view. **C**. Foreleg, outer view, with detail of inner (ventral) surface of forefemur. **D**. Abdomen, ventral. **E**. Hind leg. **F**. Lateral view, minus legs.

Abdomen as in figures 159A, D, F. Dorsal segments I and II fused, III–IX separate. Trichobothria on segments III–VII, surrounded by large basal areas (fig. 159A). Machrochaetal distribution as in figure 159A. Dorsal connexival plates I and II fused, but separate from dorsal segments themselves; III–VIII separate, VIII reduced to a small triangular plate. Terga I–VII, and to a lesser extent dorsal connexival plates bearing large, densely packed cuticular granules (fig. 159A). Sterna as in generic description, bearing cuticular granules. Second sternite separate from ventral connexival plates. Spiracles on ventral connexival plates III–VII.

Forelegs stout (fig. 159C). Ratio length to width of forefemur 1:0.56. Cuticular granules present on inner surface, interspersed with

short setae (fig. 159C). Foretibia bearing spines as in figures 159B, C. Bristle comb with approximately 17 setae. Ratio length to width of foretibia 1:0.56. Tarsus with five setae as in figures 159B, C; outer claw of medium length, about two-fifths length of inner claw. Hind leg as in figure 159E; ratio length to width of hind femur 1:0.42.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, MEXICO: Vera Cruz; 4.4 mi N of Huatusco, 4200 ft (1313 m), berlese sample of leaf and log litter, July 29–August 2, 1973 (A. Newton; AMNH).

ADDITIONAL MATERIAL EXAMINED: Same data as holotype, 3 male nymphs (in glycerine).

ETYMOLOGY: This *Alienates* is named *elongatus* because it is the only known long and slender member of this genus.

DISCUSSION: The three male nymphs are probably fifth instar and are probably of this species. Each has eyes with four or five pigmented spots.

Alienates insularis Barber

Figures 151, 154C, 155B, 160–164

Alienates insularis Barber, 1953: 2. — Barber, 1954: 11. — Štys, 1978: 243. — Kritsky, 1981: 130–132. — Vasarhelyi, 1982: 157, 168–169.

DISTRIBUTION: Florida and the Bahamas.

DIAGNOSIS: Males of *Alienates insularis* can be distinguished from their congeners by the unique wing venation (fig. 160F) and by the pointed guide (fig. 160D). Females can distinguished by the absence of eye spots (162A), the gradually widening lateral outline of the pronotum, and by the large, distinctly rectangular apodemes on sterna III and IV (fig. 162F).

REDESCRIPTION OF MALE: We add the following to Barber's description: Length 1.5–1.6 mm. General body color brown. Head slightly darker than rest of body. Eyes and ocelli dark brown. Cuticular granules very sparse, a few present on gula and on underside of thorax. Setae short, simple, and slender; most insertions normal, except expanded on all tibiae and tarsi (figs. 160J–L).

Head as in figures 160A, C. Ratio head length to pronotum length 1:0.9. Ratio head length to width across eyes 1:0.9; ratio length to width of hind lobe of head 1:2.4. Ratio length of eyes to anteocular distance 1:0.5; ratio width of eyes to synthlipsis 1:1.8. Hind margin of eye slightly emarginate, but not excavated in side view (fig. 160A).

Antenna as long as length of head and pronotum combined. Ratio segments I–IV 1:2.3:1.8:3.3.

Pronotum as in figure 160C; ratio length to width 1:1.6. Ratio width of fore to hind lobes 1:1.5; ratio length of fore to hind lobes (at midline) 1:2.8. Metanotum with reticulated sculpturing.

Abdomen as in figure 160C. Genital capsule as in figures 160D, E, 161C, G. Guide pointed at tip. Testes as in figure 160I.

Forewings with reduced venation as in figure 160F. Veins consisting of the C+Sc (Štys, 1980), the M+Cu, and a weak crossvein, the r+m, between them at level of stigma. Setae moderately long and slender at margin of wing, shorter on M+Cu vein, and present on membrane in an area near anal vein only. C+Sc continuing slightly beyond wing tip. Hind wings veinless except for thickenings at wing base; setae moderately long on distal edges of wing, but short and sparse elsewhere.

Ratio length to width of forefemur 1:0.33 (fig. 160K). Cuticular granules absent, setal insertions simple. Foretibia and tarsus with spines as in figures 160J, L, 161D, E. Setal insertions of foretibia expanded and pointed (figs. 160J, L). Bristle comb with 20 or 21 setae. Ratio length to width of foretibia 1:0.30. Outer claw of tarsus long, about three-fifths length of inner claw. Ratio length to width of hind femur 1:0.20.

DESCRIPTION OF FEMALE: Length 1.25–1.40 mm.

General body color straw yellow to very pale brown. Body surface with textured shine, covered with pale, medium length setae; slightly curved or woolly on head, thorax, and antennae; longer and straighter on abdomen and legs. Cuticular granules present on gula, mid and hind acetabula, forefemur, abdominal intersegmental membranes II–III and III–IV, and hind border of mesonotum. Setal insertions not expanded.

Head as in figures 161H, 162A. Ratio head length to pronotum length 1:0.9. Ratio head length to width (across hind lobe) 1:0.8. Ratio length to width of hind lobe of head 1:3.3. Eyes absent; neither pigmentation nor ommatidia present.

Antenna stout, shorter than head and pro-

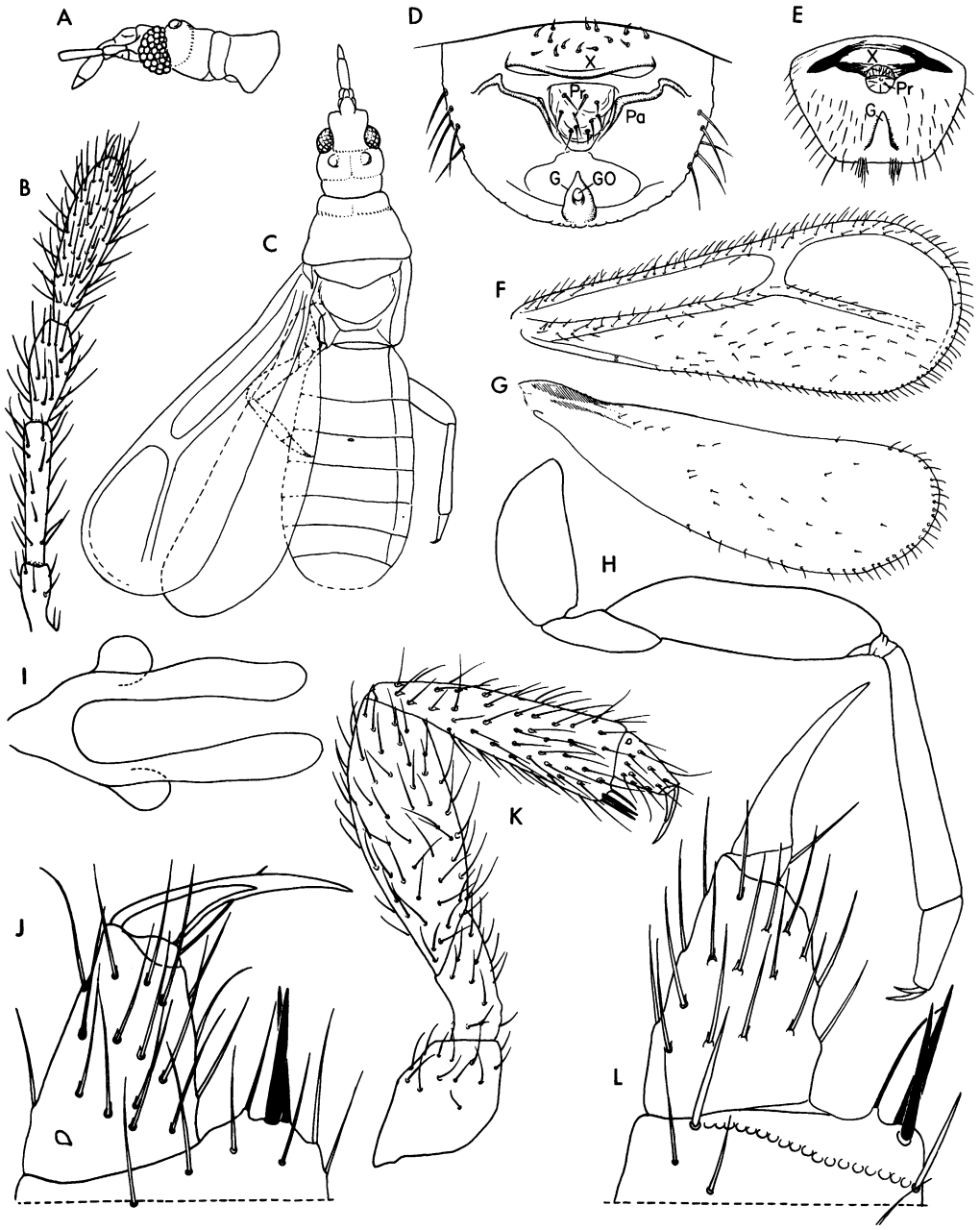


Fig. 160. *Alienates insularis*, ♂ (S. Bimini). **A**. Head and pronotum, lateral view. **B**. Antenna. **C**. Dorsal view (from slide, slightly squashed). **D**. Genital region, posterodorsal view. **E**. Genital region, posterior view (from Barber). **F**. Forewing. **G**. Hind wing. **H**. Hind leg. **I**. Testes. **J**. Apex of foreleg, outer view. **K**. Foreleg. **L**. Apex of foreleg, inner view.

notum combined (1:1.2, fig. 161H). Ratio of segments I–IV 1:1.7:1.5:3.1.

Pronotum two-lobed as in figures 161H, 162A; ratio length to width 1:1.3. Ratio width of fore to hind lobes 1:1.3; ratio length of fore to hind lobes (at midline) 1:1.9. Lateral outline of pronotum gradually widening, not abruptly steplike. Thorax as in figures 162A, C.

Abdomen as in figures 162C, E, F, 163.

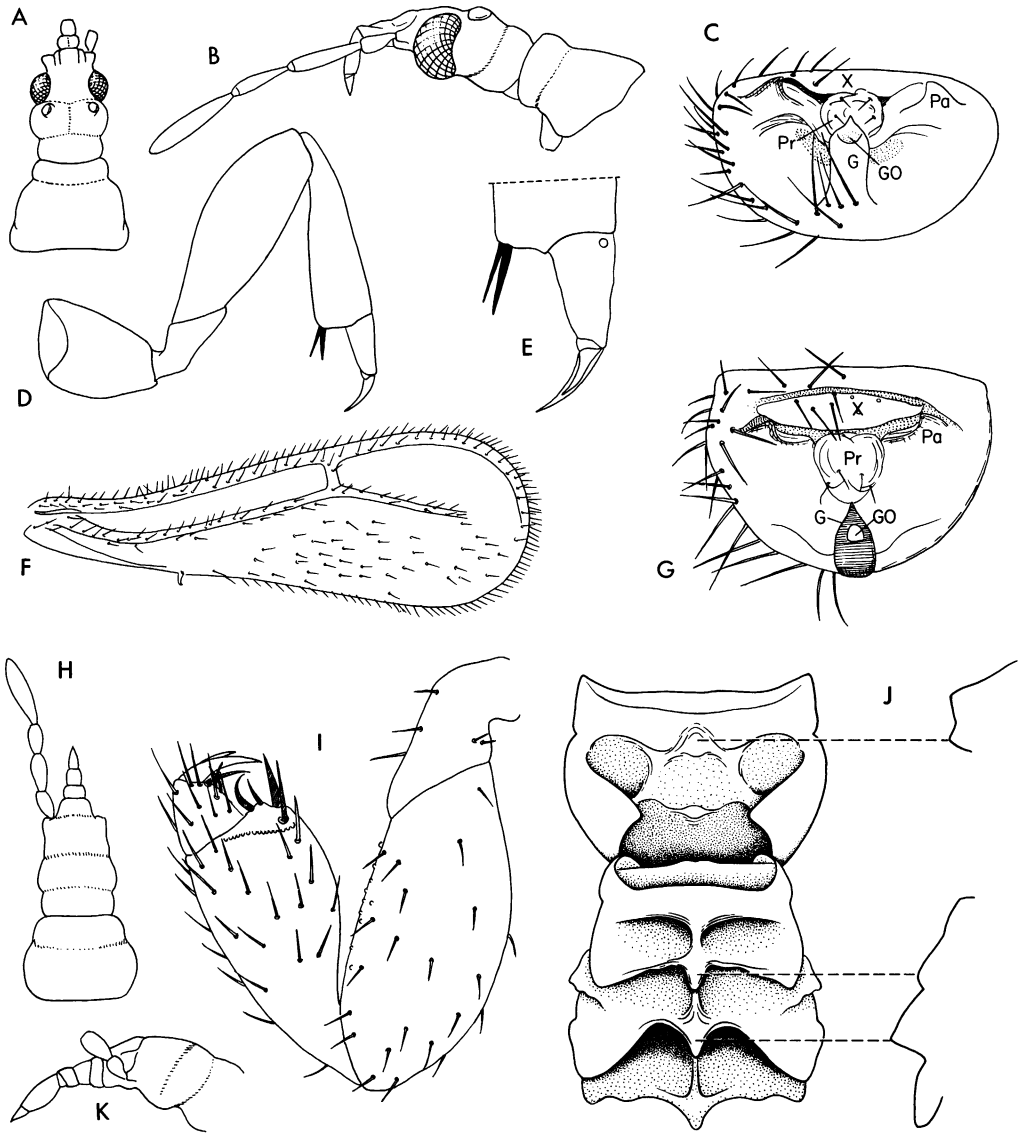


Fig. 161. *Alienates insularis* (from Florida). **A–G**. ♂. **A**. Head and pronotum. **B**. Lateral view of head and pronotum. **C**. Genital capsule, posterior view. **D**. Foreleg. **E**. Apex of foreleg, showing reduction in spines. **F**. Forewing. **G**. Genital capsule, posterodorsal view. **H**. Head and pronotum, ♀ nymph. **I**. Foreleg of same, inner surface, showing spines as in adult ♀. **J**. Thorax of female, also lateral keel shapes. **K**. Lateral view of head, ♀ nymph.

Dorsal segments I and II fused. Dorsal connexival plate VIII either present as a small and subcircular plate, or absent. Sternite II separate from ventral connexival plate II. Spiracles present on ventral connexival plates III–VII (see Discussion). Apodemes on sterna III an IV rectangular, separated centrally (fig. 162F).

Forelegs moderately stout (figs. 161I, 162H). Ratio length to width of forefemur 1: 0.45; cuticular granules present of inner surface. Foretibia and tarsus with spines as in figures 161I, 162J, L. Ratio length to width of foretibia 1:0.38. Bristle comb with 17–19 setae. Hind leg as in figure 162I; ratio length to width of hind femur 1:0.33.

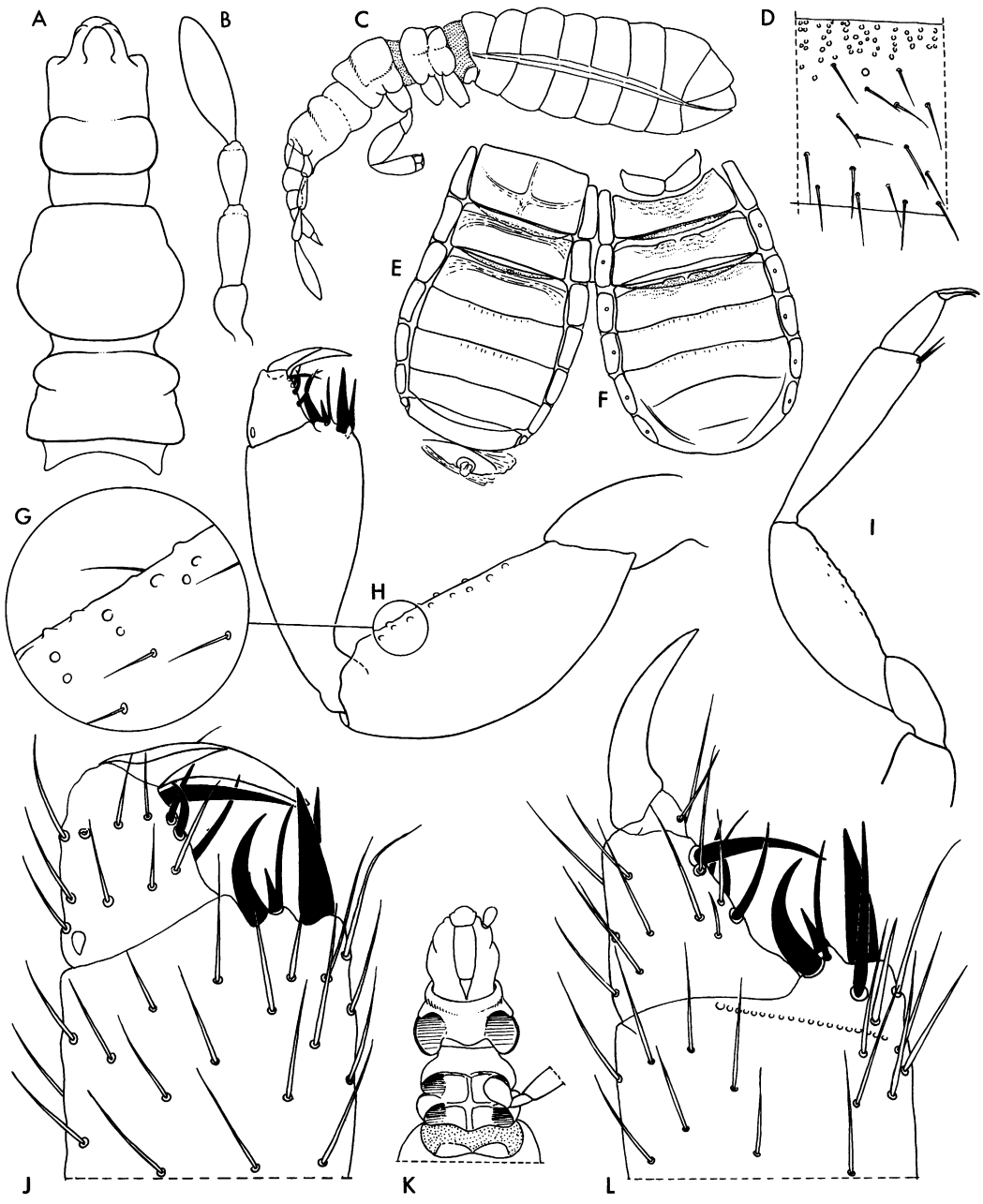


Fig. 162. *Alienates insularis*, ♀. **A**. Head and thorax. **B**. Antenna. **C**. Lateral view. **D**. Detail of sternum V. **E**. Abdomen, dorsal. **F**. Abdomen, ventral. **G**. Detail of inner (ventral) surface of forefemur. **H**. Foreleg, inner view. **I**. Hind leg. **J**. Apex of foreleg, outer view. **K**. Ventral view of head and pronotum. **L**. Apex of foreleg, inner view.

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, BWI [British West Indies]: Bahama Islands; South Bimini Island, May, 1951 (W. J. Gertsch and M. A. Cazier. AMNH), genital capsule missing.

PARATYPES AND NYMPHS: British West Indies: **Bahama Islands**: *South Bimini Island*, May, 1951 (W. J. Gertsch and M. A. Cazier: USNM), 1♂; June, 1951 (M. A. Cazier and C. and P. Vaurie; AMNH), 2♀, 1 nymph; July

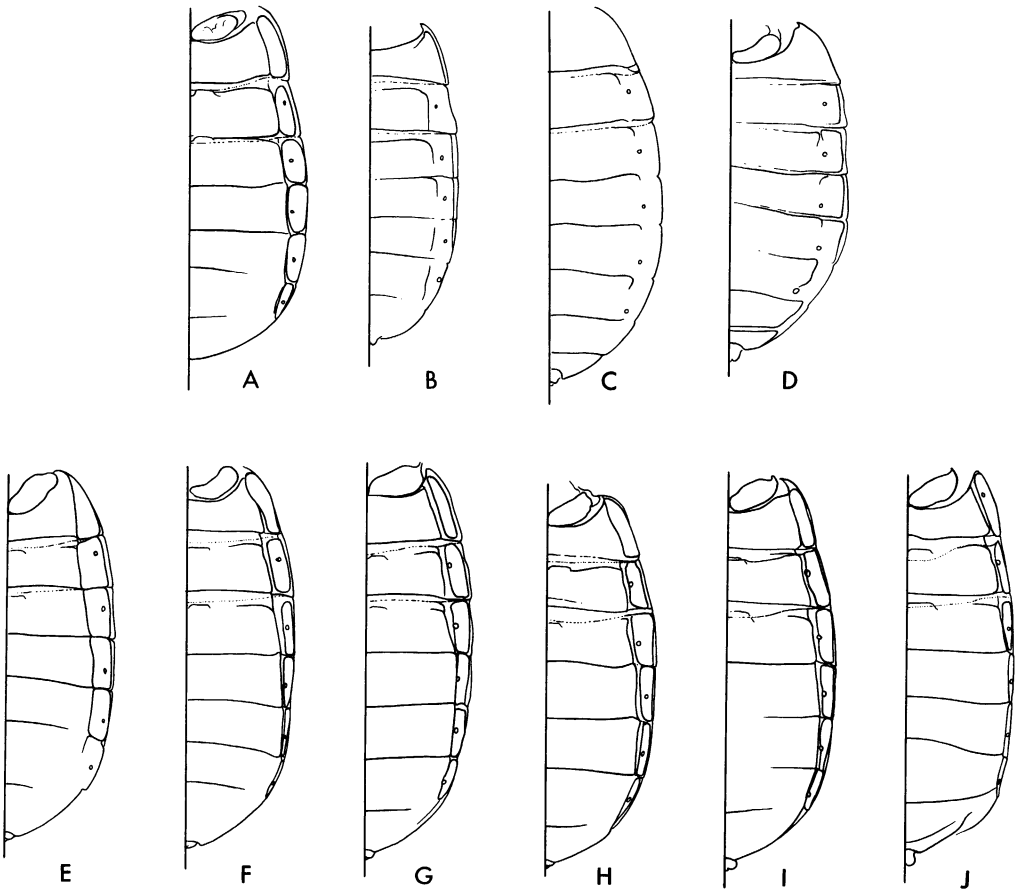


Fig. 163. *Alienates insularis*. Variations in spiracle placement and number. **A–D**. Nymphs. **E–J**. Adults. **J**. Note anomalous spiracle on ventral connexival plate II.

1951 (C. and P. Vaurie; AMNH) 1♀, 2 nymphs; August, 1952 (C. and P. Vaurie; AMNH), numerous females and nymphs. USA. – **Florida**: *Monroe Co.*: Key Largo, center of island, leaf litter berlesate, August 13, 1967 (R. Silberglied; AMNH), 1♂, 1♀, 1 nymph; upper Key Largo, berlese sample from pack rat nest (*Neotoma floridana*), May 24, 1976 (C. W. O'Brien and Marshall; AMNH), 2 male and 5 female nymphs; April 3, 1976 (J. H. Frank; AMNH), 2♀.

DISCUSSION: We have material of *Alienates insularis* from two geographical areas: South Bimini Island in the Bahamas, and Key Largo, Florida. We can find no differences between the two series; indeed, they seem nearly identical: males all have identical wing venation, pointed guides, and similar proportions; females have similar proportions, pronotal outlines, and rectangular apodemes. We thus consider them to be conspecific.

Since spiracle placement seems so unstable in females of this genus, we wondered how reliable this is as a specific character, and how it varies within a species. We studied this question in one of our longer series of slide-mounted and alcoholic samples of *Alienates insularis* from South Bimini Island. Results are illustrated in figures 163A–J. The spiracles in the 11 specimens studied nearly always appear on the ventral connexival plates, although sometimes they are in the center and sometimes along the ventral margin. In one case, the spiracle is well into the intersegmental membrane (fig. 163I). Spiracles are normally absent from both the second sternite and the second ventral connexival plates, although one specimen has them on the latter

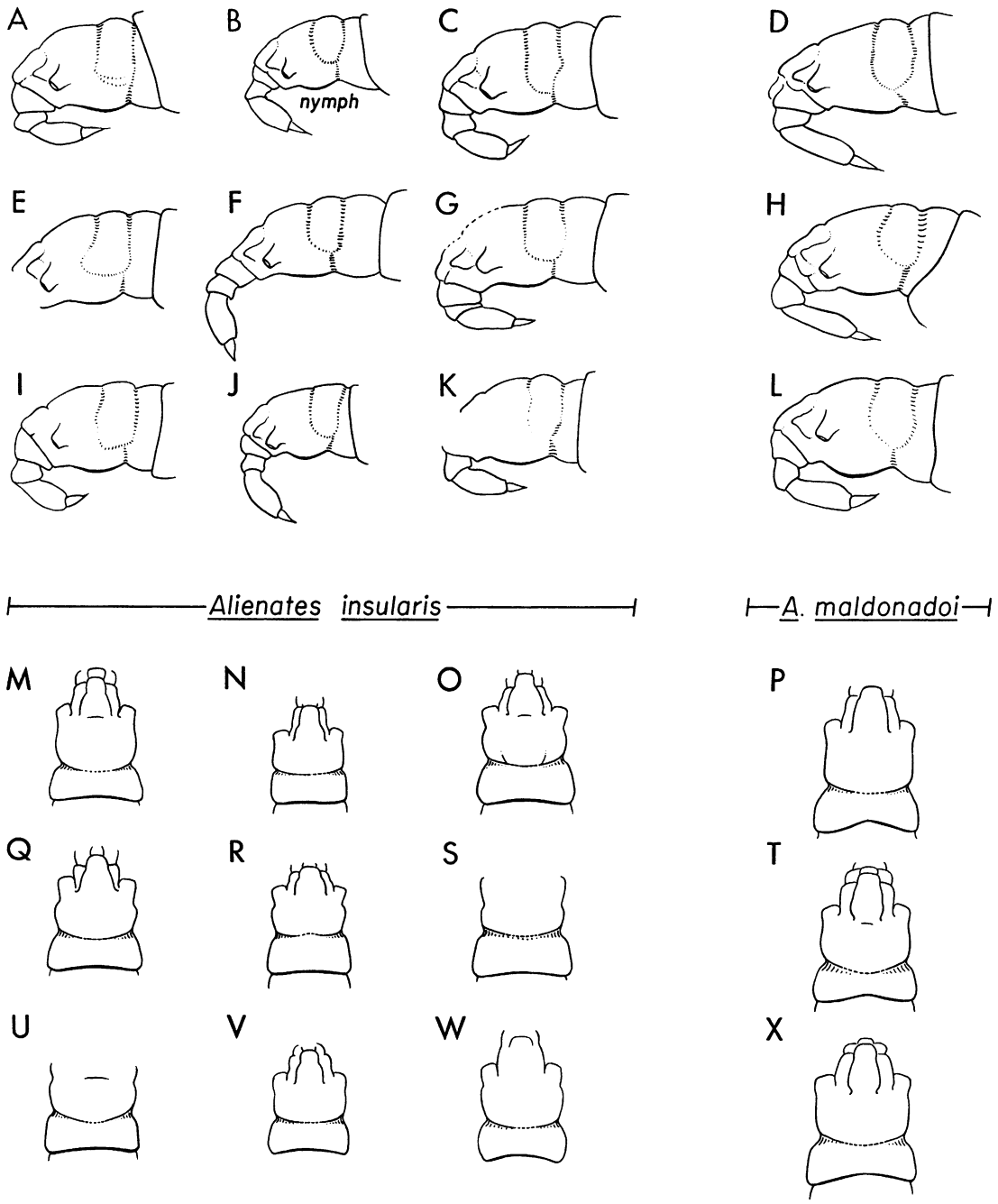


Fig. 164. Variations in dorsal and lateral head shapes in *Alienates insularis* and *A. maldonadoi*. **A–L.** Note variations in eye shape and size, and gular shape. **M–X.** Note variations in shape of posterior edge of head and lateral outline of head.

(fig. 163J). Nymphs (fig. 163A–D) seem to vary in a similar way, although the spiracles on two of them are situated more mesially, possibly in the intersegmental membranes. Nymphs tend to be poorly sclerotized and spiracle placement is not always clear.

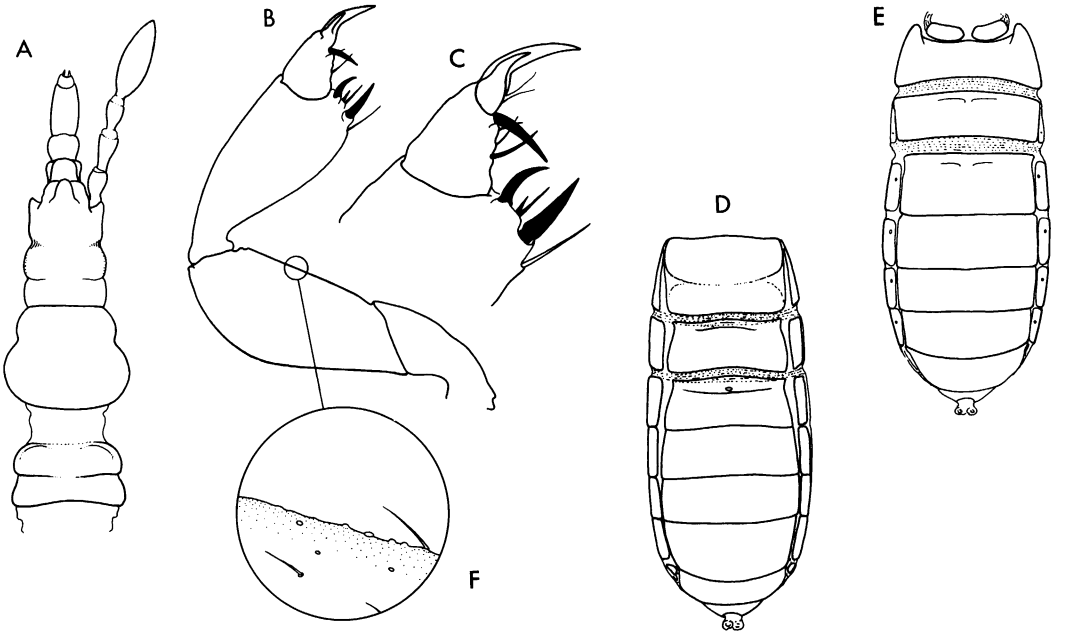


Fig. 165. *Alienates iviei*, ♀. **A**. Head and thorax. **B**. Foreleg. **C**. Apex of foreleg, outer surface. **D**. Abdomen, dorsal. **E**. Abdomen, ventral. **F**. Detail of inner (ventral) surface of forefemur.

There has been some debate as to the usefulness of the gular shape as a character in distinguishing females of different species. We have done a small study on this as well, illustrated in figure 164. We drew the shape of the gula of nine specimens (eight adult females and one female nymph), all from South Bimini Island, with the aid of a camera lucida and back-lighted the specimens to get as accurate an outline as possible. The shape of the gula varied from nearly flat (fig. 164F) to quite rounded (fig. 164J). We conclude from this that the shape of the gula is not a reliable character for separating species. This also was the case in three specimens of *A. maldonadoi* from Jamaica (figs. 164D, H, L).

A dorsal view of the heads shows slightly more consistency in the amount of emargination of the posterior border of the hind lobe. Figures 164M–W are all of *A. insularis*. These specimens seem to be more similar to one another than to the three *A. maldonadoi* specimens drawn in figures 164P, T, X. One must still be careful in using this as a character because of the subtleties of shape, the difficulties in positioning specimens similarly under the microscope, and possible overlaps between individuals.

Alienates iviei, new species
Figures 151, 165

DISTRIBUTION: U.S. Virgin Islands; St. Thomas and St. John.

DIAGNOSIS: *Alienates iviei* can be distinguished by its extremely small size (1.0–1.1 mm), its moderately elongate shape, and the large fourth antennal segment (fig. 165A). It differs from the similar *A. dudichi* by having its spiracles on the ventral connexival plates rather than on the sternites, by its warmer chestnut brown color rather than gray brown, and by its smaller size.

DESCRIPTION: Males unknown. Length of female 1.0–1.1 mm.

General body color light chestnut brown. Legs, antennae, and rostrum slightly lighter than rest of body. Setae extremely sparse and short. Cuticular granules present on several areas of body, including gula, ventral keel of pronotum, all surfaces of meso- and metanotum, scattered areas on abdominal segments

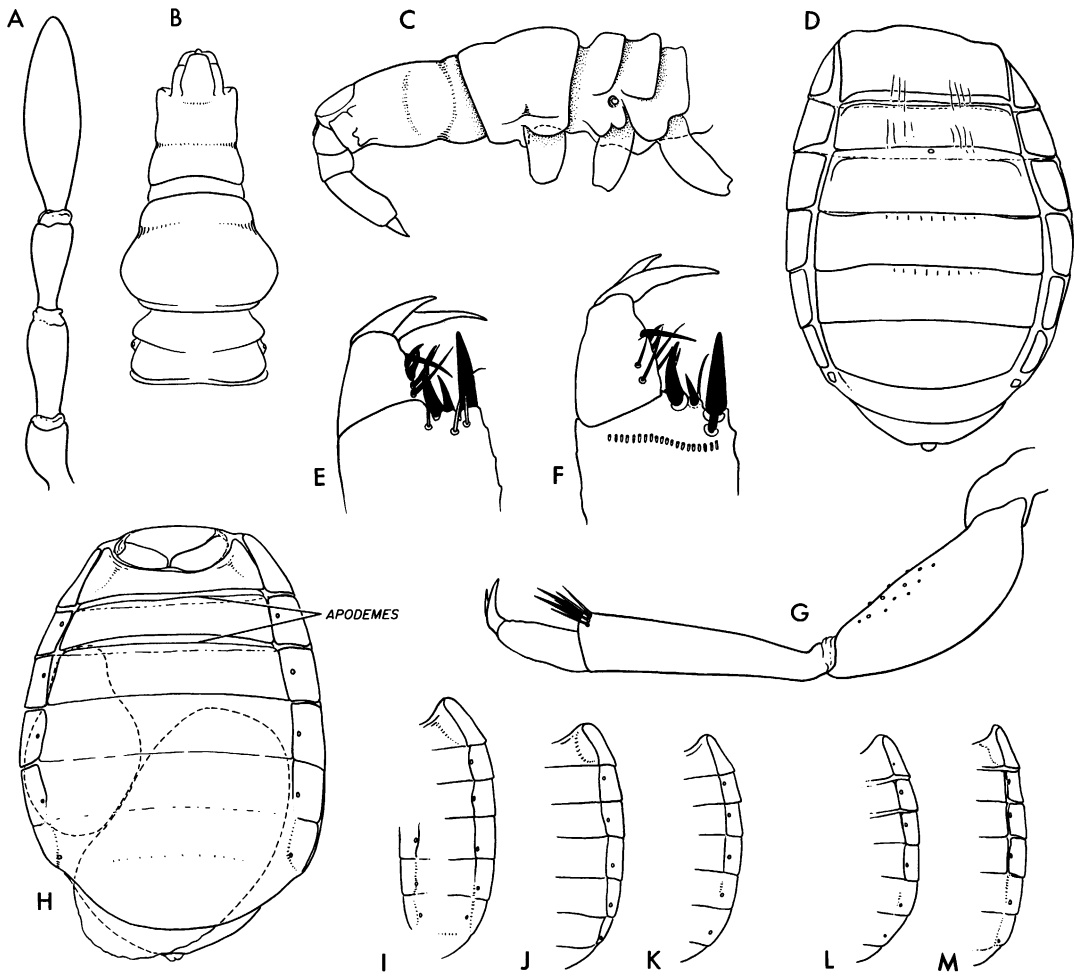


Fig. 166. *Alienates maldonadoi*, ♀ (holotype). **A**. Antenna. **B**. Head and thorax. **C**. Lateral view of head and thorax. **D**. Abdomen, dorsal. **E**, **F**. Apex of foreleg, outer and inner surfaces, respectively. **G**. Hind leg. **H**. Abdomen, ventral, showing two developing eggs. **I–M**. Variations in spiracle placement and number on ventral connexival plates (or sternites).

I–III and their intersegmental membranes, and very sparse on inner surfaces of forefemur (fig. 165F).

Head as in figure 165A. Ratio head length to pronotum length (midline) 1:1.1. Ratio head length to width (hind lobe) 1:0.9. Ratio length to width of hind lobe of head 1:2.7.

Antennae shorter than head plus pronotum (1:1.3). First three segments subequal in length, fourth segment very stout and much longer than the others. Ratio segments I–IV 1:1.1:0.9:2.3.

Pronotum as in figure 165A; ratio length to width 1:1.2. Ratio width of fore to hind lobe 1:1.2. Combined meso- and metanotum (dorsal view) more square (i.e., less transverse) than all other species but *A. elongatus*; ratio length to width 1:1.6.

Abdomen as in figures 165D, E, quite slender, ratio length to width 1:0.4. Spiracles on ventral connexival plates III–VII (fig. 165E).

Forelegs of average proportions (fig. 165B). Ratio length to width of foretibia 1:0.48; spination of tibia and tarsus typical for genus (figs. 165B, C). Ratio length to width forefemur 1:0.48; inner surface with very few cu-

ticular granules (fig. 165F). Ratio length to width of hind femur 1:0.40. Midlegs as in generic description.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, U.S. VIRGIN ISLANDS, St. Thomas: Perseverance, from dry tree hole, August 2, 1980 (no collector [most likely Ivie or Muchmore as below], AMNH) (in glycerine).

PARATYPES AND NYMPHS: U.S. VIRGIN ISLANDS: **St. Thomas**: Red Hook, from dead stump, July 27, 1980 (M. Ivie; AMNH), 1♀ (on slide). **St. John**: Cinnamon Bay Nature Trail, from kapok buttresses, June 6, 1980 (W. B. Muchmore; AMNH), 1♀ (in glycerine); Lameshur Bay, VIERS, under large tamarind tree, June 3, 1980 (W. B. Muchmore; AMNH), 1♀ (in glycerine); from kapok buttresses, March 15, 1984 (W. B. Muchmore; AMNH), 1♀; Great Lameshur Bay, from litter under and among rocks, June 5, 1979 (W. B. Muchmore; AMNH), 1 nymph (in glycerine).

ETYMOLOGY: *Alienates iviei* is named for one of its collectors, Michael Ivie.

Alienates maldonadoi, new species
Figures 151, 166, 167

DISTRIBUTION: British West Indies, Jamaica.

DIAGNOSIS: *Alienates maldonadoi* can be distinguished from its congeners by its fairly large size, heavy sclerotization, rich chestnut color, deeply emarginate posterior border of the head (fig. 166B), and extremely stout abdomen.

DESCRIPTION: Adult males unknown. Male nymph as in figure 167K.

Length of female 1.3–1.6 mm.

General body color chestnut or occasionally medium brown. Abdomen slightly lighter than head and thorax. Front of head, including tip of tylus and antenniferous tubercles, antennae, rostrum, and legs lighter yellowish brown. Entire body shiny, only a few cuticular granules present on gula, ventral surface of forefemur, metanotum, anterior edges of abdominal segments, and a few on intersegmental membranes of abdomen. All setae simple, slender, and without expanded insertions.

Head as in figures 166B, C, deeply emarginate behind. Ratio head length to pronotum length 1:1.1. Ratio head length to width (hind lobe) 1:0.8. Ratio length to width of hind lobe of head 1:3.3.

Antennae slightly shorter than head plus pronotum (1:1.1). Ratio segments I–IV 1:1.2:1.1:2.5.

Pronotum as in figure 166B, C; ratio length to width 1:1.3. Lateral outline gradually widening, not abruptly steplike (fig. 166B). Ratio width of fore to hind lobes 1:1.4; ratio length of fore to hind lobes (at midline) 1:2.3. Ratio length to width of combined meso- and metanotim 1:2.3.

Abdomen as in figures 166D, H, 167I, J, heavily sclerotized and very stout. Ratio length to width 1:1.6 or stouter. Dorsal connexival plate VIII small and triangular or absent. A few cuticular granules present dorsally on the callosity of segment I and II, and along anterior portions of segments III–VI, very few or none on intersegmental membranes. Division between ventral connexival plates VI and VII and sternites obscure. Spiracle placement as in figures 166H–M. Apodemes on sternum III straight and flat, not divided centrally (fig. 166H).

Forelegs comparatively slender (fig. 167D). Ratio length to width of foretibia 1:0.38. Foretibia bearing five spines as in figures 166E, F, 167G. Foretarsus as in figures 166E, F, 167G with one main recurved spine and five weak spines or strong setae. Bristle comb with at least 16 setae (fig. 167G). Ratio length to width of forefemur 1:0.40; a few cuticular granules present on inner surface (fig. 167D). Hind leg as in figure 167F; ratio length to width of hind femur 1:0.33.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, BRITISH WEST INDIES: JAMAICA: St. Andrew, Fairy Glade, 4300 ft (1323 m), leaf litter, May 29, 1955 (P. F. Bellinger; AMNH).

PARATYPES AND NYMPHS: BRITISH WEST INDIES: **Jamaica**: same data, 1♀ (on slide); St. Thomas, Corn Puss Gap, humus under Santa Maria tree, 2000 ft (625 m), June 27, 1954 (P. F. Bellinger; AMNH), 1♀, 1 male nymph; Clarendon, Portland Ridge, 300 ft (92 m), soil sample from dry limestone forest, July 15, 1955 (P. F. Bellinger; AMNH), 1♀; Portland, one-half mi N of Harware Gap, 3900 ft (1200 m), moss and liverwort mats, January 26, 1955 (P. F. Bellinger; AMNH),

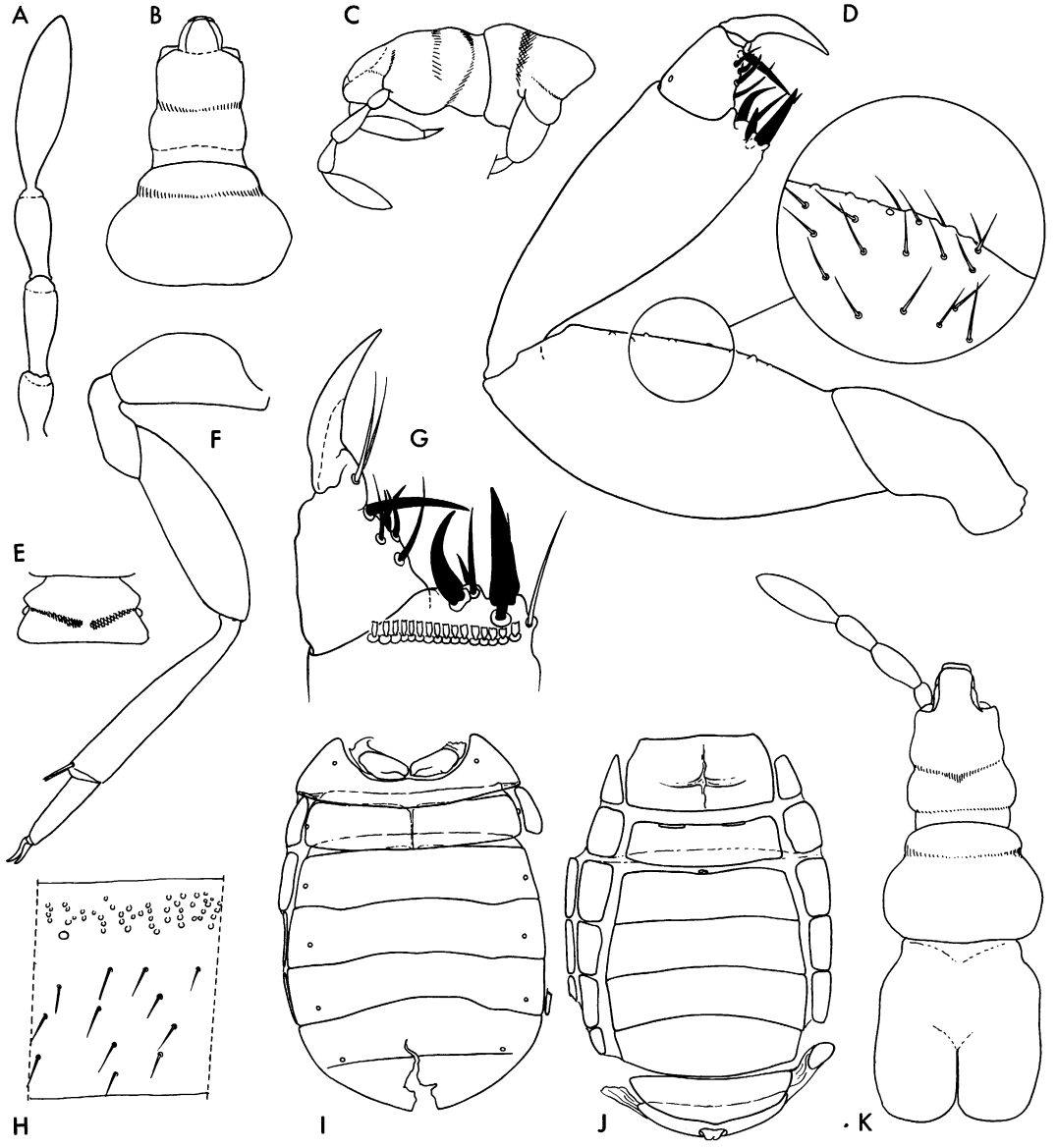


Fig. 167. *Alienates maldonadoi*. **A–J**. "anomalous" specimen, ♀. **A**. Antenna. **B**. Head and pronotum. **C**. Lateral view of head and pronotum. **D**. Foreleg, with detail of forefemoral microstructures. **E**. Meso- and metathorax. **F**. Hind leg. **G**. Apex of foreleg, inner surface. **H**. Detail of sternum V. **I**. Abdomen, ventral, showing abnormal spiracle on sternum II. **J**. Abdomen, dorsal. **K**. ♂ nymph, 5th instar.

1♀, head missing; St. Catherine Parish, 1.5 mi SW Ewarton, 313 m, April 7, 1968 (S. Peck and A Fiske; AMNH), 2♀ nymphs.

ETYMOLOGY: This species is named for Dr. J. Maldonado Capriles.

DISCUSSION: These specimens from Jamaica present us with the type of problem common in other species, and indeed other genera of this family, i.e., variability and what appears to be extreme plasticity in characters. Here it may be exhibited to the utmost. This can best be illustrated by a comparison of the two specimens that we have drawn, the holotype and a seemingly anomalous specimen.

Both were collected together in the same locality on the same day and appear to be conspecific, but show variation in four main areas: gular shape, spiracle placement, segmentation of the abdomen, and foreleg spines. Gular shape is an unreliable specific character as far as we can determine (see discussion and figures under *Alienates insularis*; fig. 164). It varies in these two specimens of *A. maldonadoi* as much as it does in the *A. insularis* specimens in our small sample.

Spiracle placement and fusion of abdominal segments also vary in *A. insularis* (see discussion and figure 163 under *A. insularis*) but not nearly as much as between these two specimens of *A. maldonadoi*. The holotype exhibits the most typical condition, with the spiracles on ventral connexival plates III–VII, and the division between the latter and the sternites of segments VI and VII poorly defined or nonexistent (fig. 166H). The "anomalous" specimen has spiracles on sterna IV–VII, on the sternum on one side and in the intersegmental membrane on the other side of segment III, and on segment II as well (fig. 167I). We have occasionally observed normal or reduced spiracles on segment II elsewhere in this genus. There is also no division between the ventral connexival plate and the sternite on segment II. Five other specimens are either the same as the holotype or intermediate in these characters (see generic discussion).

There is also a small variation in the foreleg spination, with the holotype missing the slender tibial spine (between the two large spines), which the anomalous specimen possesses. In other genera, many teratologies exist in foreleg spination, and our other specimens vary also. We therefore conclude that this would also be a risky specific character.

In conclusion, the differences between the holotype and the anomalous specimen would normally be enough to separate them into species. However, viewed in the light of the number of teratologies that seem to exist, and considering that these do not occur in any consistent pattern, we conclude for now that they are conspecific.

Alienates mexicanus, new species

Figures 151, 168–170

DISTRIBUTION: Southern Mexico.

DIAGNOSIS: Females of *Alienates mexicanus* can be distinguished from *A. insularis* and other congeners by the presence of rudimentary eye spots in most specimens (fig. 168A), and by the subtly different lateral shape of the pronotum, which is more steplike in *mexicanus* and sloping in *insularis* (compare figures 168A, 162A). The ratio of mid to hind lobe width is 1:1.31–1.36 in the former and 1:1.23–1.26 in the latter.

DESCRIPTION: Males unknown. Length of female 1.3–1.5 mm.

Color uniform yellowish brown. Body sparsely covered with short to medium length setae. Cuticular granules moderately abundant on several areas of body: gula, sides of antenniferous tubercles, ventral surfaces of femora, ventral surfaces of all thoracic segments, dorsal surfaces of meso- and metanota, and a few areas of abdomen, especially intersegmental membranes. Setal insertions not expanded.

Head as in figure 168A. Ratio head length to pronotum length 1:1.3. Ratio head length to width at hind lobe 1:0.9. Ratio length (along midline) to width of hind lobe of head 1:3. Rudimentary eye spots present, consisting of a few pigmented black spots laterally on forelobe of head.

Antennae shorter than head plus pronotum (1:1.3; fig. 168A). Ratio segments I–IV 1:1.2:0.9:2.2.

Pronotum as in figure 168A. Ratio length to width 1:1.3. Ratio width of fore to hind lobes 1:1.3; ratio length of fore to hind lobes 1:2.2. Lateral edges of forelobe of pronotum more or less parallel rather than diverging, making the lateral outline of the pronotum steplike instead of more gradually diverging. Ratio length to width of meso- and metanotum taken together 1:2.

Abdomen as in figures 168G, H. Spiracles on ventral connexival plates III–VII. Sternite II separate from ventral connexival plate.

Forelegs of medium proportions (fig. 168B). Ratio length to width of foretibia 1:0.43, bearing two main spines and three smaller ones, the innermost one curved outward (fig. 168C, D). Tarsus with one main spine, two smaller ones crossed adjacent to it, and three or four weaker spines or setae (fig. 168C–E). Outer claw three-fifths length of inner claw. Ratio length to width of forefemur 1:0.56 (slightly foreshortened). Forefemur bearing cuticular granules on inner surface (fig. 168B).

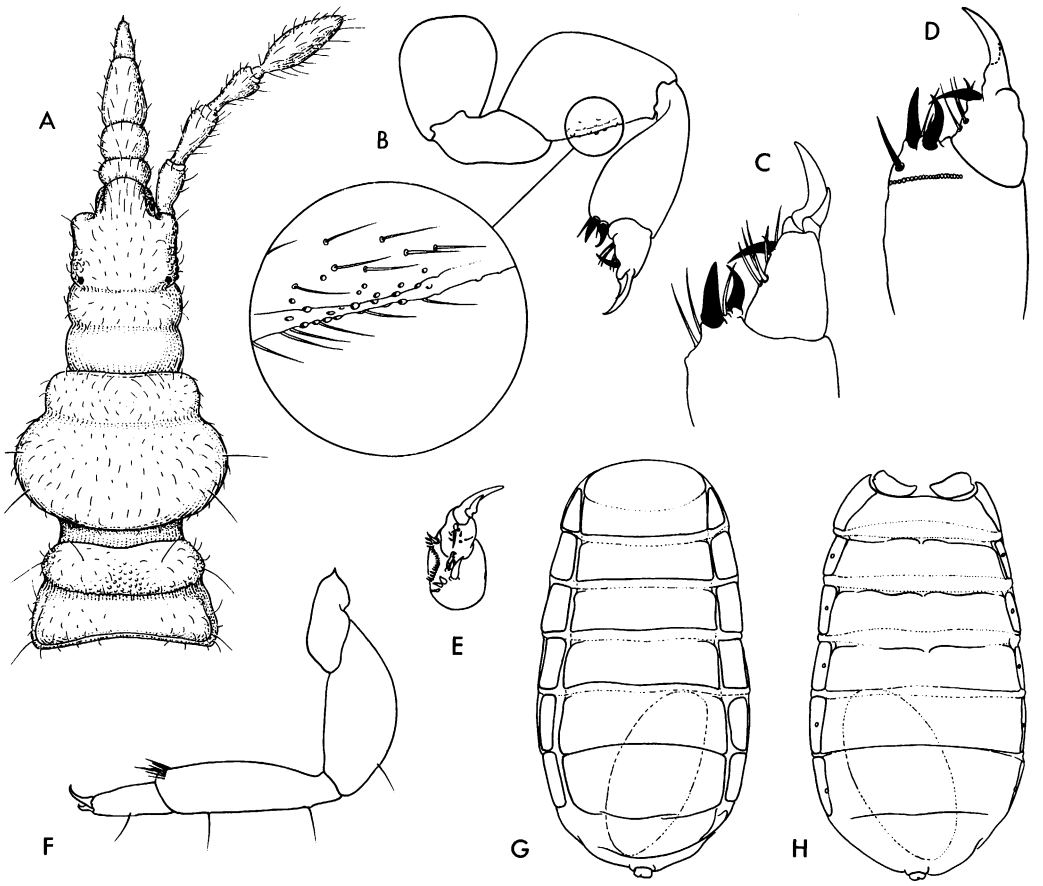


Fig. 168. *Alienates mexicanus*, ♀. **A**. Head and thorax. **B**. Foreleg, outer view, with detail of inner (ventral) surface of forefemur. **C**, **D**. Apex of foreleg, outer and inner surfaces, respectively. **E**. Apex of foreleg, end-on. **F**. Hind leg. **G**, **H**. Abdomen, dorsal and ventral views, respectively, showing outline of developing egg.

Hind leg as in figure 168F; ratio length to width of hind femur 1:0.37.

Ultimate (fifth) instar nymphs, male, and female, as in generic description (fig. 170). General shape, proportions, macrochaetal distribution, spiracle placement, and foreleg armature as in adult female. Eyes obsolete. Nymphs somewhat less sclerotized than adults, although most segments both dorsally and ventrally joined along central suture lines for most of their distance. Male with wing pads longer than wide, not joined, although contiguous medially to apices. Apices rounded.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, MEXICO: Oaxaca; 1 mi E Reforma, 33 m, berlese sample, leaf litter from tropical evergreen forest, August 15, 1973 (A. Newton; AMNH).

PARATYPES: Same data as holotype (AMNH), 21♀, 4♂ nymphs, 3♀ nymphs.

MATERIAL REFERRED TO AS NEAR *MEXICANUS*: MEXICO. – **Oaxaca**: 18.7 mi S Valle Nacional, 5200 ft (1625 m), berlese sample, cloud forest litter, August 17, 1973 (A. Newton; AMNH), 1♀; **Chiapas**: 8 mi N Pueblo Nuevo Sol, 6100 ft (1906 m), berlese litter along streams, ridge tops, August 26–27, 1973 (A. Newton; AMNH), 1♀ (slide); **Hidalgo**: Chapulhuacan, 3500 ft (1094 m), berlese sample from cloud forest leaf litter, July 5, 1976 (A. Newton; AMNH), 2♀ (slide), 4♀, 2 nymphs; 4 mi SW Chapulhuacan, 3500 ft (1094 m), berlese sample, cloud forest leaf

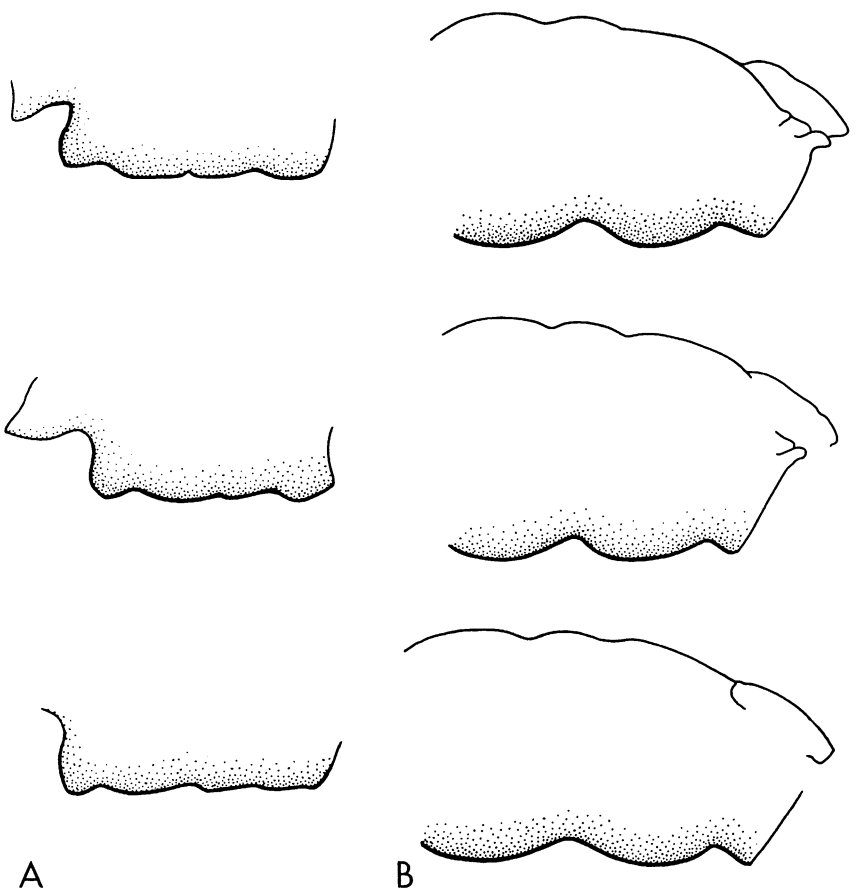


Fig. 169. **A**. Variations in meso- and metathoracic keel shape in *Alienates* nr. *mexicanus* ♀. **B**. Same, variations in gular shape, anterior toward right.

litter July 5, 1976 (A. Newton; AMNH), 1♀, 1 nymph (slide); **Veracruz**: 6 mi NE Catemaco, 1500 ft (469 m), berlese sample, rain forest leaf litter, July 7, 1976 (A. Newton; AMNH), 1♀ nymph (slide), 2♀ nymphs. We have also seen material from Belize and Costa Rica.

ETYMOLOGY: Named for its occurrence in Mexico.

DISCUSSION: We have material similar to *A. mexicanus* from five other localities in Mexico and have called it "near *mexicanus*" for the following reasons:

Similarities include the striking overall appearance, presence of eye spots, foreleg armature, abdominal spiracle placement, and segmentation. Differences are in overall size and leg proportions, and variation in the shape of the gula and in the lateral profiles of the meso- and metathoraces (figs. 169B, A, respectively). This last character is a problem, and probably not much more useful than the gular shape (see generic discussion and *A. insularis* discussion) because it varies somewhat within a single lot of specimens. Determining where intraspecific variation ends and interspecific variation begins becomes an arbitrary exercise, and in this case our information is too indefinite to make a decision.

Alienates millsi Kritsky

Figures 151–154, 171

Alienates millsi Kritsky, 1981: 130–132.

DISTRIBUTION: Cuba.

DIAGNOSIS: *Alienates millsi* can be distin-

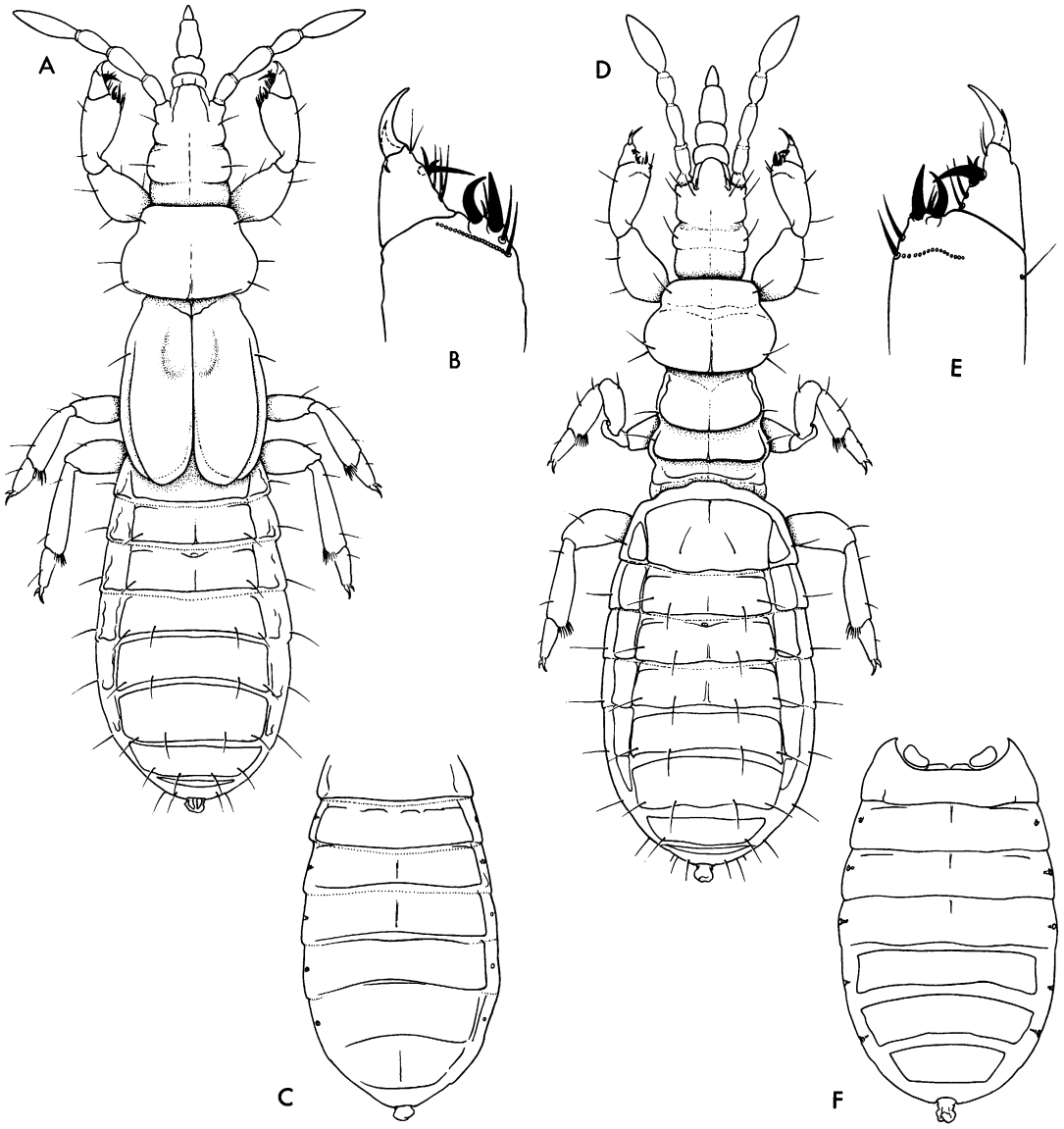


Fig. 170. *Alienates mexicanus*. **A**. 5th instar nymph, ♂, dorsal. **B**. Same, apex of foreleg, inner surface. **C**. Abdomen of ♂ nymph, ventral. **D**. 5th instar nymph, ♀, dorsal. **E**. Same, apex of foreleg, inner surface. **F**. Abdomen of ♀ nymph, ventral.

guished from *A. insularis* and other congeners by the presence of only two veins in the forewings (fig. 171G) and by the excavated hind margin of the eye (fig. 171B).

ADDITIONS TO DESCRIPTION: Females unknown.

Length of males 1.5–1.7 mm (wings extend 0.3–0.4 mm beyond abdominal tip).

General body color brown; head and thorax darker than abdomen, wings, and legs. Eyes and ocelli dark brown (in holotype they appear light because they have been cleared and slide mounted). Entire body shiny. Cuticular granules very sparse, present on humeral angles of pronotum, one or two on forefemora, absent from gula. All setae slender and simple. Setal insertions expanded and produced into points on all tarsi, tibiae, and femora (fig. 152D–F).

Head as in figures 152A, 171A, B. Ratio

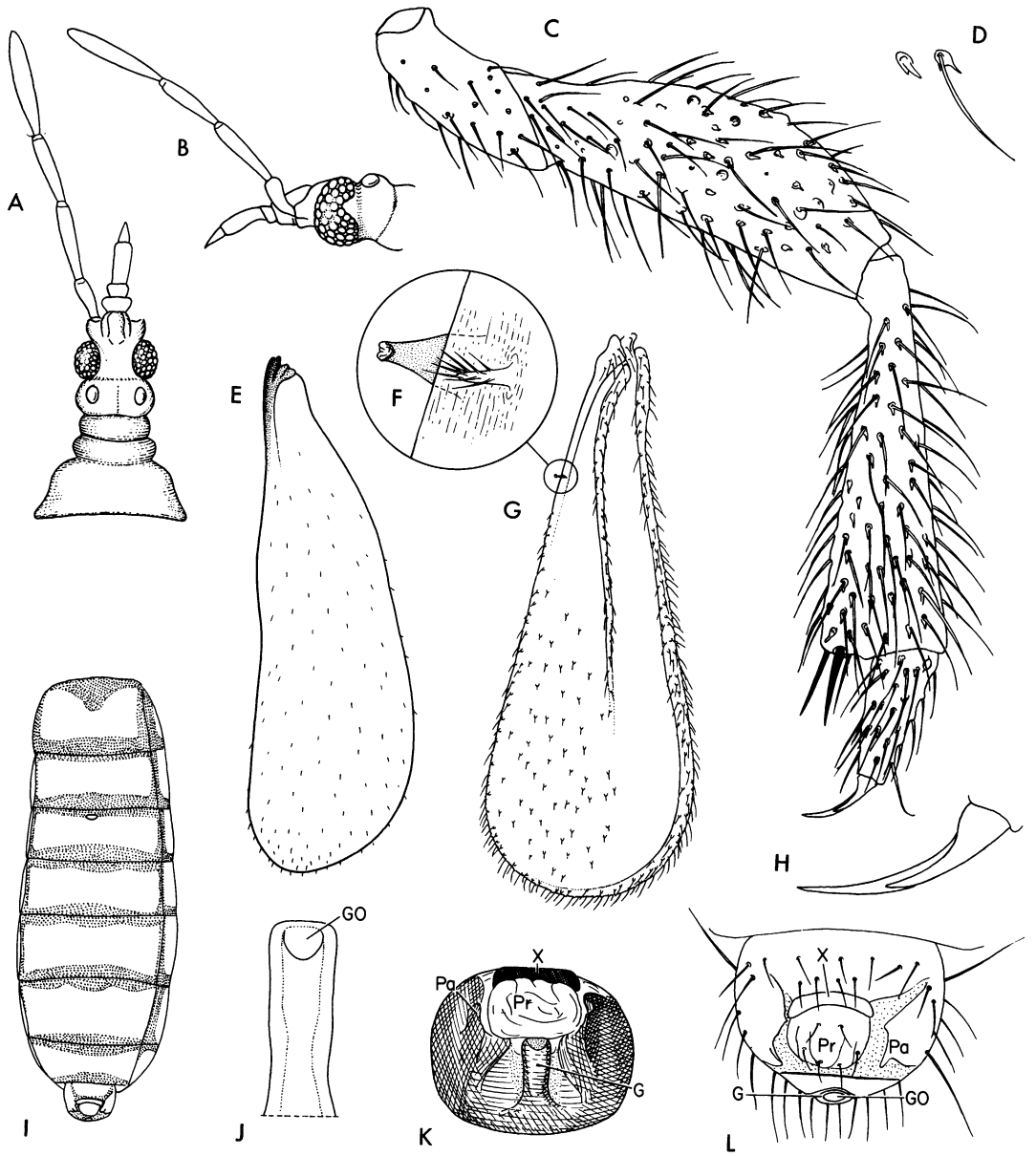


Fig. 171. *Alienates millsi*, ♂. **A**. Head and pronotum, dorsal. **B**. Lateral view of head. **C**. Foreleg, outer surface. **D**. Detail of setal base on foreleg. **E**. Hind wing. **F**. Wing coupling mechanism on hind edge of forewing. **G**. Forewing. **H**. Foretarsal claws, outer one shorter. **I**. Abdomen, dorsal. **J**. Guide. **K**. Genital capsule, posterior view. **L**. Genital capsule, dorsal view.

head length to pronotum length 1:0.9. Ratio head length to width across eyes 1:0.8; ratio length to width of hind lobe of head 1:2.4. Ratio length of eyes to anteocular distance 1:0.4; ratio eye width to synthlipsis 1:1.4. Hind margin of eye (in side view) emarginate, lacking both ommatidia and pigment (fig. 171B).

Antennae longer than head plus pronotum (1:0.7; fig. 171A). Ratio segments I–IV 1:2.2:1.9:3.

Pronotum as in figures 153A, 171A; ratio length to width 1:1.6. Ratio width of fore to hind lobes 1:1.8; ratio length of fore to hind lobes (along midline) 1:1.8.

Abdomen as in figure 171I. Genitalia as in figures 154D–F, 171J–L; guide tonguelike, truncate at tip. Parameres fused to genital capsule. Tergum X narrow, shallowly C-shaped.

Forewings with reduced venation, consisting of the C+Sc (Štys, 1980) and the unbranched Cu (fig. 171G). Sc continuing around wing past apex (in error in Kritsky, 1981). Setae with expanded insertions and present on anal half of wing only (fig. 171G). Coupling device as in figures 153E, 171F. Hind wings without veins except for thickening at wing base (fig. 171E). Short setae scattered over entire wing, most numerous at tip. Microtrichiae extremely dense, thickest at wing edges.

Ratio length to width of forefemur 1:0.28 (1:0.38; holotype measurements in parentheses, see Discussion). An occasional cuticular granule present among expanded, pointed setal insertions. Foretibia and tarsus with spines as in figures 152D, E, 171C. Tarsal spines thin and not easily distinguishable from surrounding setae. Ratio length to width of foretibia 1:0.29 (1:0.42); bristle comb with 19 or 20 setae. Outer claw slightly longer than half the length of inner claw. Ratio length to width of hind femur 1:0.21 (1:0.30).

MEASUREMENTS: See Appendix.

HOLOTYPE: Male, CUBA: Soledad, near Cienfuegos, berlese sample, June 2, 1950 (H. B. Mills; INHS); examined.

MATERIAL EXAMINED: CUBA. – Soledad, Cienfuegos, at light, August, 1964 (no collector; AMNH), 1♂; March, 1968 (AMNH), 5♂.

DISCUSSION: There is a discrepancy in the above data between the leg proportions of the holotype and our material. We have seen this type of discrepancy before in swarms of *Systelloderes* and in other genera in batches of material collected at one locality in different years or months. Since we have too little material to make a conclusive judgment about the variation within this species, and since we can find no other differences between the two, we discount this discrepancy until more is known.

Alienates muchmorei, new species

Figures 151, 172

DISTRIBUTION: U.S. Virgin Islands; St. John.

DIAGNOSIS: *Alienates muchmorei* can be easily distinguished from its congeners by its bicolorous body, which is generally light brown with a dark brown meso- and metathorax and a dark brown band on abdominal segments III–VI (figs. 172A, B). In addition, its spiracles are located on the sterna.

DESCRIPTION: Adult males unknown.

Length of females 1.3–1.4 mm.

Body bicolorous. Most body parts light to medium brown, sharply contrasting with dark brown meso- and metathorax and slightly lighter band on abdominal segments III–VI (figs. 172A, B). Band fading out centrally on tergum V and underneath confined to ventral connexival plates and edges of sternites (fig. 172F). Head, pronotum, and posterior section of abdomen of medium brown ground color; antennae, rostrum, legs, and basal portion of abdomen lighter. Setae short, simple, and of moderate density on all body parts. Cuticular granules present on head on antenniferous tubercles, gula, sides of head, and dorsally in the sulci delimiting the hind lobe. Granules also present on inner surfaces of femora, ventral and lateral surfaces of prothorax, all surfaces of meso- and metathorax, and basal abdominal segments.

Head as in figures 172A, B. Ommatidia absent, although forelobe of head bulging laterally in areas normally occupied by eyes. Tylus short and broad. Ratio length to width of hind lobe of head 1:3.2. Ratio head length to pronotum length 1:1.1. Ratio head length to width across hind lobe 1:1.

Antennae shorter than head plus pronotum (1:1.3, fig. 172A). Ratio of segments I–IV 1: 1.8:1.4:2.8.

Pronotum as in figure 172A; ratio length to width 1:1.3. Ratio width of fore to hind lobe 1:1.2; ratio length of fore to hind pronotal lobes 1:1.6. Combined meso- and metanotum moderately short and wide; ratio length to width 1:2.8.

Abdomen as in figures 172A, F. Ratio length to width 1:0.7. Spiracles on sterna III–VII. Sternum II fused with its ventral connexival plates.

Forelegs of average proportions (fig. 172C) with tarsal and tibial spination as in generic description (figs. 172D, G). Ratio length to width of forefemur 1:0.40; surface beset with cuticular granules varying in shape from rounded (many) to pointed (few). Ratio length to width of foretibia 1:0.40. Ratio length to

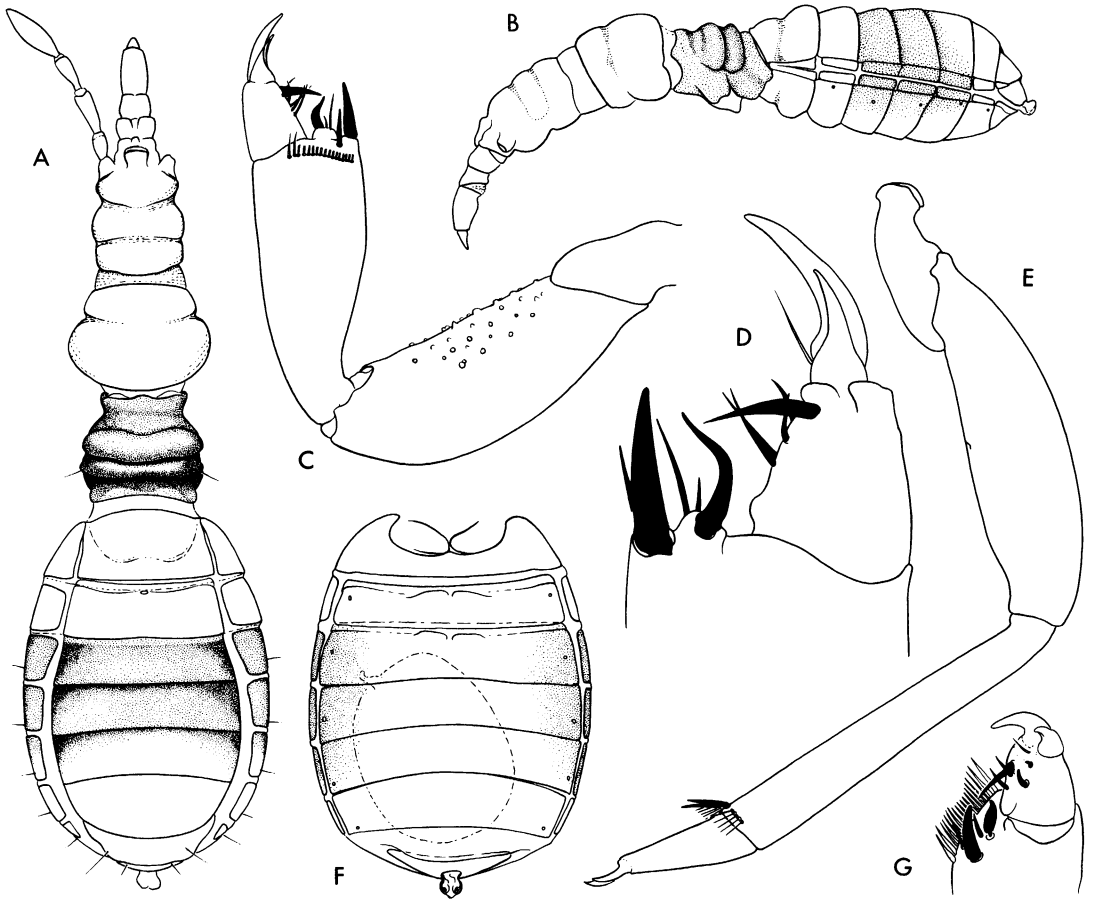


Fig. 172. *Alienates muchmorei*, ♀. **A**. Dorsal view, minus legs (note 2 colors). **B**. Lateral view. **C**. Foreleg. **D**. Apex of foreleg, outer view. **E**. Hind leg. **F**. Abdomen, ventral. **G**. Apex of different foreleg, end-on view (note that spines do not correspond in their placement with those of figure D).

width of hind femur 1:0.30 (fig. 172E). Outer tarsal claw half length of inner claw.

Nymphs as in generic description with the following additions. Fifth and fourth instar nymphs of both sexes with dark brown meso- and metathoraces, sharply contrasting with rest of body. Fifth instar male with large dark wing pads meeting medially and extending backwards to anterior edge of abdomen. Hind lobe of head, pronotum, and anterior portion of wing pads not fused medially; abdominal segments fused medially but lightly sclerotized on terga I + II, III, and IV. Eyes relatively undeveloped, with four or five pigmented ommatidia evident. Fourth instar males with somewhat lighter wing pads, although still contrasting with rest of body. Mesonotum and metanotum separate; front wing pads barely developed, extending only slightly over completely undeveloped hind wing pads. Hind lobe of head, pronotum, meso- and metanotum, and abdominal segments I–VI unfused medially. No ommatidia evident. Fourth (?) instar female nymph as above, but without wing pads or eyes. Third instar nymphs lightly sclerotized, but with meso- and metathoraces slightly darker than rest of body.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, U.S. VIRGIN ISLANDS: St. John, Europa Bay, from litter alongside boulders, March 17, 1984 (W. B. Muchmore; AMNH).

PARATYPES AND NYMPHS: Same data as ho-

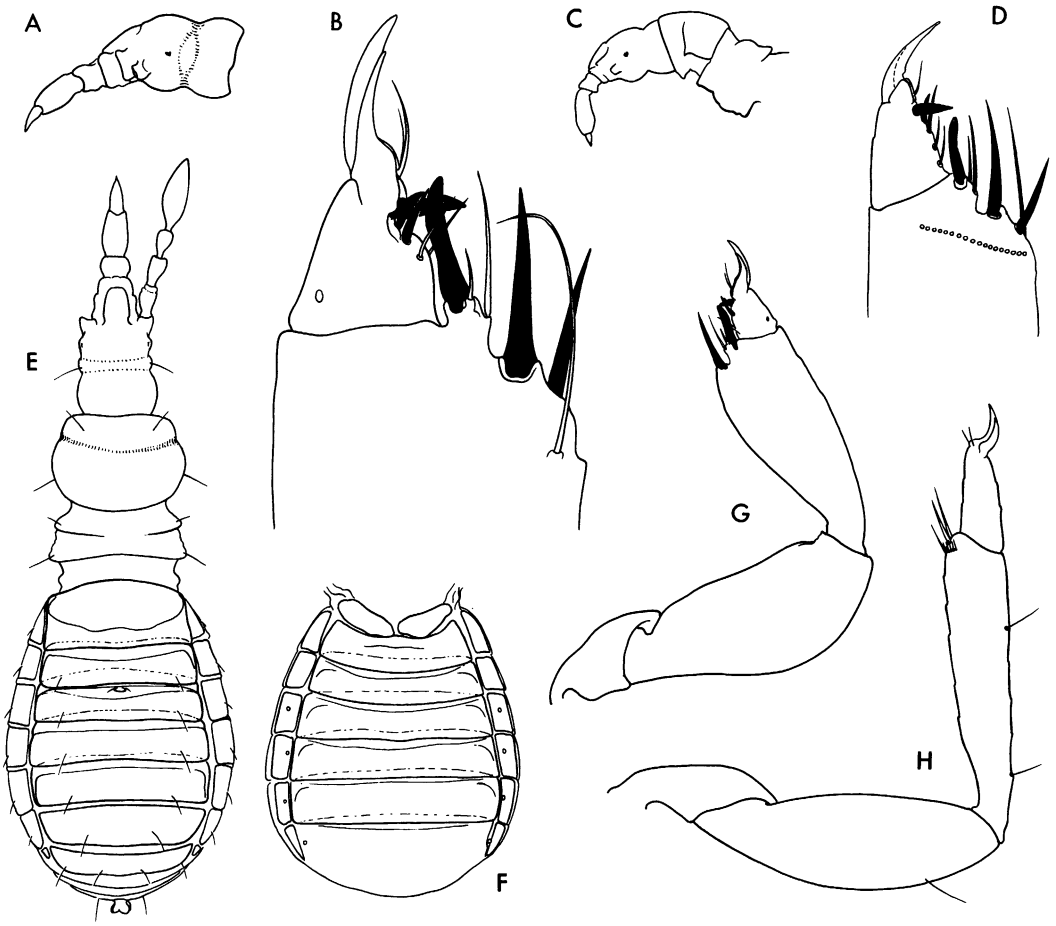


Fig. 173. *Alienates newtoni*, ♀. **A**. Lateral view of head. **B**. Apex of foreleg, outer view. **C**. Head and thorax, lateral. **D**. Apex of foreleg, inner view, ♂, nymph. **E**. Dorsal view. **F**. Abdomen, ventral view. **G**. Foreleg, outer view. **H**. Hind leg.

lotype (AMNH), 1 male nymph, 4 female nymphs (fifth instar), 2 male, 1 female nymphs (fourth instar), 3 nymphs (third instar), 3 smaller nymphs. U.S. VIRGIN ISLANDS: Great Lameshur Bay, E side, under agave, March 14, 1984 (W. B. Muchmore; AMNH), 1♀.

ETYMOLOGY: Named after its collector, W. B. Muchmore.

Alienates newtoni, new species
Figures 151, 173

DISTRIBUTION: Southern Mexico.

DIAGNOSIS: This is a small, medium brown *Alienates*, approximately 1.2 mm in length. It has foretibial spines as in figure 173B, which include a unique spoon-shaped one closest to the tarsus, eye spots within sharply jutting eye lobes (fig. 173E), and a very short hind lobe of the head.

DESCRIPTION: Males unknown (except as nymphs). Length of female 1.17–1.20 mm.

General body color uniform medium brown; ends of rostrum, legs, and antennae slightly lighter than rest of body. Body sparsely covered with short, sometimes curved setae. Cuticular granules present on gula, and ventral surfaces of all thoracic segments, conspicuously absent (or extremely vague) on inner surface of forefemur and on intersegmental membranes of abdomen.

Head as in figures 173A, C, E. Ratio head length to pronotum length 1:1.2; ratio head

length to width across hind lobe 1:0.9. Hind lobe of head extremely reduced lengthwise; ratio length to width 1:6. Eye lobes, though small, jutting out sharply laterally; eyes obsolescent, present only as small pigmented spots.

Antennae shorter than head plus pronotum (1:1.2). Ratio segments I–IV 1:1.4:1.2:2.8.

Pronotum as in figure 173E, with lateral outline gradually bulging, not steplike; ratio length to width 1:1.3. Ratio width of fore to hind lobe 1:1.3; ratio length of fore to hind lobe 1:1.5. Ratio length to width of meso- and metanotum, taken together, 1:2.8; keel on underside very prominent (fig. 173C).

Abdomen as in figures 173E, F. Abdominal segmentation as in generic description. Spiracles absent from segment III (see generic discussion), present on ventral connexival plates IV–VI, and varying in placement on segment VII, either on the sternite or the ventral connexival plate.

Forelegs of medium proportions (fig. 173G). Ratio length to width of forefemur 1:0.43; cuticular granules sparse, or if present, barely visible. Foretibia bearing spines as in figures 173B, D; spine closest to tarsus expanded apically, giving it an elongate spoon or shoe-sole shape. Bristle comb bearing approximately 18 setae. Ratio length to width of foretibia 1:0.37. Tarsus with five setae as in figure 173D; outer claw long, three-quarters length of inner claw. Hind leg as in figure 173H; ratio length to width of hind femur 1:0.30. Midleg as in generic description.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, MEXICO: Veracruz; 4.4 mi N Huatusco, 4200 ft (1313 m), berlese sample of leaf and log litter, July 29-August 2, 1973 (A. Newton; AMNH).

PARATYPES: Same data as holotype (AMNH), 7♀ (5 in glycerine, 2 on slides), 3♀ nymphs (in glycerine), 2♂ nymphs (1 in glycerine, 1 on slide).

ETYMOLOGY: *Alienates newtoni* is named for its collector, Dr. Alfred F. Newton, Jr.

DISCUSSION: The male nymphs (probably fifth instar) have the same general shape and characters as the adult females, with the exception of the normal sexually dimorphic characters: the legs and foreleg spines are slightly more slender, the pronotum is shorter, and wing pads are present. The head shape is also somewhat different; the eye lobes are not as sharp laterally and bear five or six ommatidia spread out in a crescent shape along the front margin. Also, the hind lobe of the head is somewhat longer.

Alienates roberti, new species

Figures 151, 174

DISTRIBUTION: Southern Mexico.

DIAGNOSIS: *Alienates roberti* can be distinguished from its congeners by its extremely stout forelegs (figs. 174C, D), the thick tibial spine borne on an elevated tubercle, by its relatively long pronotum (approximately 1.3 times the head length; fig. 174A), and by the presence of densely packed cuticular granules on many parts of the body (see below).

DESCRIPTION: Males unknown. Length of female 1.8–2.0 mm.

General body color light brown; legs, antennae, and rostrum slightly lighter than rest of body. Body sparsely covered with short setae. Cuticular granules present on many areas of body (figs. 174A, D), densest on gula, sides of hind lobe of head, forelobe of pronotum, meso- and metanotum, metapleuron, under surfaces of femora, abdominal segments I–VI, intersegmental membranes, and all dorsolateral terga.

Head as in figures 174A, B. Ratio head length to pronotum length (midline) 1:1.3. Ratio head length to width (hind lobe) 1:0.7; ratio length to width of hind lobe of head 1:2.8.

Antennae shorter than head plus pronotum (1:1.3). Ratio segments I–IV 1:1.1:1:2.4.

Pronotum as in figure 174A; ratio length to width 1:1.1. Ratio width fore to hind lobe 1:1.3. Ratio length fore to hind lobe 1:1.6. Ratio length to width of combined meso- and metanotum 1:1.8.

Abdomen as in figure 174E. Abdominal segmentation and spiracle placement as in generic description. Cuticular granules densest on intersegmental membranes between segments I+II and III, and III and IV.

Forelegs extremely stout (figs. 174C, D). Ratio length to width of foretibia 1:0.56. Foretibia bearing five spines as shown in figures 174C, D. Largest and outermost spines elevated on a large tubercle. Bristle comb with 21 or 22 setae. Tarsus with five spines as in

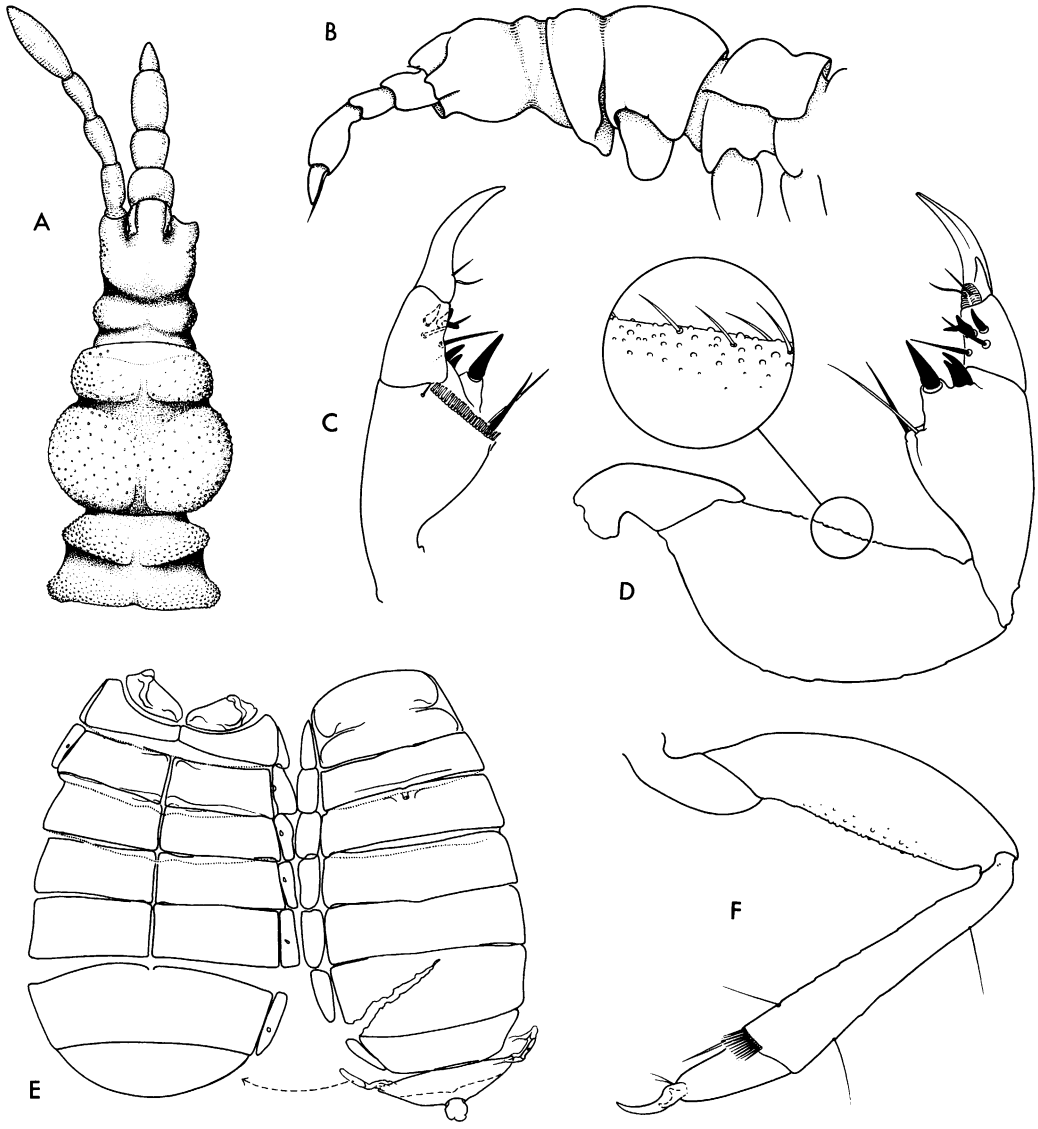


Fig. 174. *Alienates roberti*, ♀. **A**. Head and thorax, dorsal. **B**. Lateral view of head and thorax. **C**. Apex of foreleg, inner surface. **D**. Foreleg, outer surface, with detail of inner (ventral) surface of forefemur. **E**. Abdomen, ventral on left, dorsal on right. **F**. Hind leg.

figure 174D. Spine II not as long or as strongly curved as in other species. Outer claw about two-fifths length of inner claw. Ratio length to width of forefemur 1:0.53. Inner surface with minute cuticular granules (fig. 174D). Hind leg as in figure 174F, ratio length to width of hind femur 1:0.29. Midleg as in generic description.

MEASUREMENTS: See Appendix.

HOLOTYPE: Female, MEXICO: Vercruz: Fortin, Canyon Rio Metlac, tropical evergreen forest soil and leaf litter, berlese 174, August 5, 1969 (S. and J. Peck; AMNH) (in alcohol).

PARATYPES AND NYMPHS: Same data as holotype (AMNH), 1♀ (on slide), 4 nymphs in alcohol: 1 fifth instar, 3 fourth instars; 4.4 mi N Huatusco, 4200 ft, berlese leaf and log litter, July 29–August 2, 1973 (A. Newton; AMNH), 1♀ nymph.

ETYMOLOGY: *Alienates roberti* is named for Dr. Robert E. Schmidt, the junior author's husband, in recognition of his encouragement in this project.

DISCUSSION: Even though abdominal sterna I–VI are poorly sclerotized along the midlines, we feel the specimens we examined are adults. The insect is heavily sclerotized, the division line is faint and narrow, and the proepisternum and proepimeron are fused.

REFERENCES

Agassiz, J. L. R.
1846. Nomenclatoris zoologici index universalis ... 4°. Soloduri: Jent et Gassman. viii + 393 pp.

Alayo, P.
1967. Catálogo de la fauna Cubana. XXI. Hemípteros de Cuba. V. Familias Nabidae y Henicocephalidae. Mus. "Felipe Poey", La Habana, Trabajos de Divulgacion No. 46: 13 pp.

Ashmead, W. H.
1892a. Doings of societies. Entomol. News 3: 190–191.
1892b. Notes on the genus *Enicocephalus* Westwood, and descriptions of a new species from Utah. Proc. Entomol. Soc. Washington 2: 328–330.

Barber, H. G.
1939. Insects of Porto Rico and the Virgin Islands. Hemiptera-Heteroptera (excepting the Miridae and Corixidae). *In* New York Acad. Sci. Scientific Survey Porto Rico Virgin Is. 14: 263–441.
1953. A new subfamily, genus, and species belonging to the family Enicocephalidae (Hemiptera, Heteroptera). Am. Mus. Novitates 1614: 1–4.
1954. A report on the Hemiptera Heteroptera from the Bimini Islands, Bahamas, British West Indies. (Enicocephalidae) Am. Mus. Novitates 1682: 11.

Berg, C.
1883. Addenda et emendanda ad Hemiptera Argentina. Continuatio. An. Soc. Cient. Argentina 16: 105–125.
1893. Lebensweise von *Henicocephalus*. Berl. Entomol. Z. 38: 362.

Bergroth, E. E.
1889. Note sur le genre *Henschiella* Horvath. Rev. Entomol. 8: 319.
1893. Notes Hémiptèrologiques. Rev. Entomol. 12: 153–155.
1903. Neue myrmecophile Hemipteren. Wien. Entomol. Z. 22: 253–256.
1913. On some North American Hemiptera. Entomol. News 24: 263–267.
1916a. New and little-known Heteropterous Hemiptera in the United States National Museum. Proc. USNM 51(2150): 215–239.
1918. Studies in Philippine Heteroptera I. Philippine J. Sci. (D) 13: 43–126.
1927. Hemiptera Heteroptera from New Zealand. Trans. Proc. New Zealand Inst. 57: 671–684.

Blanchard, E.
1852. Order 7 Hemípteros. *In* C. Gay: Historia fisica y politica de Chile ... Zoologia 7: 113–320. Paris: Imprenta de Maulde y Renou.

Breddin, G.
1897. Hemipteren. *In* Hamburger Magalhaensische Sammelreise. Hamburg: L. Friederichsen & Co. pp. 1–36.

Bruner, S. C.
1924a. A new *Enicocephalus*. Bull. Brooklyn Entomol. Soc. 19: 39.
1924b. Una nueva especie de la familia Enicocephalidae (Hemiptera). Mem. Soc. Cubana Hist. Nat. "Felipe Poey" 6: 53–59.

Carayon, J.
1950. Observations sur l'accouplement, la ponte et l'éclosion chez les Hémiptères Henicocephalides de l'Afrique tropicale. Bull. Mus. Nat. Hist. Nat., ser. 2, 22(6): 739–745.
1951. Ecologie at regime alimentaire d'Hémiptères Hénicocéphalides africains. Bull. Soc. Entomol. de France 56: 39–44.
1962. Observations sur l'appareil odorifique des Héteroptères, particulierment celui des Tingidae, Vianaididae, et Piesmatidae. Cahiers des Naturalistes. Bull. Nat. Parisiens (n.s.) 18(1): 1–16.
1971. Notes et documents sur l'appareil odorant metathoracique des Hémiptères. Ann. Soc. Entomol. France (n.s.) 7(4): 737–770.
1984. Les androconies de certains Hémiptères Scutelleridae. Ann. Soc. Entomol. France (n.s.) 20(2): 113–134.

Champion, G. C.
1898. [Enicocephalidae]. *In* Biologia Centrali-Americana. Rhynochota, Hemiptera-Heteroptera 2: 158–162.

China, W. E.
1963. Hemiptera-Heteroptera collected by the Royal Society Expedition to South Chile 1958–1959. Ann. Mag. Nat. Hist. 5(13): 705–723.
Drake, C. J. and H. M. Harris
1927. Three new species of Enicocephalidae. Ohio J. Sci. 27: 102–103.
Hickman, V. V. and J. L. Hickman
1981. Observations on the biology of *Oncylocotis tasmanicus* (Westwood) with descriptions of the immature stages (Hemiptera, Enicocephalidae). J. Nat. Hist. 15: 703–715.
Jeannel, R.
1942(1941). Les Henicocephalides. Monographie d'un groupe d'Hémiptères hématophages. Ann. Soc. Entomol. France 110: 273–368.
1943. Les Henicocephalides de Fernando-Po (Hémiptères) Bull. Soc. Entomol. France 48: 114–117.
1944(1943). Nouveau Henicocephalides sudamericains. Bull. Soc. Entomol. France 48: 125–128.
Johannsen, O. A.
1909. North American Henicocephalidae. Psyche 16: 1–4.
Karsch, F.
1893(1892). Einige neue Wanzen der Aethiopischen Region. Berl. Entomol. Z. 37: 481–486.
Kerzhner, I. M.
1988a. Infraotryad Enicocephalomorpha. *In* P. A. Ler (ed.), Opredelitel' nasekomykh Dal'nego Vosoka SSSR v chesti tomakh. Tom. II. Ravnokrylye i poluzhestkokrylye. Nauka, Leningrad. 972 pp.
1988b(1987). Novye i moloizvestnye poluzhestkokrylye nasekomye s Dal'nego Vostoka SSSR. Akad. Nauk SSSR, Dal'nevostochnyi nauchnyj tsentr, Vladivostok. 83 pp.
Kirkaldy, G. W.
1901. An addition to the Rhynchotal fauna of New Zealand (*Henicocephalus maclachlani*). Entomol. Mon. Mag., ser. 2, 12: 217–219.
Knab, F.
1909. Swarming of a reduviid. Proc. Entomol. Soc. Washington 10: 7–8.
Kritsky, G.
1976. The Enicocephalidae (Hemiptera) in Illinois. Trans. Ill. State Acad. Sci. 69: 192–193.
1977a. Observations on the morphology and behavior of the Enicocephalidae (Hemiptera). Entomol. News 88(5&6): 105–110.
1977b. Two new genera of Enicocephalidae (Hemiptera). Entomol. News 88:(7&8): 161–168.
1978a. The north American and Caribbean species of *Systelloderes* (Hemiptera: Enicocephalidae). Entomol. News 89: (2&3): 65–73.
1978b. A new species of *Hymenocoris* from Mexico (Hemiptera: Enicocephalidae). Entomol. News 89:(2&3): 74–76.
1978c. The neotropical species of *Oncylocotis* (Hemiptera: Enicocephalidae). Pan. Pac. Entomol. 54(3): 194–198.
1979. A revision of the genus *Enicocephalus* (Hemiptera: Enicocephalidae). J. Agric. Univ. Puerto Rico 63: 91–99.
1981. Two new species of *Alienates* (Hemiptera: Enicocephalidae). Entomol. News 92: 130–132.
Lethierry, L., and G. Severin
1896. Catalogue Générale des Hémiptères. Brussels 3: 67.
Maldonado, J.
1948. A new *Enicocephalus* from Puerto Rico (Hemiptera, Enicocephalidae). Proc. Entomol. Soc. Washington 50(6): 159–160.
Polhemus, D. A.
1988. Observations on the swarming behavior of *Euchelichir longpipes* Jeannel in northern Madagascar (Heteroptera: Enicocephalidae). 96(1): 122–123.
Say, T.
1832. Descriptions of new species of heteropterous Hemiptera from North America. New Harmony, Indiana. 39 pp.
Schuh, R. T.
1970. Swarming in an undescribed Enicocephalid (Hemiptera) from Costa Rica. Entomol. News 81(3): 66–68.
Stål. C.
1860. Bidrag till Rio Janeiro-traktens Hemipter-fauna. K. Vetensk. Akad. Handl. 2(7): 3–84.
1866. Hemiptera Africana III. Holmiae: Officina Norstedtiana. 200 pp.
Štys, P.
1968(1967). A review of the genus *Henschiella* Horv. (Heteroptera: Enicocephalidae). Acta Univ. Carol. Biol. 1967: 327–347.
1969a(1968). Notes on the classification and nomenclature of Ethiopian Enicocephalidae (Heteroptera). Entomol. Mon. Mag. 104: 280–284.
1969b. Revision of fossil and pseudofossil En-

icocephalidae (Heteroptera). Acta Entomol. Bohemoslovaca 66: 352–365.

1970a(1968). Three new aberrant species of *Systelloderes* Blanch. from the Old World, and notes on tribal classification of the Enicocephalinae (Heteroptera, Enicocephalidae). Acta Univ. Carol. Biol. 1968: 435–454.

1970b. A review of the palaearctic Enicocephalidae (Heteroptera). Acta Entomol. Bohemoslovaca 67(4): 223–240.

1970c. A new species of the genus *Hoplitocoris* Jeannel from Ethiopia (Heteroptera: Enicocephalidae). Acta Entomol. Mus. Nat. Pragae 13(1968): 75–85.

1977. Female of *Aenictopechys necopinatus* (Heteroptera, Enicocephalidae) Vestnick Ceskoslovenské Spolecnosti Zoologické 41(3): 200–210.

1978(1977). An annotated list of the genera of Enicocephalidae (Heteroptera). Acta Entomol. Mus. Nat. Pragae 39: 241–252.

1980. *Australostolus monteithi* gen. n., sp. n. - first record of an Australian aenictopecheine bug (Heteroptera, Enicocephalidae). Acta Entomol. Bohemoslov. 77: 303–321.

1981a. A new subgenus and two new species of *Hoplitocoris* from the Philippine Islands (Heteroptera, Enicocephalidae). Acta Entomol. Bohemoslov. 78: 87–104.

1981b. A new relict subfamily, genus and species of Enicocephalidae from New Caledonia (Heteroptera). Acta Entomol. Bohemoslov. 78: 412–429.

1981c. Unusual sex ratios in swarming and light-attracted Enicocephalidae (Heteroptera). Acta Entomol. Bohemoslov. 78: 430–432.

1982a(1980). *Oncylocotis neotenicus* sp. n. from Sumatra—an extremely micropterous species of Enicocephalidae (Heteroptera). Acta Univ. Carol. Biol. 1980: 485–489.

1982b(1980). New genus, two new species, females and larvae of Monteithostolinae from New Caledonia (Heteroptera, Enicocephalidae). Acta Univ. Carol. Biol. 1980: 491–515.

1985(1981). Phallopiratinae - A new subfamily of plesiomorphic Enicocephalidae based on a new genus and four new species from the Oriental region (Heteroptera). Acta Univ. Carol. Biol. 1981: 269–310.

1986. A new plesiomorphic micropterous genus and species of Enicocephalidae from Papua, New Guinea (Heteroptera). Acta Entomol. Bohemoslov. 83: 62–73.

1988. A new aenictopecheine bug from Tasmania (Heteroptera, Enicocephalidae). Vestnick Ceskoslovenské Spolecnosti Zoolické 52: 302–315.

1989. Fylogenetická systematika nejprimitivnejsick plostic (Heteroptera: Enicocephalomorpha, Dipsocoromorpha). Práce Slov. Entomol. Spol. 8.

Uhler, P. R.

1892. Observations on some remarkable Heteroptera of North America. Trans. Maryland Acad. Sci. 1: 179–184.

Usinger, R. L.

1932. Miscellaneous studies in the Henicocephalidae (Hemiptera). Pan-Pacific Entomol. 8: 145–156.

1939. A new genus of Pacific Island Enicocephalidae with new species from the Hawaiian and Philippine Islands (Hemiptera). Proc. Haw. Entomol. Soc. 10(2): 267–270.

1945. Classification of the Enicocephalidae (Hemiptera, Reduvioidea). Ann. Entomol. Soc. Am. 38(3): 321–342.

Usinger, R. L., and P. Wygodzinsky

1960. Insects of Micronesia. Heteroptera. Enicocephalidae. B. P. Bishop Museum, Honolulu 7(5): 219–230.

Vasarhelyi, T.

1982. *Alienates dudichi* sp. n. from the Island St. Lucia (Heteroptera: Enicocephalidae). Acta Zool. Acad. Sci. Hung. 28 (1–2): 157–170.

Villiers, A.

1952a. Un nouveau *Systelloderes* du Venezuela (Hemiptera, Henicocephalidae). Bull. Mus. Nat. Hist. Nat., ser. 2, 25: 95–96.

1952b. Un nouveau *Systelloderes* de Madagascar (Hemiptera, Henicocephalidae). Memoires de L'institut Scientifique de Madagascar, sèr. E, 1(1): 101–102.

1956. Les Henicocephalidae (Heteroptera) de la collection de l'Institut Francais d'Afrique Noire. Mem. Soc. Roy. Entomol. Belgique 27: 484–494.

1958. Faune de Madagascar. 7 Insectes Hémiptères Enicocephalidae. Tananarive-Tsimbazaza, Institut de Recherches Scientifiques, 79 pp.

1959. Hémiptères Henicocephalides du Musée de Dundo. Publ. Cult. Comp. Diamantes Angola 45: 105–122.

1960. Revision des *Systelloderes* Africains. Rev. Francaise Entomol. 27(2): 155–162.

1961. Un Henicocephalid myrmecophile de l'Afrique australe: *Composoderes stuckenbergi*, n. sp. (Hemiptera). Ann. Natal Mus. 15(4): 69.

1963(1962). Hemiptera (Heteroptera): Heni-

cocephalidae. South African Animal Life 9: 324–336.

1968a. Hémiptères Henicocephalidae Explorations de Parc National Albert, 2° sér., 21(3): 45–64, Bruxelles.

1968b. Trois nouveaux *Systelloderes* d'Amerique Intertropicale (Hémiptères, Henicocephalidae). Ann. Mus. Civico Storia Nat. Genova 77: 338–341.

1969. Revision des Hémiptères Henicocephalidae Africains malagaches. Ann. Mus. R. Afrique Centr. Tervuren, sér. in-8°, Sci. Zool. 176: 1–232.

1978. Sur quelques hétéroptères de Guadaloupe (Henicocephalidae, Reduviidae). Ann. Soc. Entomol. Fr. (n.s.) 14: 727–734.

Walker, F.

1873. Catalogue of the specimens of Hemiptera-Heteroptera in the collection of the British Museum. 8: 22–23.

Westwood, J. O.

1837. Descriptions of several new genera of exotic hemipterous insects. Trans. Entomol. Soc. London 2: 18–24.

Wolcott, G. N.

1948. Insects of Puerto Rico. Hemiptera. J. Agric. Univ. P.R. 32(1): 210.

Woodward, T. E.

1956. The Heteroptera of New Zealand. Part II. The Enicocephalidae. Trans. Roy. Soc. New Zealand 84: 391–430.

Wygodzinsky, P.

1949. Redescription of *Gamostolus subantarcticus* (Berg, 1883) (Enicocephalidae, Hemiptera). Rev. Brasil. Biol. 9: 353–358.

Wygodzinsky, P., and P. Štys

1970. A new genus of Aenictopecheine bugs from the Holarctic (Enicocephalidae, Hemiptera). Am. Mus. Novitates 2411: 1–17.

1982. Two new primitive genera and species of Enicocephalidae from Singapore (Heteroptera). Acta Entomol. Bohemoslovaca 79: 127–142.

APPENDIX
Enicocephalid Measurements
(F = female; M = male; h = holotype; a = allotype; p = paratype)

Alienates Females: Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head
brevilobus	F (h+p)	2	.06/.05-.06	.09/.08-.09	.07/.06-.08	.15/.14-.15	.36/.34-.37	.18/.18-.18
dudichi	F (p)	1	.06	.06	.05	.13	.30	.13
elongatus	F (h)	1	.08	.09	.08	.13	.36	.18
insularis								
Bimini	F (p+3)	4	.05/.05-.05	.09/.09-.10	.09/.08-.10	.18/.18-.20	.41/.39-.45	.23/.23-.23
Florida	F	1	.05	.08	.06	.15	.34	.21
iviei	F (h+p)	2	.05/.05-.05	.06/.05-.06	.05/.04-.05	.12/.10-.13	.27/.24-.29	.14/.13-.14
maldonadoi	F (h+2p)	3	.08/.08-.08	.09/.09-.10	.08/.08-.09	.19/.18-.20	.44/.42-.46	.23/.21-.24
mexicanus	F (h+3p)	4	.06/.06-.06	.08/.08-.08	.06/.06-.08	.13/.13-.14	.34/.33-.35	.20/.18-.23
muchmorei	F (h+3p)	4	.05/.05-.05	.09/.09-.09	.07/.06-.08	.14/.14-.15	.35/.34-.37	.19/.18-.20
newtoni	F (h+2p)	3	.05/.05-.05	.07/.06-.08	.06/.05-.06	.14/.14-.15	.32/.30-.34	.18/.18-.18
roberti	F (h)	1	.09	.10	.09	.21	.49	.25

Species	Sex	N	Width head across eye lobe	Length eye lobe	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Length pronotum forelobe
brevilobus	F (h+p)	2	.17/.16-.18	---	.19/.18-.20	.05/.04-.05	.24/.23-.25	.11/.10-.11
dudichi	F (p)	1	.11	.08	.13	.05	.15	.05
elongatus	F (h)	1	.13	.06	.14	.06	.18	.05
insularis								
Bimini	F (p+3)	4	.15/.15-.16	---	.18/.16-.20	.05/.05-.06	.21/.20-.22	.07/.06-.08
Florida	F	1	.15	.09	.18	.05	.17 (?)	.06
iviei	F (h+p)	2	.11/.10-.11	.07/.05-.08	.12/.11-.13	.05/.04-.05	.15/.14-.15	.05/.04-.05
maldonadoi	F (h+2p)	3	.16/.15-.18	.11/.10-.11	.19/.18-.20	.06/.05-.06	.24/.22-.27	.07/.06-.09
mexicanus	F (h+3p)	4	.13/.13-.14	.08/.08-.09	.15/.14-.16	.05/.05-.05	.20/.20-.21	.06/.06-.06
muchmorei	F (h+3p)	4	.16/.15-.16	---	.19/.18-.19	.06/.05-.06	.21/.21-.21	.08/.08-.08
newtoni	F (h+2p)	3	.15/.14-.15	.08/.08-.09	.15/.15-.15	.03/.03-.03	.20/.20-.20	.08/.08-.09
roberti	F (h)	1	.18	.13	.18	.06	.33	.13

Alienates Females: Measurements (continued)

Species	Sex	N	Length pronotum hind lobe	Width pronotum forelobe	Width pronotum hind lobe	Length meso- and metanotum	Width meso- and metanotum
brevilobus	F (h+p)	2	.14/.13-.14	.24/.23-.25	.29/.28-.29	.12/.11-.13	.25/.24-.26
dudichi	F (p)	1	.10	.15	.21	.10	.20
elongatus	F (h)	1	.13	.16	.23	.14	.18
insularis							
Bimini	F (p+3)	4	.14/.14-.15	.20/.20-.21	.26/.25-.28	.10/.09-.11	.24/.23-.26
Florida	F	1	.11 (?)	.18	.24 (?)	.10	.21
iviei	F (h+p)	2	.10	.15/.14-.15	.18	.10/.09-.10	.15/.15-.15
maldonadoi	F (h+2p)	3	.17/.16-.18	.22/.21-.25	.30/.29-.33	.13/.11-.15	.30/.28-.35
mexicanus	F (h+3p)	4	.14/.13-.14	.19/.18-.20	.26/.25-.26	.12/.11-.13	.23/.23-.24
muchmorei	F (h+3p)	4	.13/.13-.13	.22/.21-.23	.26/.26-.26	.09/.08-.09	.24/.23-.24
newtoni	F (h+2p)	3	.12/.12-.13	.20/.20-.20	.25/.24-.25	.09/.09-.10	.25/.25-.26
roberti	F (h)	1	.20	.26	.35	.18	.33

Species	Sex	N	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
brevilobus	F (h+p)	2	.15/.14-.16	.06/.06-.06	.18/.16-.19	.08/.08-.08	.21/.19-.23	.06/.06-.06
dudichi	F (p)	1	.13	.06	.14	.06	.15	.05
elongatus	F (h)	1	.14	.08	.18	.10	.15	.06
insularis								
Bimini	F (p+3)	4	.19/.18-.20	.07/.06-.08	.19/.18-.21	.09/.08-.09	.22/.21-.23	.07/.06-.08
Florida	F	1	.16	.07	.17 (?)	.08	---	---
iviei	F (h+p)	2	.10/.10-.10	.05/.04-.05	.11/.10-.11	.05/.05-.05	.10/.10-.10	.04/.04-.04
maldonadoi	F (h+2p)	3	.20/.19-.20	.08/.08-.08	.23/.20-.25	.09/.09-.10	.23/.21-.24	.08/.08-.08
mexicanus	F (h+3p)	4	.17/.15-.19	.07/.06-.08	.18/.18-.19	.10/.10-.10	.18/.18-.18	.07/.06-.08
muchmorei	F (h+3p)	4	.17/.16-.18	.07/.06-.08	.19/.18-.20	.08/.07-.08	.20/.18-.20	.06/.06-.06
newtoni	F (h+2p)	3	.15/.14-.15	.05/.05-.06	.16/.15-.18	.07/.06-.08	.16/.15-.18	.05/.04-.06
roberti	F (h)	1	.23	.13	.31	.16	.30	.09

Alienates Males: Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes	Length eye
barberi	M (h)	1	.08	.11	.11	.20	.50	.20	---	.06
insularis										
Bimini	M (p)	1	.06	.13	.11	.20	.50	.19	.16	.08
Florida	M	1	.07	.14	.11	.21	.53	.23	.18	.08
millsi	M	3	.08/.08-.08	.16/.15-.18	.14/.14-.15	.23/.21-.24	.60/.60-.61	.22/.21-.23	.17/.16-.18	.09/.09-.09

Species	Sex	N	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Length pronotum forelobe	Length pronotum hind lobe
barberi	M (h)	1	---	.04	---	---	.08	.16	.05	.11
insularis										
Bimini	M (p)	1	.04	.05	.09	.18	.06	.19	.05	.14
Florida	M	1	.05	.04	.08	.18	.10	.20	.06	.14
millsi	M	3	.05/.05-.05	.04/.04-.04	.07/.06-.08	.16/.16-.16	.07/.06-.08	.16/.15-.16	.06/.05-.06	.10/.09-.11

Species	Sex	N	Width pronotum forelobe	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
barberi	M (h)	1	---	---	.19	.05	.20	.05	.21	.05
insularis										
Bimini	M (p)	1	.19	.29	.18	.05	.23	.06	.23	.05
Florida	M	1	.19	.30	.21	.06	.20	.06	.28	.06
millsi	M	3	.17/.16-.18	.30/.30-.30	.22/.21-.23	.06/.06-.06	.21/.20-.23	.06/.05-.06	.25/.25-.25	.05/.05-.06

Boreostolus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
americanus									
CO. (macrop.)	M(h)	1	.23	.63	.68	.54	2.10	.80	.41
OR. (microp.)	M	3	.24/.23-.25	.71/.63-.75	.72/.63-.78	.51/.48-.55	2.18/1.97-2.25	.88/.80-.93	.41/.38-.44
OR. (macrop.)	F(a+1)	2	.25/.25-.25	.63/.63-.63	.66/.63-.68	.53/.51-.55	2.06/2.01-2.10	.90/.90-.90	.46/.43-.48
WA. (macrop.)	F	1	.23	.65	.63	.55	2.06	.85	.45
OR. (brachy.)	F	1	.23	.70	.70	.55	2.18	.85	.45
OR. (microp.)	F	4	.26/.25-.26	.74/.70-.78	.73/.68-.79	.59/.58-.60	2.32/2.24-2.43	.94/.90-1.00	.45/.43-.46

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
americanus										
CO. (macrop.)	M(h)	1	.18	.09	.23	.24	.39	.25	.85	.95
OR. (microp.)	M	3	.14/.13-.15	.07/.06-.08	.25/.24-.28	.28/.25-.30	.39/.35-.41	.27/.25-.29	.86/.73-.98	.86/.75-.95
OR. (macrop.)	F(a+1)	2	.19/.18-.20	.10/.09-.10	.20/.20-.20	.27/.25-.28	.43/.43-.43	.31/.28-.33	.84/.83-.85	.88/.85-.90
WA. (macrop.)	F	1	.18	.09	.20	.28	.43	.28	.80	.84
OR. (brachy.)	F	1	.19	.10	.21	.25	.39	.26	.88	.85
OR. (microp.)	F	4	.15/.14-.15	.07/.06-.08	.27/.25-.28	.32/.30-.34	.43/.41-.44	.28/.25-.31	.96/.88-1.05	.93/.90-.98

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
americanus									
CO. (macrop.)	M(h)	1	1.10	.88	.30	1.13	.45	1.00	.28
OR. (microp.)	M	3	.82/.70-.89	.95/.91-1.03	.35/.28-.39	1.22/1.08-1.35	.51/.41-.60	1.08/1.00-1.13	.30/.25-.35
OR. (macrop.)	F(a+1)	2	.99/.90-1.08	.99/.95-1.03	.36/.33-.38	1.17/1.10-1.23	.46/.45-.46	1.02/.93-1.10	.28/.28-.28
WA. (macrop.)	F	1	.95	.98	.33	1.13	.40	1.00	.25
OR. (brachy.)	F	1	1.00	.95	.23	1.15	.44	1.05	.24
OR. (microp.)	F	4	.90/.88-.94	1.06/.95-1.20	.38/.35-.40	1.29/1.18-1.45	.55/.50-.60	1.07/.98-1.13	.33/.33-.33

Brevidorsus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
arizonensis									
Tucson and Sinaloa	M	3	.13/.13-.13	.38/.35-.43	.34/.33-.35	.34/.34-.35	1.19/1.14-1.24	.47/.46-.48	.32/.31-.33
Guasave	M	1	.15	.58	.48	.48	1.69	.58	.40
Sonora	M	1	.14	.48	.40	.40	1.42	.53	.34

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum hind lobe
arizonensis										
Tucson and Sinaloa	M	3	.20/.19-.21	.13/.11-.15	.10/.10-.10	.06/.03-.09	.29/.28-.30	.15/.14-.15	.32/.30-.34	.34/.33-.35
Guasave	M	1	.25	.18	.10	.05	.33	.18	.40	.43
Sonora	M	1	.20	.14	.13	.06	.31	.15	.29	.38

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
arizonensis									
Tucson and Sinaloa	M	3	.44/.41-.45	.48/.48-.48	.13/.13-.14	.48/.45-.50	.13/.13-.14	.53/.51-.55	.13/.13-.13
Guasave	M	1	.43	.63	.15	.58	.15	.73	.15
Sonora	M	1	.49	.55	.13	.48	.13	.58	.15

Chiricocoris Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
dybasi	F(h+1)	2	.23/.23-.23	.42/.40-.43	.58/.55-.60	.47/.45-.48	1.69/1.66-1.71	.93/.85-1.00	.41/.38-.43

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe hind	Maximum length pronotum	Width pronotum mid lobe
dybasi	F(h+1)	2	.19/.18-.19	.09/.08-.09	.19/.18-.19	.24/.23-.25	.39/.38-.40	.28/.28-.28	.72/.70-.73	.77/.75-.78

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
dybasi	F(h+1)	2	1.00/.94-1.05	1.04/.90-1.18	.44/.43-.45	.97/.93-1.00	.49/.48-.50	1.12/1.05-1.18	.33/.30-.35

Enicocephalus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
boraceianus	F (h)	1	.20	.33	.35	.43	1.30	.76	.55
cubanus									
Dom. Rep.	M	1	.19	.33	.55	.43	1.50	.63	.45
Haiti (Big)	M	1	.23	.43	.65	.58	1.90	.75	.54
Cuba	F	7	.18/.18-.20	.35/.34-.36	.51/.46-.53	.45/.43-.46	1.45/1.16-1.54	.65/.64-.68	.47/.44-.50
Jamaica	F	2	.19/.18-.20	.35/.34-.35	.49/.48-.50	.45/.45-.45	1.48/1.44-1.50	.74/.68-.80	.47/.45-.48
Dom. Rep.	F	1	.19	.34	.48	.40	1.41	.68	.48
"marimutti"	F	1	.21	.39	.52	.30	1.42	.85	.52
"yvonnae"	F	1	.18	.30	.45	.24	1.17	.73	.44
dominicus	M (h)	1	.20	.24	1.18	.75	2.37	.63	.44
exophthalmus	M (h+p)	2	.24/.23-.25	.82/.78-.86	.84/.80-.88	.58/.55-.60	2.48/2.36-2.59	.77/.73-.81	.50/.50-.50
flavicollis	M (h)	1	.15	.30	.35	.35	1.15	.65	.40
guarani	F (h+2p)	3	.20/.20-.20	.42/.40-.44	.55/.53-.60	.48/.48-.50	1.63/1.60-1.65	.78/.78-.79	.55/.55-.55
lenkoi	M (h+p)	2	.15/.14-.15	.32/.30-.34	.36/.33-.38	.38/.38-.38	1.19/1.16-1.24	.68/.68-.68	.41/.41-.41
	F (a+p)	2	.15/.15-.15	.32/.31-.32	.36/.36-.36	.38/.38-.38	1.21/1.21-1.21	.72/.70-.73	.45/.44-.45
neblinensis	M (h+p)	2	.14/.13-.15	.23/.23-.23	.26/.26-.26	.26/.26-.26	.89/0.88-0.90	.45/.43-.48	.30/.30-.30
ningulus									
R.J. area	M (a+p)	2	.15/.15-.15	.33/.30-.35	.34/.33-.35	.39/.38-.40	1.21/1.18-1.23	.55/.55-.55	.41/.40-.41
	F (h+4p)	5	.16/.15-.18	.32/.30-.34	.35/.30-.38	.38/.36-.43	1.21/1.14-1.30	.62/.60-.63	.17/.17-.17
Pernambuco	M	2	.15/.15-.15	.29/.28-.30	.33/.31-.35	.38/.38-.38	1.16/1.13-1.18	.64/.63-.65	.40/.40-.40
pilosus	F (h)	1	.20	.40	.48	.48	1.56	.85	.48
"emarginatus"	M	2	.13/.13-.13	.27/.25-.28	.32/.30-.33	.35/.34-.35	1.06/1.04-1.08	.68/.63-.73	.40/.40-.40
schuhi									
Sao Paulo	F (h+p)	2	.25/.25-.25	.56/.53-.58	.67/.66-.68	.56/.53-.59	2.03/1.99-2.08	.97/.95-.98	.65/.64-.65
R.J.	F	2	.20/.19-.20	.48/.46-.49	.57/.56-.58	.52/.51-.53	1.76/1.73-1.79	.89/.88-.90	.59/.58-.60
semirufus									
macrop.	M (h+1)	2	.18/.18-.18	.28/.28-.28	.44/.43-.45	.35/.34-.35	1.25/1.24-1.25	.55/.55-.55	.40/.39-.40
macrop.	F	1	.20	.39	.48	.40	1.47	.70	.44
brachyp.	F	3	.21/.20-.23	.42/.40-.44	.55/.50-.60	.49/.48-.50	1.67/1.60-1.75	.70/.69-.71	.43/.43-.44
sturmi									
macrop.	F (h)	1	.28	.79	.83	.66	2.56	1.13	.65
microp.	F (2p)	2	.29/.28-.30	.78/.78-.79	.81/.78-.84	.65/.65-.65	2.53/2.50-2.55	1.11/1.09-1.13	.64/.64-.65
taeuberi	M (h)	1	.15	.28	.35	.38	1.16	.63	.29
tupi	M (h+p)	2	.17/.16-.18	.29/.28-.30	.37/.36-.38	.14(1 only)	1.18(1 only)	.72/.71-.73	.48/.48-.48
	F (a+p)	2	.18/.18-.18	.39/.38-.40	.46/.43-.48	.42/.38-.45	1.43/1.35-1.50	.88/.88-.88	.55/.54-.55
usingeri	M (p)	1	.20	.43	.55	.45	1.67	.63	.50
wygodzinskyi	M (h+p+2)	4	.21/.20-.23	.44/.38-.48	.83/.78-.90	.54/.50-.58	2.02/1.95-2.08	.67/.65-.70	.44/.43-.45

Enicocephalus Measurements (continued)

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
boraceianus	F	1	.19	.14	.16	.28	.58	.33	1.03	.93
cubanus										
Dom. Rep.	M	1	.18	.13	.13	.20	.39	.26	.80	.61
Haiti (Big)	M	1	.21	.14	.19	.26	.48	.28	1.05	.73
Cuba	F	7	.16/.14-.19	.12/.10-.15	.17/.15-.18	.23/.20-.28	.46/.40-.49	.27/.24-.29	.85/.78-.93	.74/.69-.78
Jamaica	F	2	.16/.15-.16	.11/.10-.11	.19/.18-.19	.25/.25-.25	.49/.48-.49	.27/.26-.28	.89/.88-.89	.78/.78-.78
Dom. Rep.	F	1	.16	.11	.16	.25	.45	.26	.85	.79
"marimutti"	F	1	.17	.11	.20	.30	.48	.27	.97	.88
"yvonnae"	F	1	.15	.09	.17	.26	.45	.27	.79	.73
dominicus	M	1	.20	.14	.14	.16	.39	.26	.75	.63
exophthalmus	M	2	.22/.21-.23	.17/.16-.18	.16/.14-.18	.17/.15-.18	.42/.39-.45	.24/.23-.25	.69-.65-.74	.67/.65-.68
flavicollis	M	1	.18	.11	.13	.18	.38	.25	.78	.53
guarani	F	3	.17/.16-.18	.13/.13-.13	.20/.20-.20	.30/.30-.30	.59/.58-.61	.33/.33-.35	1.06/1.04-1.08	.93/.90-.95
lenkoi	M	2	.12/.11.13	.10/.10-.10	.14/.13-.14	.21/.21-.21	.43/.43-.43	.24/.23-.24	.75/.73-.78	.66/.65-.66
	F	2	.13/.13-.13	.10/.10-.10	.15/.15-.15	.25/.24-.25	.48/.48-.48	.25/.25-.25	.80/.79-.80	.74/.73-.75
neblinensis	M	2	.13/.13-.13	.08/.08-.08	.09/.09-.09	.15/.15-.15	.30/.30-.30	.20/.20-.20	.52/.50-.54	.41/.40-.41
ningulus										
R. J. area	M	2	.16/.15-.16	.10/.10-.10	.14/.13-.14	.21/.20-.21	.40/.39-.40	.25/.24-.25	.79/.78-.79	.63/.60-.65
	F	5	.12/.11-.13	.10/.09-.10	.15/.14-.18	.23/.23-.25	.44/.40-.48	.26/.25-.26	.82/.78-.88	.76/.70-.80
Pernambuco	M	2	.14/.14-.14	.10/.10-.10	.11/.11-.11	.20/.20-.20	.39/.39-.40	.24/.23-.25	.72/.70-.74	.63/.63-.63
pilosus										
"emarginatus"	F	1	.14	.10	.20	.28	.50	.24	.88	.74
	M	2	.15/.15-.15	.11/.11-.11	.10/.10-.10	.19/.18-.19	.39/.38-.40	.24/.23-.25	.72/.68-.75	.57/.53-.60
schuhi										
Sao Paulo	F	2	.22/.20-.23	.14/.13-.15	.25/.25-.25	.37/.35-.39	.63/.63-.63	.39/.38-.40	1.32/1.30-1.33	1.15/1.14-1.15
R. J.	F	2	.20/.19-.20	.14/.14-.14	.24-.23-.24	.32/.30-.33	.60/.60-.60	.36/.34-.38	1.19/1.18-1.20	1.02-1.01-1.03
semirufus										
macrop.	M	2	.17/.16-.18	.11/.11-.11	.11/.10-.11	.17/.16-.18	.38/.38-.38	.26/.26-.26	.71/.69-.73	.58/.55-.61
macrop.	F	1	.15	.10	.20	.24	.43	.29	.85	.75
brachyp.	F	3	.14/.14-.15	.08/.08-.09	.22/.21-.23	.27/.25-.29	.44/.43-.46	.25/.25-.26	.78/.75-.83	.80/.76-.83
sturmi										
macrop.	F	1	.21	.14	.31	.36	.65	.45	1.45	1.14
microp.	F	2	.22/.21-.23	.14/.14-.15	.31/.31-.31	.37/.36-.38	.64/.64-.65	.46/.43-.48	1.47/1.44-1.50	1.13/1.13-1.13
taeuburi	M	1	.12	.06	.11	.16	.34	.21	.60	.46
tupi	M	2	.20/.20-.20	.14/.14-.14	.13/.13-.13	.20/.20-.20	.42/.40-.44	.26/.25-.26	.84/.83-.85	.66/.65-.66
	F	2	.20/.19-.20	.14/.14-.14	.16/.15-.16	.27/.26-.28	.53/.53-.53	.30/.29-.30	1.00/1.00-1.00	.88/.85-.90
usingeri	M	1	.25	.19	.13	.13	.39	.25	.75	.33
wygodzinskyi	M	4	.17/.16-.18	.10/.10-.10	.18/.16-.19	.24/.23-.25	.42/.40-.43	.26/.25-.28	.86/.83-.88	.73/.66-.81

Enicocephalus Measurements (continued)

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
boraceianus	F	1	1.10	.80	.25	.88	.30	.90	.26
cubanus									
Dom. Rep.	M	1	.90	.80	.15	.80	.18	1.03	.16
Haiti (Big)	M	1	1.14	.98	.20	.98	.23	1.13	.18
Cuba	F	7	.90/.80-.98	.75/.73-.79	.23/.21-.25	.80/.75-.83	.26/.24-.29	.87/.80-.93	.20/.19-.21
Jamaica	F	2	.87/.85-.89	.74/.73-.74	.26/.25-.26	.80/.80-.80	.29/.28-.29	.84/.80-.88	.23/.23-.23
Dom. Rep.	F	1	.91	.70	.26	.78	.29	.83	.21
"marimutti"	F	1	1.03	.79	.24	.79	.27	.97	.15
"yvonnae"	F	1	.82	.67	.21	.77	.26	---	---
dominicus	M	1	.81	.93	.21	.85	.23	.93	.21
exophthalmus	M	2	.90/.85-.95	1.05/.98-1.13	.24/.23-.25	.95/.90-1.00	.27/.25-.28	1.04/.95-1.13	.21/.20-.21
flavicollis	M	1	.80	.75	.18	.83	.20	---	---
guarani	F	3	1.13/1.10-1.15	.94/.93-.95	.29/.28-.30	.95/.91-.99	.30/.29-.30	1.01/.98-1.05	.24/.23-.25
lenkoi	M	2	.87/.83-.90	.59/.58-.60	.19/.18-.19	.64/.63-.65	.18/.18-.18	.67/.65-.68	.17/.16-.18
	F	2	.89/.88-.90	.59/.58-.60	.20/.19-.20	.69/.68-.70	.20/.19-.20	.75/.75-.75	.20/.19-.20
neblinensis	M	2	.62/.60-.63	.52/.50-.53	.13/.13-.13	.52/.50-.53	.13/.13-.13	.58/.55-.60	.10/.10-.10
ningulus									
R. J. area	M	2	.95/.94-.96	.68/.65-.70	.16/.15-.16	.69/.66-.71	.15/.15-.15	.87/.85-.88	.16/.15-.16
	F	5	.94/.91-.98	.67/.58-.75	.19/.18-.21	.69/.66-.73	.20/.18-.21	.82/.78-.86	.20/.18-.23
Pernambuco	M	2	.87/.85-.88	.64/.63-.65	.15/.15-/15	.67/.65-.68	.17/.15-.18	.80/.80-.80	.16/.16-.16
pilosus	F	1	.90	.88	.23	.83	.23	.78	.20
"emarginatus"	M	2	.83/.80-.85	.64/.60-.68	.14/.14-.14	.71/.68-.73	.15/.14-.15	.69/.63-.75	.17/.16-.18
schuhi									
Sao Paulo	F	2	1.44/1.40-1.47	1.10/1.08-1.11	.36/.33-.39	1.15/1.10-1.20	.42/.39-.45	1.23/1.20-1.25	.34/.33-.35
R. J.	F	2	1.32/1.28-1.35	1.03/1.00-1.05	.33/.30-.36	1.05/1.00-1.10	.40/.38-.41	1.09/1.03-1.15	.32/.30-.33
semirufus									
macrop.	M	2	.83/.80-.85	.68/.68-.68	.17/.15-.18	.72/.70-.74	.19/.18-.19	.84/.78-.90	.15/.14-.15
macrop.	F	1	.90	.75	.23	.83	.28	.85	.21
brachyp.	F	3	.71/.69-.73	.76/.75-.78	.25/.23-.28	.85/.83-.88	.32/.30-.34	.87/.85-.88	.25/.25-.26
sturmi									
macrop.	F	1	1.61	1.39	.39	1.40	.36	1.49	.28
microp.	F	2	1.65/1.60-1.70	1.41/1.38-1.43	.37/.36-.38	1.36/1.33-1.38	.35/.35-.35	1.46/1.45-1.47	.27/.25-.28
taeuberi	M	1	.74	.68	.13	.64	.16	.76	.11
tupi	M	2	1.03/1.00-1.06	.73	.19	.70	.19	.78/.75-.80	.15/.11-.18
	F	2	1.07/1.05-1.08	.77/.75-.78	.27/.25-.28	.88/.85-.90	.33/.33-.33	.92/.85-.98	.10
usingeri	M	1	.41	.75	.16	.80	.23	.93	.18
wygodzinskyi	M	4	.90/.85-.95	.85/.80-.88	.21/.20-.21	.91/.85-1.00	.24/.23-.28	1.02/.95-1.05	.19/.18-.23

Gamostolus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
subantarcticus									
Punta Arenas									
and south	M	3	.27/.26-.28	.53/.50-.55	.60/.55.-63	.49/.48-.50	1.89/1.84-1.94	.88/.85-.90	.55/.54-.58
	F	3	.34/.30-.38	.69/.60-.75	.75/.65-.80	.58/.50-.63	2.37/2.05-2.56	1.08/1.03-1.10	.71/.68-.73
"cotype"	F	1	.30	.63	.68	.56	2.17	1.20	.70
Osorno	F	1	.33	.66	.73	.63	2.34	1.08	.70
	M	1	.28	.60	.64	.55	2.06	.93	.55

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
subantarcticus										
Punta Arenas										
and south	M	3	.24/.23-.25	.14/.13-.15	.13/.13-.14	.28/.28-.29	.49/.48-.50	.28/.25-.30	.77/.75-.79	1.02/.95-1.10
	F	3	.28/.28-.29	.15/.14-.15	.19/.18-.23	.42/.40-.43	.73/.69-.78	.28/.25-.30	1.16/1.08-1.28	1.31/1.25-1.35
"cotype"	F	1	.30	.15	.20	.40	.68	.43	1.18	1.45
Osorno	F	1	.24	.13	.18	.45	.68	.38	1.08	1.25
	M	1	.23	.14	.13	.28	.50	.33	.80	.98

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
subantarcticus									
Punta Arenas									
and south	M	3	1.28/1.18-1.35	1.14/1.08-1.18	.37/.36-.38	1.08/1.05-1.15	.46/.45-.48	1.38/1.25-1.48	.27/.25-.29
	F	3	1.58/1.48-1.68	1.51/1.38-1.60	.59/.53-.63	1.50/1.43-1.63	.68/.58-.78	1.80(1 only)	.40(1 only)
"cotype"	F	1	1.75	1.45	.50	1.50	.43	1.33	.40
Osorno	F	1	1.50	1.50	.53	1.48	.73	1.53	.38
	M	1	1.30	1.18	.43	1.20	.48	1.68	.28

Hymenocoris Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
brunneocephalus formicina	M(h+p)	2	.25(1 only)	.80	.78	---	---	.80/.80-.80	.46/.45-.46
CA (typical)	M	5	.28/.28-.28	1.00/.98-1.03	.91/.88-.93	.64/.60-.70	2.83/2.78-2.88	.84/.75-.93	.37/.34-.40
Auberry	M	1	.23	.85	.88	.58	2.54	.78	.35
Adobe Cr.	M	1	.30	1.08	1.00	.78	3.16	.95	.45
ARIZONA	M	1	.28	.90	.80	.63	2.61	.80	.34
MEX., Baja	M	1	.28	.90	.75	.58	2.51	.85	.36
CA. San Bruno	F	2	.24/.23-.25	.83/.73-.93	.91/.83-.98	.60(1 only)	2.40	1.13/1.00-1.25	.42/.38-.45

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
brunneocephalus formicina	M(h+p)	2	.29/.28-.29	.18/.18-.18	.20/.20-.20	.11/.10-.11	.37/.35-.38	.28/.28-.28	.56/.53-.59	.57/.56-.58
CA. (typical)	M	5	.19/.16-.20	.11/.10-.13	.24/.19-.28	.14/.11-.16	.37/.33-.40	.28/.26-.30	.56/.50-.60	.55/.45-.58
Auberry	M	1	.19	.11	.20	.13	.35	.25	.55	.48
Adobe Cr.	M	1	.25	.14	.30	.18	.41	.30	.73	.65
ARIZONA	M	1	.19	.10	.24	.14	.34	.26	.54	.48
MEX., Baja	M	1	.19	.10	.29	.16	.39	.30	.64	.54
CA. San Bruno	F	2	.10/.09-.10	.04/.04-.04	.45/.39-.51	.34/.30-.38	.42/.41-.43	.34/.30-.38	.90/.85-.95	.88/.80-.95

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
brunneocephalus formicina	M(h+p)	2	.83/.83-.83	.93/.90-.95	.25/.24-.25	.94/.93-.95	.25/.25-.25	.96(1 only)	.19
CA. (typical)	M	5	.93/.79-1.00	1.07/.98-1.13	.26/.23-.29	1.01/.93-1.05	.24/.20-.26	1.16/.98-1.30	.17/.14-.20
Auberry	M	1	.83	.95	.24	.88	.21	1.05	.18
Adobe Cr.	M	1	1.10	1.20	.31	1.15	.33	1.35	.19
ARIZONA	M	1	.80	1.00	.23	.95	.19	1.00	.13
MEX., Baja	M	1	.90	1.05	.26	1.00	.25	1.08	.16
CA. San Bruno	F	2	.79/.73-.85	1.22/1.15-1.28	.49/.48-.50	1.18/1.05-1.30	.62/.55-.68	1.23(1 only)	.30(1 only

Lysenicocephalus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
chemsaki	M(h)	1	.14	.35	.39	---	---	.46	.34
macneilli	M(h)	1	---	---	---	---	---	.65	.38

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
chemsaki	M(h)	1	.19	.13	.09	.09	.29	.18	.33	.38
macneilli	M(h)	1	.25	.15	.13	.08	.33	.21	.44	.43

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
chemsaki	M(h)	1	.53	.53	.15	.50	.15	.60	.14
macneilli	M(h)	1	.58	.65	.20	.65	.20	---	---

Neoncylocotis Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
albovenosus	M	3	.15/.14-.15	.31/.30-.33	.42/.40-.43	.33/.33-.33	1.21/1.18-1.21	.75/.73-.75	.37/.36-.38
	F	3	.16/.15-.18	.38/.38-.40	.47/.45-.50	.37/.35-.38	1.38/1.33-1.43	.88/.86-.90	.40/.40-.41
alvarengai	M	1	.13	.20	.26	.23	.82	.50	.28
annulipes	F	2	.17/.16-.18	.38/.38-.38	.38/.38-.39	.34/.34-.35	1.27/1.26-1.28	.86/.85-.88	.40/.40-.40
clavisetosus	M	3	.16/.15-.16	.39/.38-.43	.38/.38-.39	.29/.26-.30	1.22/1.20-1.24	.85/.84-.85	.41/.40-.41
concolor	F	1	.15	.39	---	---	---	.81	.45
nr.con.(BM)	F	1	.15	.40	.34	.30	1.19	.85	.43
nr.con.(Pan)	F	2	.14/.14-.14	.41/.40-.41	.29/.29-.30	.31/.30-.31	1.15/1.13-1.16	.76/.74-.78	.40/.40-.40
meridionalis	F	1	.16	.40	.34	.33	1.23	.84	.43
mexicanus	F	3	.15/.14-.15	.30/.29-.30	.29/.27-.32	.28/.28-.29	1.02/1.00-1.04	.72/.65-.76	.41/.38-.42
montanus	M	6	.15/.14-.15	.32/.30-.34	.38/.35-.40	.28/.26-.29	1.20/1.08-1.20	.74/.71-.78	.34/.31-.35
pisinnus	F	4	.11/.10-.11	.19/.18-.20	.21/.20-.23	.22/.21-.23	.73/.69-.76	.55/.54-.56	.31/.31-.31
rhyparus	M	1	---	---	---	---	---	.68	---
rubripes	M	4	.13/.13-.14	.23/.23-.24	.26/.25-.28	.28/.28-.28	.90/.88-.91	.62/.60-.63	.34/.34-.35
slateri	F	2	.13	.28/.28-.29	.29/.29-.30	.26	.96/.94-.99	.69/.68-.71	.38/.38-.39
nr. slateri	F	3	.12/.11-.13	.24/.21-.29	.25/.21-.28	.26/.26-.26	.87/.80-.95	.65/.61-.73	.36/.36-.36
stannardi	F	6	.15/.14-.15	.31/.31-.33	.28/.25-.30	.30/.28-.33	1.00/1.00-1.10	.68/.65-.70	.36/.34-.39
weyrauchi	F	4	.18/.15-.20	.51/.48-.55	.48/.45-.50	.38/.38-.39	1.55/1.46-1.60	1.06/1.03-1.10	.48/.48-.49

Neoncylocotis Measurements (continued)

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
albovenosus	M	3	.15/.15-.16	.09/.09-.09	.14/.14-.14	.19/.19-.20	.38/.38-.39	.26/.25-.28	.75/.74-.78	.61/.60-.63
	F	3	.14/.13-.15	.09/.09-.10	.18/.18-.20	.22/.21-.23	.43/.43-.45	.29/.28-.30	.83/.80-.88	.70/.66-.75
alvarengai	M	1	.11	.07	.09	.14	.31	.18	.50	.48
annulipes	F	2	.13/.13-.14	.08/.08-.08	.18/.18-.18	.25/.25-.25	.43/.43-.43	.28/.28-.29	.78/.78-.79	.68/.68-.68
clavisetosus	M	3	.17/.16-.18	.10/.10-.10	.15/.15-.16	.21/.20-.21	.40/.40-.41	.30/.30-.30	.86/.83-.90	.68/.65-.70
concolor	F	1	.15	.10	.15	.25	.45	.28	.75	.73
nr. con.(BM)	F	1	.14	.09	.16	.25	.45	.28	.80	.75
nr. con.(Pan)	F	2	.13/.13-.13	.09/.09-.10	.15/.15-.15	.21/.20-.23	.44/.44-.45	.27/.26-.28	.71/.68-.75	.68/.65-.71
meridionalis	F	1	.15	.10	.15	.23	.48	.28	.85	.78
mexicanus	F	3	.13/.11-.14	.09/.09-.10	.13/.12-.16	.22/.20-.24	.43/.42-.45	.24/.21-.26	.63/.57-.67	.66/.60-.72
montanus	M	6	.13/.13-.15	.09/.08-.09	.15/.14-.15	.17/.16-.18	.35/.34-.36	.25/.23-.25	.73/.70-.75	.54/.53-.58
pisinnus	F	4	.10/.10-.10	.06/.06-.06	.10/.10-.10	.19/.19-.19	.35/.35-.35	.18/.18-.20	.51/.50-.53	.53/.51-.55
rhyparus	M	1	.11	---	.10	.18	.34	.23	---	.50
rubripes	M	4	.13/.13-.13	.08/.06-.09	.10/.10-.11	.19/.18-.21	.34/.33-.35	.23/.23-.24	.64/.60-.66	.57/.54-.58
slateri	F	2	.10/.10-.10	.08/.08-.08	.15/.15-.15	.23/.23-.24	.41/.40-.43	.24/.24-.25	.65/.63-.68	.67/.66-.68
nr. slateri	F	3	.12/.11-.13	.08/.08-.08	.12/.11-.13	.21/.21-.21	.40/.40-.40	.23/.21-.25	.60/.58-.63	.61/.58-.63
stannardi	F	6	.11/.10-.11	.08/.06-.09	.14/.13-.15	.21/.20-.23	.40/.38-.43	.23/.21-.25	.62/.60-.63	.64/.63-.66
weyrauchi	F	4	.17/.15-.19	.10/.10-.13	.24/.23-.25	.28/.28-.29	.49/.48-.50	.35/.33-.38	.94/.90-1.03	.84/.83-.88

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
albovenosus	M	3	1.01/.99-1.04	.78/.75-.83	.21/.20-.23	.81/.80-.83	.17/.15-.19	.95/.95-.96	.17/.15-.19
	F	3	1.03/1.00-1.05	.83/.80-.88	.28	.86/.85-.88	.23/.21-.24	.99/.98-1.00	.23
alvarengai	M	1	.68	.53	.15	.50	.11	.60	.11
annulipes	F	2	.91/.91-.91	.76/.75-.78	.23/.23-.23	.76/.75-.78	.20/.20-.20	.90/.88-.93	.19/.19-.20
clavisetosus	M	3	1.19/1.13-1.25	1.05/1.00-1.10	.23/.23-.23	.97/.93-1.03	.19/.18-.20	1.18/1.08-1.23	.18/.16-.19
concolor	F	1	1.03	.80	.25	.83	.25	.88	.19
nr. con.(BM)	F	1	1.04	.78	.25	---	.25	.88	.20
nr. con.(Pan)	F	2	.98/.95-1.00	.77/.75-.79	.20/.20-.20	.74/.73-.76	.21/.19-.23	.93/.88-.94	.14/.13-.15
meridionalis	F	1	1.05	.88	.26	.86	.29	1.05	.23
mexicanus	F	3	.89/.82-.94	.73/.71-.75	.21/.20-.23	.69/.60-.75	.21/.19-.24	.80/.76-.85	.15/.14-.16
montanus	M	6	.88/.83-.94	.74/.68-.80	.21/.20-.21	.75/.70-.78	.16/.14-.18	.93/.88-.98	.16/.15-.18
pisinnus	F	4	.70/.70-.70	.48/.48-.50	.17/.15-.19	.51/.50-.53	.17/.16-.18	.57/.55-.58	.14
rhyparus	M	1	.84	---	---	---	---	---	---
rubripes	M	4	.89/.85-.90	.66/.64-.68	.18/.18-.19	.69/.68-73	.17/.15-.18	.84/.78-.90	.15/.15-.15
slateri	F	2	.93/.93-.93	.63/.63-.63	.23/.23-.23	.63/.60-.66	.21/.20-.21	.79/.78-.80	.18/.18-.19
nr. slateri	F	3	.82/.80-.85	.56/.53-.61	.19/.18-.23	.59/.53-.63	.18/.16-.20	.71/.65-.78	.17/.15-.19
stannardi	F	6	.86/.83-.91	.67/.65-.70	.21/.19-.21	.64/.63-.68	.20/.19-.21	.77/.73-.80	.16/.15-.18
weyrauchi	F	4	1.30/1.25-1.38	1.06/1.00-1.13	.30/.28-.33	1.00/.93-1.13	.28/.26-.30	1.22/1.13-1.35	.26/.23-.28

Tornocrusus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
aguilari	F (h)	1	.20	.29	.33	.29	1.11	.48	.36
browni	F (h)	1	.18	.33	.31	.29	1.11	.55	.40
incaicus	M (h)	1	.20	.38	.39	.35	1.32	.49	.41
occidentalis	M (h+2p)	3	.22/.20-.23	.34/.33-.35	.38/.38-.38	.32/.31-.33	1.26/1.22-1.29	.52/.50-.55	.41/.40-.41
	F (a)	1	.25	.45	.45	.38	1.53	.60	.51
penai	M (3p)	3	.23/.20-.25	.39/.38-.40	.43/.41-.45	.36/.34-.38	1.41/1.35-148	.54/.53-.56	.45/.45-.45
	F (a)	1	.28	.43	.50	.38	1.59	.60	.51
sturmi	F (h)	1	.25	.43	.48	.42	1.58	.65	.49
stysi	M (h)	1	.18	.28	.30	.33	1.09	.45	.35
venezolanus	F (h)	1	.21	.33	.36	.33	1.30	.49	.43

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum length pronotum	Width pronotum mid lobe
aguilari	F (h)	1	.11	.06	.10	.24	.35	.10	.43	.55
browni	F (h)	1	.15	.06	.05	.28	.36	.10	.39	.58
incaicus	M (h)	1	.18	.10	.04	.21	.39	.16	.45	.51
occidentalis	M (h+2p)	3	.17/.16-.18	.10/.10-.10	.08/.08-.08	.21/.20-.21	.38/.38-.38	.12/.10-.13	.43/.43-.43	.52/.50-.53
	F (a)	1	.19	.09	.10	.34	.48	.13	.58	.65
penai	M (3p)	3	.17/.16-.18	.10/.10-.11	.05/.05-.05	.24/.23-.25	.41/.40-.43	.15/.14-.15	.54/.53-.55	.60/.58-.63
	F (a)	1	.18	.10	.08	.31	.50	.15	.65	.73
sturmi	F (h)	1	.15	.08	.09	.34	.48	.15	.53	.68
stysi	M (h)	1	.15	.09	.06	.18	.33	.13	.40	.63
venezolanus	F (h)	1	.15	.08	.06	.28	.40	.11	.44	.60

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
aguilari	F (h)	1	.63	.60	.20	.65	.35	.70	.18
browni	F (h)	1	.65	.50	.20	.63	.33	.75	.20
incaicus	M (h)	1	.63	.60	.20	.75	.25	1.05	.15
occidentalis	M (h+2p)	3	.60/.59-.61	.65/.63-.68	.22/.20-.23	.69/.66-.70	.30/.30-.30	.97/.95-.98	.18
	F (a)	1	.76	.80	.28	.93	.48	1.10	.25
penai	M (3p)	3	.72/.68-.75	.76/.73-.80	.27/.25-.30	.81/.80-.83	.35/.30-.38	1.13/1.08-1.18	.22/.21-.24
	F (a)	1	.85	.83	.33	.98	.48	1.05	.25
sturmi	F (h)	1	.78	.83	.28	.90	.40	1.00	.21
stysi	M (h)	1	.68	.70	.26	.70	.30	.91	.16
venezolanus	F (h)	1	.65	.68	.23	.75	.41	.80	.21

Urnacephala Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total length antenna	Length head	Width head across eyes
californica									
holotype	M	1	.23	.65	.43	.40	1.71	.58	.26
others	M	5	.19/.15-.23	.58/.48-.68	.39/.33-.43	.40/.35-.45	1.56/1.31-1.79	.62/.56-.70	.28/.25-.30

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind lobe head	Length hind lobe head	Maximum Length pronotum	Width pronotum mid lobe
californica										
holotype	M	1	.14	.08	.18	.11	.30	.26	.38	.33
others	M	5	.17/.15-.19	.10/.08-.11	.16/.13-.20	.09/.08-.13	.30/.29-.30	.25/.23-.29	.35/.33-.38	.31/.28-.33

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
californica									
holotype	M	1	.55	.58	.10	.48	.09	.70	.09
others	M	5	.50/.48-.54	.59/.53-.68	.12/.11-.13	.52/.48-.58	.11/.10-.13	.57/.55-.60	.10/.09-.11

Xenicocephalus Measurements (mean/range in mm)

Species	Sex	N	Length antennal segment I	Length antennal segment II	Length antennal segment III	Length antennal segment IV	Total Length antenna	Length head	Width head across eyes
sp. (nymph V)	-	1	.30	.88	.68	.80	2.66	1.15	.70

Species	Sex	N	Length eye	Width eye	Anteocular distance	Synthlipsis	Width hind Lobe head	Length hind Lobe head	Maximum length pronotum	Width pronotum mid lobe
sp. (nymph V)	-	1	.24	.13	.30	.45	.71	.43	1.08	---

Species	Sex	N	Width pronotum hind lobe	Length fore tibia	Width fore tibia	Length fore femur	Width fore femur	Length hind femur	Width hind femur
sp. (nymph V)	-	1	1.50	1.20	.34	1.25	.56	1.53	.33

INDEX OF SCIENTIFIC NAMES

Boldfaced page numbers refer to main discussion of taxon in text. Names in italics are synonyms.

Aenictopecheinae, 13, 14, 16, 18, 21, 22, 24, 25, 30, 31, 36, **38**
Aenictopechys Breddin, 30, 31
aguilari (Villiers) (Tornocrusus), 63, **65**, 71, 258
albovenosus, n. sp. (Neoncylocotis), 20, 22, 29, 164, **167**, 169, 170, 171, 172, 173, 174, 176, 256, 257
Alienates Barber, 8, 9, 11, 14, 15, 16, 18, 19, 21, 23, 28, 29, 33, 34, 35, 36, 37, 126, 207, 208, 211, 214, 244, 245, 246
Alienatinae, 13, 16, 21, 24, 26, 27, 30, 33, 34, 36, **207**
alvarengai, n. sp. (Neoncylocotis), 27, 166, 173, 174, 256
americanus Wygodzinsky and Štys (Boreostolus), 9, 17, 20, 21, 25, 27, 29, 38, 39, 40, 41, 42, 43, 44, **45**, 47, 48, 49, 50, 51, 61, 247
angustatus Champion (Systelloderes), 9, 86
annulipes (Champion) (Neoncylocotis), 167, **175**, 176, 256
arizonensis Kritsky (Brevidorsus), 18, 20, 27, 29, 32, 87, **92**, 93, 94, 95, 96, 248
Australostolus Štys, 30, 31

barberi Kritsky (Alienates), 214, 215, 216, 246
biceps (Say) (Systelloderes), 86
boraceianus, n. sp. (Enicocephalus), 27, **107**, 111, 118, 250
Boreostolus Wygodzinsky and Štys, 8, 15, 16, 17, 19, 21, 26, 28, 30, 31, 34, 36, **38**, 39, 46, 247
borneensis Štys (Phallopirates), 33
braziliensis (Kritsky) (Neoncylocotis), 5, 189, 192
Brevidorsus Kritsky, 8, 11, 12, 16, 19, 26, 28, 33, 34, 35, 37, **87**, 89, 160, 196, 248
brevilobus, n. sp. (Alienates), 27, 212, 215, **216**, 217, 244, 245
browni, n. sp. (Tornocrusus), 64, 65, **71**, 72, 258
brunneocephalus, n. sp. (Hymenocoris), 146, **145**, 152, 153, 254

californica, n. sp. (Urnacephala), 20, 23, 27, 29, 33, 194, 195, 196, 197, **198**, 199, 200, 201, 202, 259
chemsaki, n. sp. (Lysenicocephalus), 27, 160, **161**, 162, 163, 255
Chinella Usinger, 103, 104
Chiricocoris, n. gen., 5, 8, 16, 19, 25, 28, 35, 36, 37, **95**, 97, 249
clavisetosus, n. sp. (Neoncylocotis), 29, 165, 166, 167, 171, 173, **176**, 177, 178, 256
Compsoderes Jeannel, 85
concolor (Champion) (Neoncylocotis), 167, **179**, 180, 256
crassatus Usinger (Systelloderes), 86
cubanus Bruner (Enicocephalus), 5, 105, **107**, 112, 113, 114, 145, 250, 251, 252
culicis (Uhler) (Systelloderes), 19, 20, 22, 23, 25, 27, 29, 86, 87, 88, 89, 90, 91

dominicus Bruner (Enicocephalus), 103, 104, **113**, 115, 250, 251, 252
doriai Villiers (Systelloderes), 86
dorsalus Kritsky (Systelloderes), 86
dudichi Vasarhelyi (Alienates), 214, 215, **217**, 218, 226
dybasi, n. sp. (Chiricocoris), 20, 25, 27, 29, 95, **97**, 98, 99, 100, 101, 102, 244, 245, 249

elongatus, n. sp. (Alienates), 215, **218**, 219, 227, 244, 245
emarginatus (Champion) (Enicocephalus), 5, 103, 127
Enicocephalinae, 13, 14, 16, 21, 22, 24, 26, 30, 33, 34, 36, **85**
Enicocephalini, 33, 34, 86, **87**
Enicocephalus Westwood, 8, 11, 15, 16, 17, 18, 19, 21, 28, 32, 33, 34, 37, **103**, 104, 106, 204, 250, 251, 252
Euchelichir Jeannel, 29
exophthalmus, n. sp. (Enicocephalus), 104, 105, **116**, 117, 139, 250, 251, 252

flavicollis Westwood (Enicocephalus), 103, 105, **116**, 118, 250, 251, 252
formicinus Uhler (Hymenocoris), 9, 10, 11, 12, 13, 17, 20, 23, 26, 27, 29, 32, 33, 34, 143, 145, 146, 147, 148, **149**, 150, 151, 154, 155, 156, 157, 158, 159, 160, 199, 254

Gamostolini, **38**
Gamostolus Bergroth, 8, 15, 16, 19, 20, 21, 26, 28, 30, 31, 36, **46**, 253
giganticus, n. sp. (Xenicocephalus), 27, 200, 204, **205**
grandes Kritsky (Systelloderes), 9, 86
guarani, n. sp. (Enicocephalus), 107, **118**, 119, 250, 251, 252
guigliae Villiers (Systelloderes), 86

harroyi Villiers (Systelloderes), 86
Henicocephalus Agassiz, 50, 103
hintoni Kritsky (Hymenocoris), 145, 146, **159**, 160
Hymenocoris Uhler, 8, 11, 12, 14, 15, 16, 19, 21, 28, 33, 34, 37, **142**, 145, 146, 160, 196, 203, 254
Hymenodectes Uhler, 85

incaicus, n. sp. (Tornocrusus), 63, 64, **73**, 74, 258
insularis Barber (Alienates), 15, 18, 34, 208, 211, 212, 213, 214, 215, **220**, 221, 222, 223, 224, 225, 230, 233, 244, 245, 246
inusitatus Drake and Harris (Systelloderes), 86
iowensis Drake and Harris (Systelloderes), 11, 87
iviei, n. sp. (Alienates), 215, 217, **226**, 244, 245

jamaicensis Kritsky (Systelloderes), 87

lateralus Kritsky (Systelloderes), 87
lenkoi, n. sp. (Enicocephalus), 9, 105, **119**, 120, 121, 123, 135
Lomagostus Villiers, 30, 31, 65, 68
longiceps Jeannel (Systelloderes), 87
Lysenicocephalus, n. gen., 5, 8, 11, 12, 15, 16, 19, 26, 28, 33, 34, 35, 37, **160**, 161, 162, 196, 255

maclachlani group (Systelloderes), 4
macneili, n. sp. (Lysenicocephalus), 161, **162**, 164, 255
magnus Woodward (Phthirocoris), 34
maldonadoi, n. sp. (Alienates), 213, 214, 215, 225, 226, 227, **228**, 229, 230, 244, 245
Maoristolus Woodward, 30
marimutti Kritsky (Enicocephalus), 5, 108, 112
Megenicocephalus Usinger, 204
meridionalis, n. sp. (Neoncylocotis), 167, **180**, 181, 256
mexicanus (Kritsky) (Neoncylocotis), 167, **182**, 231, 233, 182, 190, 256
mexicanus, n. sp. (Alienates), 215, **230**, 231, 232, 233, 244, 245
millsi Kritsky (Alienates), 17, 20, 23, 27, 29, 33, 209, 210, 211, 214, **232**, 234, 246
montanus, n. sp. (Neoncylocotis), 25, 167, **183**, 184, 256
monteithi Štys (Australostolus), 7, 26, 30
Monteithostolinae, 33, 34
Monteithostolini, 30
Monteithostolus Štys, 30, 32, 33, 34
moschatus Blanchard (Systelloderes), 85, 87
moschatus group (Systelloderes), 4
muchmorei, n. sp. (Alienates), 213, 214, **235**, 236, 244, 245

neblinensis, n. sp. (Enicocephalus), 105, **121**, 122, 250, 251, 252
necopinatus Štys (Aenictopechys), 34
Neoncylocotis, n. gen., 5, 8, 11, 16, 17, 18, 19, 21, 28, 32, 33, 34, 37, **164**, 166, 168, 194, 256, 257
Nesenicocephalus Usinger, 11
newtoni, n. sp. (Alienates), 215, **237**, 244, 245
ningulus, n. sp. (Enicocephalus), 16, 20, 24, 29, 32, 103, 105, 108, 109, 110, 119, **123**, 124, 125, 135, 250, 251, 252
nitidus Usinger (Systelloderes), 87
Nymphocoris Woodward, 30

occidentalis, n. sp. (Tornocrusus), 22, 63, 64, **73**, 75, 76, 258
Oncylocotis Stål, 11, 29, 166

palawanicus Štys (Phallopirates), 32
penai, n. sp. (Tornocrusus), 18, 20, 22, 25, 27, 29, 60, 63, 64, 66, 67, 68, 69, 70, **77**, 79, 80, 258
petrophila Štys (Phthirocorisella), 32
Phallopirates Štys, 32
Phallopiratinae, 30
Phthirocorinae, 30
pilosus (Champion) (Enicocephalus), 5, 103, 104, 105, **126**, 127, 128, 129, 250
pisinnus, n. sp. (Neoncylocotis), 166, **185**, 256

rhyparus (Stål) (Neoncylocotis), 167, **186**, 187, 256
roberti, n. sp. (Alienates), 215, **238**, 239, 244, 245
rubripes, n. sp. (Neoncylocotis), 166, **186**, 188, 256

schuhi, n. sp. (Enicocephalus), 106, **127**, 130, 131, 250, 251, 252
semirufus Barber (Enicocephalus), 105, **130**, 132, 250, 251, 252
sikhotalinensis Wygodzinsky and Štys (Boreostolus), 9, 45, 61
slateri, n. sp. (Neoncylocotis), 167, **189**, 190, 256, 257
spurculus Stål (Systelloderes), 87
stannardi (Kritsky) (Neoncylocotis), 5, 167, 182, **189**, 191, 256
sturmi, n. sp. (Enicocephalus), **133**, 134, 250, 251, 252
sturmi, n. sp. (Tornocrusus), 9, 10, 21, 22, 60, 63, 64, **78**, 81, 82, 105, 258
stysi Kritsky (Tornocrusus), 51, 59, 63, 64, **83**, 84, 85, 258
subantarcticus (Berg) (Gamostolus), 11, 17, 18, 20, 21, 22, 25, 27, 29, **50**, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 253
Systelloderes Blanchard, 4, 5, 7, 8, 9, 11, 15, 16, 18, 19, 21, 28, 32, 33, 34, 35, 37, **85**, 89, 91, 116, 235
Systelloderini, 4, 5, 33, **85**, 86
Systelloderus Stål, 85

taeuberi Jeannel (Enicocephalus), 105, **135**, 250, 251, 252
tasmanicus (Westwood) (Oncylocotis), 7, 9, 12
tenuis Jeannel (Systelloderes), 87
terrenus Drake and Harris (Systelloderes), 86
Tornocrusus Kritsky, 8, 15, 16, 19, 21, 26, 28, 30, 31, 34, 36, **51**, 63, 64, 65, 68, 145, 258
tortonesei Villiers (Systelloderes), 87

tupi, n. sp. (Enicocephalus), 7, 11, 105, 106, 136, **137**, 138, 250, 251, 252

Urnacephala, n. gen., 5, 8, 11, 12, 15, 16, 19, 21, 26, 28, 33, 34, 35, 92, 160, **194**, 195, 203, 259
usingeri Maldonado (Enicocephalus), 105, 116, 130, **139**, 250, 251, 252
Usingeriella Wygodzinsky, 29
uvarovi group (Systelloderes), 4

venezolanus, n. sp. (Tornocrusus), 64, 65, **83**, 86, 258

weyrauchi, n. sp. (Neoncylocotis), 166, 180, **192**, 193, 256
wygodzinskyi Villiers (Enicocephalus), 32, 33, 104, **140**, 141, 142, 250, 251, 252

Xenicocephalus, n. gen., 4, 5, 8, 16, 18, 19, 28, 35, 36, 37, **200**, 204, 205, 206, 207, 260

yvonneae (Kritsky) (Enicocephalus), 5, 108, 112

SUBJECT INDEX

abdomen, 21, 100
acetabulum, 16, 90, 101
antenna, 16, 69, 96, 108, 209
anterior supracoxal lobes, 21
aptery, 8, 13, 15, 36, 208, 211

brachyptery, 8, 31, 37, 42, 46, 49, 69, 71, 131, 132
bristle comb, 24, 28, 29, 41, 94, 151, 211
bristle comb, foretibial, 99
bristle comb, hind leg, 67, 89

chaetotaxy, 25
claw, foretarsal, 28
claws, tarsal, 25, 27
costal fracture, forewing, 13, 35
coupling groove, fore and hind wing, 17, 19, 21
coupling groove, forewing to body, 55, 90, 150
coupling groove, hind wing to body, 90, 150
coupling groove, hind wing, 67
coupling groove, wing to body, 17, 19, 21, 42
coupling mechanism, forewing, 34, 57, 68, 89, 98
coupling mechanism, wing, 94
cuticle, structures of, 18, 24, 55, 56, 57, 68, 69, 90, 96, 100, 110, 171, 199
cuticular granules, 24, 28, 108

dimorphism, sexual, 25, 26

eggs, 9, 12, 13, 227, 231
epimeron, 21
episternum, 21
eyes, 13, 15
eyes, females, 35

foreacetabulum, 16, 147
forefemur, 41, 54, 99, 151
foreleg, 25, 41, 54, 66, 88, 93, 96, 99, 148, 170, 209, 212
forelegs, Aenictopecheinae, 24
forelegs, Alienatinae, 24
forelegs, Enicocephalinae, 24
foretarsus, 28, 54, 93, 196, 209
foretibia, 41, 54
foretibial spines, 13
forewing, 31, 35, 44, 68, 89, 94, 96, 98, 109, 150, 170, 210
forewing, basal cells, 35
forewing, discal cells, 35
forewing, teratological, 125, 128

genital capsule, 44, 91, 94, 100
genital plates, 30
genitalia, Aenictopecheinae, female, 22, 30, 31, 44, 58, 70
genitalia, Aenictopecheinae, male, 22, 30, 31, 44, 58, 69
genitalia, Alienatinae, female, 30, 34
genitalia, Alienatinae, male, 23, 211
genitalia, Enicocephalinae, female, 22, 34
genitalia, Enicocephalinae, male, 30
genitalia, Enicocephalini, female, 110, 151, 172
genitalia, Enicocephalini, male, 23, 96, 110, 142, 151, 172, 199
genitalia, Monteithostolus, 30, 32, 33
genitalia, Systelloderes, female, 34, 91
genitalia, Systelloderini, male, 23, 86, 91
glandular (?) openings, 25
gonopore, 33
guide, 32, 33
gular shape, 213, 225, 226, 230

habitat, 7, 8, 9, 10
head, 14, 15, 40, 53, 66, 87, 93, 96, 98, 108, 147, 169, 196, 209, 212
head, posterior border, 213
head proportions, 15
head shape, 225, 226
hindtibia, 99
hind tibiae, bristle combs, 28, 31
hind tibiae, spines, 28
hind wing, edge, 18
hypermacroptery, 112

keel, thoracic, shape, 213

leaf litter, 8
leaf sheaths, 216
leg, 14, 25
leg, hind, 41, 29, 96
leg, proportions, 235
legs, proportions, 184
lights, 8, 11, 198

macroptery, 8, 15, 31, 38, 46, 50
male genital plates, 13
measurement methodology, 14
mesepimeron, 19, 21
mesonotum, 110, 172
mesosternum, 19, 21, 35
mesothorax, 19, 21, 42, 67, 150, 210
metanotum, 110, 172
metathorax, 19, 21, 42, 67, 150, 210
metepimeron, 21
metepisternum, 21
microptery, 8, 13, 15, 37, 40, 41, 42, 43, 44, 46, 47, 49
microtrichiae, 18, 24
morphometrics, 25

nymphs, 12, 44, 45, 46, 49, 51, 59, 63, 82, 83, 97, 102, 104, 111, 144, 145, 159, 166, 194, 202, 206, 207, 213, 222, 224, 229, 231, 233, 236, 238

ocelli, 13, 15, 31
odor, 7, 11
ommatidia, 212
ontogenesis, 25
oviposition, 12

paramere, 13, 30, 31, 32, 33, 35, 69
phallus, 13, 30, 35
phygophore, 85
plate, infradistal, 32, 33
plate, medial, 32, 33
plate, proximal, 32, 33
plate, supradistal, 23, 32, 33, 35, 86
plate, ventral connexival, 69, 70, 90, 110, 171, 199, 212, 224, 227
proctiger, 30, 32, 33, 91
proepimeron, 31
pronotum, 13, 14, 16, 40, 53, 55, 66, 87, 93, 96, 98, 108, 110, 147, 169, 172, 196, 209, 210, 212
pronotum, shape of, 35
proportions, 15, 25
prothorax, 16, 19, 42, 67, 147, 150
pseudosternite, 32
pterothoracic segments, 19
pygophore, 30, 32, 33, 96
pygophore, dorsal bridge, 31

rostrum, 69, 98

scent gland, 20
scent gland, dorsal abdominal, 100
scent gland, auricle, 55, 150
scent gland, diastomian type, 21
scent gland, median orifice, 171
scent gland, metathoracic, 19, 20, 55, 62
scent gland, omphalian type, 21
scent gland, thoracicoabdominal, 21, 43, 56, 61, 62, 68, 70, 150
sclerites, secondary, 31
scutellum, 55, 196
sensilla, trichoid, 32
seta, parempodial, 28
setae, 32
sex ratio, 9
sexual dimorphism, 13, 15, 16, 147
shape, gular, 15, 225, 232
shape, head, 225
shape, mesothoracic keel, 232
soil, 10, 216
sperm, 9, 12
spermatheca, 9, 12, 31, 62
spicules, 25, 28
spination of forelegs, teratological, 144
spination of foretibia, teratological, 54, 153, 157
spine "a", 25, 31, 66
spines, 29, 41, 94, 151, 211
spines, forelegs, anomalous, 230
spines, foretarsal, 27, 31, 35, 66, 88, 99, 108, 148, 170
spines, foretibial, 25, 26, 27, 35, 54, 66, 88, 89, 93, 96, 99, 108, 109, 148, 170, 196, 209
spines, hind tibial, 41, 67, 89
spines, tarsal, 25, 27, 41, 54
spines, thoracicoabdominal, 211
spines, tibial, 25
spiracle, 19, 21, 23, 54, 57, 67, 70, 90, 100, 171, 199, 210
spiracle, placement, 213, 214, 224, 227, 230
sterna, 90
supracoxal lobe, 21
swarming, 7, 9, 145
swarms, 8, 11

tab, median, 34
tab, median, ventrite, 91
tarsal claw, 24
tarsus, 13, 34, 41
tarsi, hind, 28, 35
tarsi, mid, 35
teratology, 59
tergum, 33, 34, 35, 85, 92, 96, 156, 161, 162, 163, 164, 195, 196
thoracicoabdominal junction, 43
thorax, 17, 90, 197, 212
tibia, hind, 28, 57, 94, 109, 151, 172, 197, 211
tibiae, mid, 28
tubercles, antenniferous, 14
tubercles, setiferous, 208

valvifers, 30, 34
valvulae, 30, 34
valvulae, first, 31, 44, 58, 70, 91
valvulae, second, 44, 58, 70, 91
venation of forewing, normal, 18
venation of forewing, reduced, 216, 221, 222, 234
venation of forewing, teratological, 59, 70, 83, 104, 113, 114, 116, 117, 126, 135, 136, 137, 140, 141, 145, 166, 178, 181, 187, 188, 193
venation of hind wing, 18
venation of hind wing, teratological, 81

wing coupling mechanism, 17, 18, 19, 20, 43, 109, 150, 163, 170, 197, 210
wing polymorphism, 13, 15
wing teratology, 127
wing, hind, edge, 19, 43, 57, 68, 89, 94, 98, 109, 150, 170, 197, 210
wing, shedding, 8, 11, 37, 107, 118, 129, 134, 137
wing, teratologies, 118

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.