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NATURAL HISTORY SURVEY
The Systematics, Evolution and Zoogeography
of
Staphylinid Beetles
Associated with Army Ants
(Coleoptera, Staphylinidae)

Charles H. Seevers

Fieldiana: Zoology
Volume 47, Number 2
Published by
Chicago Natural History Museum
March 22, 1965
The Systematics, Evolution and Zoogeography of Staphylinid Beetles Associated with Army Ants (Coleoptera, Staphylinidae)

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Library of Congress Catalog Card Number: 65–18865

PRINTED IN THE UNITED STATES OF AMERICA
BY CHICAGO NATURAL HISTORY MUSEUM PRESS
# CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Introduction</strong></td>
<td>141</td>
</tr>
<tr>
<td><strong>Acknowledgements</strong></td>
<td>144</td>
</tr>
<tr>
<td><strong>The Army Ants (Dorylinae)</strong></td>
<td>147</td>
</tr>
<tr>
<td>Tribes Cheliomyrmicini, Ecitonini, Dorylini, and Aenictini</td>
<td>148</td>
</tr>
<tr>
<td>Behavior Cycles of Representative Dorylines</td>
<td>150</td>
</tr>
<tr>
<td><strong>Evolutionary Considerations</strong></td>
<td>155</td>
</tr>
<tr>
<td>Mechanisms of Social Integration</td>
<td>156</td>
</tr>
<tr>
<td>Morphological Specializations</td>
<td>157</td>
</tr>
<tr>
<td>Types of Abdominal Petioles</td>
<td>158</td>
</tr>
<tr>
<td>Limuloid Dorylophiles</td>
<td>159</td>
</tr>
<tr>
<td>Regressive Specializations</td>
<td>160</td>
</tr>
<tr>
<td><strong>The Dorylophilous Tribe Dorylomimini (Aleocharinae):</strong></td>
<td>161</td>
</tr>
<tr>
<td>Organization, Phylogeny, and Zoogeography</td>
<td></td>
</tr>
<tr>
<td>Introduction</td>
<td>161</td>
</tr>
<tr>
<td>Dorylomimini of the Ethiopian Region</td>
<td>165</td>
</tr>
<tr>
<td>Dorylomimini of the Oriental Region</td>
<td>166</td>
</tr>
<tr>
<td>Dorylomimini of the New World</td>
<td>167</td>
</tr>
<tr>
<td><strong>The Tribe Myrmedoniini (Aleocharinae): Convergent Evolution of Dorylphilous Groups</strong></td>
<td>170</td>
</tr>
<tr>
<td>Tribal Composition</td>
<td>170</td>
</tr>
<tr>
<td>The Dorylphilous Components of the Tribe</td>
<td>171</td>
</tr>
<tr>
<td><strong>The Old World Dorylphilous Tribe Pygostenini (Aleocharinae)</strong></td>
<td>174</td>
</tr>
<tr>
<td><strong>The Neotropical Ecitophilous Tribe Ecitogastrini (Aleocharinae)</strong></td>
<td>175</td>
</tr>
<tr>
<td><strong>The Neotropical Ecitophilous Tribe Ecitocharini (Aleocharinae)</strong></td>
<td>175</td>
</tr>
<tr>
<td><strong>The Ethiopian Tribe Deremini (Aleocharinae)</strong></td>
<td>176</td>
</tr>
<tr>
<td><strong>Ecitophilous Paederinae, Staphylinidae, and Tachyporinae</strong></td>
<td>176</td>
</tr>
<tr>
<td><strong>Systematic Section</strong></td>
<td>181</td>
</tr>
<tr>
<td>Genera of Dorylphilous Staphylinidae</td>
<td>181</td>
</tr>
<tr>
<td>Subfamily Alecharinae</td>
<td>186</td>
</tr>
<tr>
<td>Key to Old World Tribes with Dorylphilous Genera</td>
<td>186</td>
</tr>
<tr>
<td>Key to New World Tribes with Ecitophilous Genera</td>
<td>186</td>
</tr>
<tr>
<td>Tribe Dorylomimini</td>
<td>187</td>
</tr>
</tbody>
</table>
## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>A Key to the New World Genera</td>
<td>207</td>
</tr>
<tr>
<td>Tribe Myrmedoniini</td>
<td>232</td>
</tr>
<tr>
<td>A Key to the New World Genera</td>
<td>233</td>
</tr>
<tr>
<td>New World Ecitophilous Groups</td>
<td>236</td>
</tr>
<tr>
<td>Old World Dorylophilous Groups</td>
<td>274</td>
</tr>
<tr>
<td>Tribe Ecitocharini, new tribe</td>
<td>287</td>
</tr>
<tr>
<td>Tribe Deremini, new tribe</td>
<td>294</td>
</tr>
<tr>
<td>Tribe Ecitogastrini</td>
<td>300</td>
</tr>
<tr>
<td>Tribe Pygostenini</td>
<td>303</td>
</tr>
<tr>
<td>Tribe Phyllodinardini</td>
<td>309</td>
</tr>
<tr>
<td>Tribe Trilobitideini</td>
<td>312</td>
</tr>
<tr>
<td>Tribe Aleocharini</td>
<td>314</td>
</tr>
<tr>
<td>Subfamily Paederinae; Tribe Paederini</td>
<td>315</td>
</tr>
<tr>
<td>Subfamily Staphylininae</td>
<td>323</td>
</tr>
<tr>
<td>Tribe Staphylinini</td>
<td>328</td>
</tr>
<tr>
<td>Tribe Qediini</td>
<td>329</td>
</tr>
<tr>
<td>Subfamily Tachyporinae; Tribe Vatesini</td>
<td>332</td>
</tr>
<tr>
<td>Subfamily Oxytelinae</td>
<td>339</td>
</tr>
<tr>
<td>Position uncertain: <em>Synaecictus</em> Patrizi</td>
<td>341</td>
</tr>
<tr>
<td><strong>BIBLIOGRAPHY</strong></td>
<td>343</td>
</tr>
</tbody>
</table>
INTRODUCTION

As one of the dominant groups of insect predators the beetle family Staphylinidae has attained great success. Representatives of its more than 28,000 recorded species occur in almost every inhabitable terrestrial area of the world, and occupy important places in many types of ecological communities. Most staphylinids live in decaying organic materials where there is an abundance of larvae and other soft-bodied arthropods and where their predatory activities are generalized in character. Some members of the family have achieved notable success in adapting to such specialized ecological systems as ant and termite societies. Successful adaptation to insect societies requires some measure of obligatory social integration, and inquilinous species in all likelihood must conform to species specific physiological integrative mechanisms of a chemo-tactic nature. The success of the Staphylinidae in adjusting to life in insect social systems is indicated by the fact that the number of independently evolved groups of termitophilous and myrmecophilous species exceeds that of any other family of organisms.

This monograph attempts to explore certain aspects of the evolution of one category of myrmecophilous Staphylinidae—those associated with army ants (Dorylinae) of the world. The central theme is the evolution and zoogeography of interspecies systems composed of doryline ant societies and their staphylinid dorylophiles. As the basis for a synthesis it has been necessary for me to restudy the classification of more than one hundred dorylophilic genera, and to reorganize the categories, usually tribes, to which they belong. The results of these systematic studies lead me to conclude that there are more than twenty independently evolved groups of dorylophilous Staphylinidae (Table 1). Ideally, each of the groups should be monophyletic and be based on the successful establishment of a single dorylophilous species at some remote geologic time.

A majority of dorylophilous Staphylinidae belong to the subfamily Aleocharinae, an extremely large and complex taxon. Inasmuch as the tribal classification of this subfamily has developed as
an artificial system—based principally on tarsal segmentation—it did not provide a sound basis for studies on phylogeny. I have devoted considerable time to the tribal classification of the entire subfamily Aleocharinae with a view to proposing a system that is phylogenetically defensible, but in this monograph I must confine my attention to the dorylophiles. The classification of the genera of dorylophilous Aleocharinae in current catalogues has two major weaknesses: the expedient use of a few characters such as tarsal segmentation to place most of the genera; and, at the other extreme, the use of highly specialized abdominal characters as a basis for establishing small, often monobasic, tribes. Two examples may show how the current classification either brings together convergently adapted dorylophiles or separates allied genera. In one instance, the large heterogeneous tribe Myrmedoniini includes genera of dorylophiles which I believe should be assigned to five tribes: Myrmedoniini (s.s.), Ecitocharini, Deremini, Dorylomimini, and Phyllopinardini. In another case, I propose to expand the tribe Dorylomimini to include 33 genera selected from about a dozen tribes of current catalogues. Expansion of the Dorylomimini—a tribe proposed by Wasmann for a few African genera but ignored by cataloguers—submerges a number of small tribes. The taxonomists who studied and classified the dorylophilous Staphylinidae were either staphylinid specialists who adhered rigidly to an artificial tribal system, or non-specialists who had little acquaintance with free-living Aleocharinae. The former placed the dorylophilous genera in existing tribes on the basis of tarsal segmentation, while the latter tended to emphasize the highly specialized condition of the dorylophile abdomen and to propose new categories. The view that a tribe should be characterized by a community of characters was largely overlooked by specialists and non-specialists alike.

The literature on the dorylophiles is largely devoted to descriptions of new genera and species and scant attention has been given to problems of phylogeny, evolution, and zoogeography. Between 1889 and 1925 Wasmann laid the foundation of our present knowledge of the dorylophiles, as he received and described many new forms from Africa and the Americas. He also wrote extensively about adaptive features of dorylophiles and proposed such concepts as amical selection and symphilic instinct. Wasmann was a strong proponent of “ameisenmimikry” and believed that mimicry is an adaptation designed to deceive the host ants and to thus insure admission of the mimics to the colony. Wheeler disagreed with Wasmann on his concept of mimicry and participated in a heated
controverisy in which he and Heikertinger supported one viewpoint and Wasmann and Reichensperger another.

Wasmann believed in the independent origins of the Old and New World dorylophile faunas. In a discussion of adaptational types (Wasmann, 1912a, p. 470) he stated, “... the genera which represent these types in the two hemispheres do not stand in any closer systematic relationship to each other. Their similarity, therefore, rests upon convergence as the result of similar conditions for adaptation.” In the course of the present studies, I have attempted to marshal the evidence, pro and con, that bears on Wasmann’s proposition; this will be presented in later sections. At this point it may be stated that present evidence does not conclusively demonstrate that the army ant subfamily Dorylinae is a monophyletic group with a pantropical dorylophile fauna, or that, on the contrary, it is a polyphyletic group with independently derived dorylophile faunas. In an earlier work on the termophilous staphylinid fauna (Seevers, 1957), I was able to show that there are several pantropical termite-termophile interspecies systems, in refutation of assertions by both Wasmann and Warren that the Old and New World termophilic faunas were independently evolved.

In recent years two studies on the dorylophilous fauna have been initiated and partially completed—one by Dr. David Kistner on the Old-World Pygostenini, and another by Dr. Carl Rettenmeyer on the New World eciitophiles. Kistner (1958) published a thorough revision of the Pygostenini and discussed the phyletical and host relationships of the genera of that tribe. He is continuing his research program on the Pygostenini and other dorylophiles in the course of several trips to Africa to study the ecology and behavior of these guests. Rettenmeyer’s investigations of the eciitophiles of Barro Colorado Island, Panama Canal Zone, have produced comprehensive collections of many arthropods and numerous observations of the ecology and behavior of the guests.

The largest section of this paper is devoted to the classification of the dorylophilous genera. My classification is not a literature-based one but is the result of studies of all but a few recorded genera. I have intentionally avoided a dependence on the literature in order to provide a fresh outlook, and my classification differs in numerous respects from that of current catalogues. The extent of the suggested changes may be noted in the summary of genera at the beginning of the systematic section; more than one-half of the genera have been shifted to different categories. My review of the genera in
the systematic section stresses mainly those characters deemed of important in classification and no attempt has been made to present a comprehensive comparative morphological study.

Inasmuch as a high percentage of the dorylophilous genera are reasonably well illustrated in the literature, it has not seemed essential to figure all of them in this work. On the whole, the dorylophilous genera are among the best illustrated Staphylinidae, and so the interested reader may easily become acquainted with the general characteristics of many genera by consulting a few papers. Nearly one-half of the genera are reasonably well illustrated in the literature, it has not seemed essential to figure all of them in this work. On the whole, the dorylophilous genera are among the best illustrated Staphylinidae, and so the interested reader may easily become acquainted with the general characteristics of many genera by consulting a few papers. Nearly one-half of the genera are illustrated by photographs in five papers—Wasmann (1904, 1915a, 1916, 1917), and Borgmeier (1949). Many illustrations are found in papers by Wasmann, Borgmeier, Bruch, Reichensperger, Kistner, and others.

The Chicago Natural History Museum collection, on which this study was largely based, contains about 85 per cent of the Old-World genera of dorylophilous Staphylinidae and about 96 per cent of the New-World genera. This collection of specialized Staphylinidae is part of the comprehensive Museum collection of this family now numbering some 14,000 species. The collection of the late Dr. Max Bernhauer of Vienna, Austria, forms the major part of the world-wide collection but I have secured most of the dorylophiles from other sources, chiefly by gift or exchange. Other collections studied during the course of the investigations include: the Wasmann collection (Maastricht, The Netherlands), Reichensperger collection (Bad Gödesberg, Germany), Mann and Nevermann collections (Washington, D.C.), Fenyes collection (San Francisco, California), Cameron and Sharp collections (London, England).

The drawings are original and were prepared by the author.

ACKNOWLEDGEMENTS

The research for this monograph and its preparation were completed during the tenure of three grants from the National Science Foundation (1954–1964) for studies on the Systematics of the Staphylinidae. As they enabled me to study types and other material in European and American museums—for other projects as well as this one—the grants are gratefully acknowledged. For their kind cooperation during my visits to study collections, I am much indebted to Dr. R. M. Kruytzer, former director of the Natuurhistorisch Museum, Maastricht, The Netherlands; Mr. E. B. Britton, British Museum (Natural History); the late Dr. August Reichensperger,
Bad Gödesberg, Germany; Dr. J. F. Gates Clarke and Dr. O. L. Cartwright, United States National Museum; and Dr. Edward R. Ross and Mr. Hugh Leach, California Academy of Sciences. Dr. Thomas Borgmeier (Rio de Janeiro, Brazil), whose collection of neotropical ecitophiles is outstanding, was especially helpful in lending and exchanging important specimens, and through the gift to the Chicago Natural History Museum of a number of holotypes (acknowledged at appropriate places in the systematic section). For the privilege of studying important recent collections of dorylophiles, I am very grateful to Dr. T. C. Schneirla (American Museum of Natural History) for material from Mexico, Panama, Arizona, the Philippines, and Thailand; Dr. Carl W. Rettenmeyer (Kansas State University) for extensive collections from Panama, Costa Rica, and Kansas; Mr. Roger D. Akre (Kansas State University) for unusually interesting species from Costa Rica and Kansas; and Dr. David Kistner (Chico State College) for the loan of African specimens. The availability of the remarkable Bernhauer collection of Staphylinidae at Chicago Natural History Museum is an important factor in my taxonomic studies, and the thoughtful and generous cooperation of Dr. Rupert L. Wenzel, Curator of Insects, is a very encouraging feature of my Museum associations. I am especially grateful to my wife, Frances, for aid in preparing the manuscript and for essential encouragement in research activities.
THE ARMY ANTS (DORYLINAE)

The Old and New World army ants have always been grouped in the subfamily Dorylinae, an arrangement that implies a common origin. Even though using this classification, myrmecologists have not always considered the subfamily to be monophyletic. Borgmeier (1954) recognized four tribes of Dorylinae—Dorylini and Aenictini of the Old World, and Cheliomyrmicini and Ecitonini of the Americas—but indicated that the Old and New World tribes were not very closely allied. In personal communication, Borgmeier informed me that he considered the two faunas to have originated independently. Brown (1954), in a general review of the ant subfamilies, pointed out that the origin (or origins) of the Dorylinae is uncertain. In personal communication, Brown has favored the concept of two or more origins for the army ants.

Wheeler (1928) was one of the chief proponents of a monophyletic concept of the Dorylinae and suggested that the American tribe Cheliomyrmicini links the neotropical and palaeotropical army-ant faunas. Borgmeier (1955) rejected the latter hypothesis. After an analysis of the behavior cycles of the American genus Eciton and the Ethiopian driver ants (subgenus Anomma), Schneirla (1957) concluded that the patterns are probably homologous, i.e., derived from a common ancestral pattern. Zoogeographic evidence does not support the case for monophyly as there are no tribes or genera that occur in both Old and New Worlds. As the army-ant faunas of both hemispheres are probably quite old, a common ancestor, if it existed, probably was of Mesozoic stock.

Although studies on the dorylophile faunas of the different tribes of army ants cannot contribute directly to a solution of the doryline phylogeny problems, they may provide important circumstantial evidence bearing on them. If the subfamily Dorylinae is diphyletic, the dorylophile fauna of each independently evolved group must also have been independently derived. Evidence presented in this monograph is by no means conclusive but does allow one to infer the possibility of pantropical distributions for one or more dorylophile groups.
The tribe Dorylomimini as herein organized contains staphylinid genera associated with each of three doryline tribes; it is distributed in the Ethiopian, Oriental, Neotropical, and Nearctic Regions. The Myrmedoniini contains genera in the Oriental and American faunas that may be closely allied, and the Old World Pygostenini and the New World Ecitogastrini may have had a common ancestor.

As a background for a synthesis of doryline-dorylophile relationships, a brief review of the doryline ant genera and some comments on representative behavior patterns is in order. The remarkable behavior cycles of army ants are of importance to an understanding of some conditions of life to which the dorylophiles have adapted.

Tribe Cheliomyrmicini

This small category includes one genus and five species; the genus ranges from Mexico to the Amazon Region. Borgmeier (1955) agreed with Wheeler that these are the most generalized of American army ants. These rarely collected ants have not been investigated for possible ecitophiles although Wheeler reported finding one beetle, possibly Vatesus, in a colony.

Tribe Ecitonini

This is a relatively homogeneous group as evidenced by the fact that all species were placed in the genus Eciton until Borgmeier (1955) in a revision of the tribe raised the four subgenera to generic rank. Phyletic relations within the tribe have not been discussed in these terms but the morphological considerations in Borgmeier's revision provide some idea of the relations of the genera. The diagrams that are presented in this paper to illustrate host-guest relations are not to be construed as indicating the differentiation of genera in the order given. The arrangement does reflect some ideas on relationship discussed by Borgmeier but is chiefly a device for presenting data. Reichensperger (1930) and Borgmeier (1955) agreed that Neivamyrmex is the most generalized genus of Ecitonini. After a study of the wing venation of the tribe, Brown and Nutting (1950) stated that the genera might almost be placed in a straight line.

Genus Neivamyrmex Borgmeier (= Acamatus Emery)

Borgmeier (1955) listed about 110 species of this genus and arranged them in 14 groups. The species are generally characterized by hypogaeic nesting habits and nocturnal emigrations, so many
are poorly known. The worker caste is generally the only one collected and all castes are recorded for only 12 species. Compared with the other genera of the tribe, relatively few species have extensive ranges. However, the species of particular interest in this work, i.e., those with recorded ecitophiles, may have wide ranges. These include:

*legionis* F. Smith; from Amazon Region to Argentina.
*pseudops* Forel; Brazil and Argentina.
*pilosus* F. Smith; from Arizona and Texas to Argentina.
*spinolai* Westwood; from Costa Rica to Argentina.
*halidayi* Shuckard; from Mexico to Argentina.

Two species that are widely distributed in the southern United States have exceptionally broad ranges in the hemisphere—from 45° N. Lat. in the upper Mississippi Valley to 45° S. Lat. in Patagonia. The genus, as well as the entire tribe, is primarily a tropical group, and the species of the temperate climate are doubtless secondarily adapted to these conditions.

*Neivamyrmex* harbors a rich fauna of ecitophiles and the many unexplored societies of the genus should provide for many interesting discoveries.

Genus *Labidus* Jurine

Borgmeier recognized eight species of this genus, which ranges from the southern United States to Argentina. Societies of two species have exceptionally rich ecitophile faunas: *Labidus praedator* F. Smith, distributed from Mexico (San Luis Potosí) to Argentina (Misiones), and *Labidus coecus* Latreille, ranging from Texas to Argentina. Both species are probably polytypic; two subspecies of the former are recognized.

Genus *Nomamyrmex* Borgmeier

The two species of this small genus may occur throughout most of the Neotropical Region. *Nomamyrmex esenbecki* Westwood, with three subspecies, ranges from Texas to Argentina.

Genus *Eciton* Latreille

This genus comprises the large, epigaeic army ants of tropical America. Because of their above-ground activities they are the most frequently encountered of the American army ants. The remarkable behavior cycle of the members of this genus, which has been so carefully studied by Schneirla, will be discussed later in this sec-
tion. More than one-half of the species of Eciton have very broad ranges and several are probably polytypic. The species of major importance in this work are:

- *burchelli* Westwood; from Mexico to Paraguay; 5 subspecies.
- *dulcius* Forel; from Panama to Argentina; 2 subspecies.
- *hamatum* Fabricius; from Mexico to Brazil and Bolivia.
- *mexicanum* Roger; from Mexico to Argentina; 6 subspecies.
- *quadriglume* Haliday; from Amazon Region to Argentina.
- *vagans* Olivier; from Mexico to Argentina; 7 subspecies.

**Tribe Dorylini**

Most myrmecologists have grouped the species of this Old World tribe in a single genus, *Dorylus*. Raignier and Van Boven (1955) recognized six subgenera of *Dorylus*, of which three concern us in this work: *Dorylus s.s.*, *Anomma*, and *Typhlopane*. *Dichthadia*, *Rhagmus*, and *Alaopone* do not to my knowledge have recorded staphylinid dorylophiles. By far the most diversified dorylophile fauna is associated with the subgenus *Anomma*, the renowned driver ants of equatorial Africa. The hypogaeic societies of *Dorylus*, s.s., also harbor an interesting fauna, noteworthy in particular for the regressive evolutionary modifications of its members. The tribe is largely confined to Africa but some species do occur in the Oriental Region.

**Tribe Aenictini**

This tribe, containing two genera, *Aenictus* Emery and *Aenictogiton* Emery, was separated from the Dorylinae by Borgmeier (1954). *Aenictus* is widely distributed in both Ethiopian and Oriental Regions, and in many areas of the latter Region is the only genus of army ants. Studies on this tribe may determine whether or not there is a phyletic link between the Old and New World army ants.

**Behavior Cycles of Representative Dorylines**

The following review of the most noteworthy features of the ecology and behavior of army ants is drawn largely from publications by Schneirla (1949, 1956, 1957, 1958), whose outstanding field studies on *Eciton* and *Neivamyrmex* have clarified many phases of army ant life.

The dorylines are characterized by a nomadic way of life and carnivorous habits; many species have relatively large colonies. While all species are probably nomadic to some degree, there is considerable variation in the frequency, regularity, and duration of
emigrations. All have stable nests between emigrations, usually in situations well-sheltered ecologically. Doryline colonies have a single queen and distinctive wasp-like males. Mass forages provide arthropod food in quantity.

In discussion of American army ants, Schneirla emphasized the major importance of active broods (active larvae and newly emerged workers) in regulating the nomadic phase and foraging activities of the colony. Schneirla rejected the food-exhaustion hypothesis as a basis for nomadism and proposed instead that the cyclic variations in foraging and nomadism are dependent on brood activities. Orientation within the colony is on a non-visual, contact chemical basis, and workers have the ability to lay down chemical trails and to utilize them in foraging.

Behavioral Cycle of Eciton

The two species of *Eciton* studied by Schneirla, *burchelli* and *hamatum*, are forest-dwelling, epigaeic species living in colonies of large size (estimated to consist of more than a million individuals in *burchelli*, and about 250,000 in *hamatum*). Throughout the year these species pass through alternating statary and nomadic phases of behavior.

**Statary Phase:** A colony remains at the same nesting site (bivouac) for about three weeks. The bivouac consists of a great mass of ants in a sheltered place such as a hollow log, and no construction work takes place. The colony is not very excitable and only small daily raids are sent out. Prior to entering this phase the queen began maturing a brood of oocytes and her abdomen became greatly distended. The queen lays eggs during the second week of the statary period and near the end of the third week the eggs hatch and produce a brood of small larvae. About the same time, a pupal brood, from larvae of the previous statary phase, emerges from cocoons as callow workers. Schneirla contends that the new crop of emerging workers and hatching larvae excites the entire colony to nomadism and brings the statary period to an end.

**Nomadic Phase:** During this period, which lasts for 12–15 days in *hamatum*, and 16–18 days in *burchelli*, the entire colony emigrates nightly to a new bivouac site and forms a huge exposed cluster of workers on a tree trunk or log. Workers hanging from the support and from one another by tarsal claws surround the queen and larval brood. At dawn each day *hamatum* typically sends out three columns of raiders to seek out and capture immature insects; *burchelli*
raids in a swarm some 20-25 meters wide which fans out from a single trail. At dusk the entire colony emigrates along one of the trails to the next bivouac site, generally about 140 meters away in *burchelli* and 200 or more in *hamatum*. When the larval brood hatched during the previous statary period reaches maturity the nomadic phase is ended and the colony seeks a secluded site for another statary phase. By this time most of the larvae have completed the first stages of cocoon spinning.

**Behavior of Neivamyrmex nigrescens**

Schneirla (1958) reported that this species has a nomad-statary cycle similar to that of *Eciton* and that during the active season a nomadic phase is set off by the maturation of a pupal brood and the emergence of callow workers. The nomadic phase is longer in this species than in *Eciton* probably because the larvae do not spin cocoons when pupating and the larval excitation is therefore prolonged. The bivouacs of this species are, as in most species of the genus, subterranean.

**Behavior of Labidus**

The activities of *Labidus coecus* are almost entirely subterranean while *Labidus praedator* raids and emigrates above ground. It seems likely that the genus was primarily hypogaeic in behavior and that the *praedator* pattern was secondarily acquired. *L. coecus* forages in galleries just beneath the surface of the ground or under large stones; its columns advance under covered galleries which the workers rapidly construct from earth. Bates traced the galleries for 100-200 yards and noted that when a rotten log was reached the workers poured forth to search every crevice for prey. *Labidus praedator* bivouacs in subterranean places but raids above ground in a manner similar to *Eciton burchelli*; it is characterized by Schneirla as a swarm raider. When emerging from a bivouac the ants may form a swarm more than 3 meters in width. Advancing in a meandering fashion the swarm is followed by a series of loosely formed columns that lead to the rear. As the swarm moves rapidly along, workers climb to the summit of low trees and search through masses of decaying material for apterus insects and larvae.

**Behavior of Dorylus (Anomma)**

In his paper comparing the cycles of *Anomma* and *Eciton*, Schneirla (1957) brought out some of the salient features of the
behavior of Dorylus (Anomma) wilverthi Emery. Colonies of this species occur in either tropical forest or open savannah of equatorial Africa and are estimated to consist of as many as 22,000,000 ants. Having strong subterranean tendencies wilverthi remains in the nest, enlarged by digging, for a period of 20–25 days. Prey-seeking raids, with advance swarms as much as 12 meters in width, are sent out during this statary period. Food consists of dismembered arthropods and as many as one-fourth of returning workers carry such booty.

The nomadic phase of the Anomma cycle is much shorter than in Eciton and the entire colony moves to a new nest site in a continuous movement of two or three days’ duration. Overnight bivouacs do not characterize this behavior cycle. Emigrations seem to be stimulated, as in Eciton, by the maturation of a pupal brood and emergence of a crop of callow workers. The queen is moderately physogastric at all times and has to be dragged along by the workers during emigration, usually in underground runways. Peak egg-laying occurs after migration and may be at the rate of three or four million per month. Schneirla regards the Anomma cycle as homologous to that of Eciton and probably derived from a common ancestral pattern.
EVOLUTIONARY CONSIDERATIONS

The discussion in this section deals with three general topics: adaptations associated with dorylophily; phylogenies of independently evolved groups (usually tribes) of dorylophilous Staphylinidae; and the evolution of interspecies systems. The dorylophilous staphylinid fauna is a polyphyletic assemblage; so one is in effect dealing with a series of interspecies associations, each comprising a monophyletic group of beetles and its hosts. Theoretically, each interspecies system began with the adjustment of a single staphylinid species to the social life of a single army-ant host species. From each such relationship there may have evolved an entire category of obligatory guests associated with the descendants of the original host species. The greater the degree of host specificity maintained during the evolution of such a system the more likely the system was to maintain its integrity. Much may be deduced about the phyletic histories of some of these systems from an analysis of present-day faunas. Changes in host affinity by some species during the evolution of the system would not necessarily alter the main picture but might well have resulted in the establishment of new systems with new lineages.

It is unfortunate that so little is known about the ecological relationships of dorylophilous beetles. Many species are admirably adapted to army-ant societies, as evidenced by their obligate relationship, but their precise niche in the ecological system is not often known. Wasmann drew many inferences from morphological data but these are often open to criticism. He recognized three categories of inquilines presumably differing in degree of integration with insect societies. In Wasmann's terms, synechthrans are predators not tolerated by the colony; synoeketes are commensals that are tolerated but do not enter into trophallactic relations with the hosts; symphiles are closely integrated species that, as a rule, secrete exudates sought by the hosts. While it may be relatively easy to decide that physogastric termiophiles and trichome-bearing myrmecophiles are symphiles, it is quite difficult to classify inquilines that do not have
obvious exudatory mechanisms. As the dorylophilous Staphylinidae fall in the latter category, it is usually presumptuous to decide that a given species is a synoekete or a symphile. Many of Wasmann’s decisions are very difficult to justify. There is probably some validity in the use of the term “synechthran” to categorize the large number of species that seem to have a “fringe” relationship to the army-ant colonies. For example, the debris piles formed in proximity to the bivouacs of Eciton attract a variety of species. These species, whatever their niche, might be called synechthrans.

Mechanisms of Social Integration

This is a topic about which very little is known. Most of the dorylophiles considered in this study are apparently well integrated with their host societies, and the species are either host specific or occur with a limited number of related host species. It seems likely that the dorylophiles are physiologically adapted to specific chemo-tactic integrative mechanisms, but observations and experiments are needed to clarify the matter. To what extent such adaptations are acquired or genetically determined is problematical, but one would certainly suspect a strong genetic influence.

The dorylophilous Staphylinidae lack a feature common to many myrmecophiles: clusters of glandular hairs (trichomes) on some part of the body. Trichomes are rarely found among dorylophilous insects and to my knowledge only certain neotropical histerids have them. It is probable that exchanges of exudates among members of the carnivorous doryline societies are less important than in the Formicinae and other nest-dwelling ants, and that the dorylophiles were not subjected to selection pressure to develop trichomes. Patrizi (1948) has observed, though, that the African genus, Smectonia, in observation colonies seemed to respond to solicitation by driver ants (Anomma) which stroked the underside of the thorax and coxal region, but whether or not a secretion was elicited was not determined.

It would be interesting to know how the developmental cycles of dorylophilous Staphylinidae are integrated with the activities of the ant society. Some special adaptational features of larval and pupal development may be required for life in nomadic societies. Larvae of the neotropical genus, Vatesus, march in the columns of Eciton, but those of other genera may have to be carried during emigrations.
Morphological Specializations

Many obligate dorylophilous genera are generalized in appearance and differ little in this respect from their free-living relatives. It may be surmised that their obligate relationship is based on some genetically determined physiological adaptations of a subtle nature. On the other hand there seems to have been strong selection pressures for the development of a myrmecoid body form, as evidenced by the presence of this type in several independently derived series.

The degree to which dorylophilous beetles resemble their hosts is variable and often a matter of subjective judgment. Species which were thought by Wasmann to bear a strong resemblance to their hosts were considered by Wheeler to have a superficial resemblance at best. In this paper the term “myrmecoid” is used to refer to those genera with petiolate or subpetiolate abdomens. The dorylophilous species may resemble closely their hosts in one or more ways—coloration, integumental sculpture, antennal form, structure of the thorax—but the most distinctive feature of the myrmecoid type is the petiolate abdomen having one or more slender petiolar segments and an enlarged ant-like “gaster.”

In the light of the fact that the myrmecoid body type was repeatedly selected during the evolution of the dorylophilic fauna, there can be little doubt of its important adaptive value. The strength of the selection pressure favoring this abdominal specialization is indicated not only by the number of independent origins but also by the number of morphological devices utilized to form it. The remarkable adaptability of the staphylinid abdomen is well shown in this fauna. The pliability of the abdomen is not only manifested in the Aleocharinae, a subfamily noteworthy for variety of abdominal types, but even in the more conservative subfamily Staphylininae. In the latter group the distinctive genus *Ecitophytes*, with a petiolate abdomen, represents a real departure from the subfamily pattern.

I have concluded that the present dorylophilous staphylinid fauna includes at least a dozen independently derived myrmecoid groups as evidenced by the fact that petioles of myrmecoid abdomens—although perhaps superficially similar in appearance—are constructed in a variety of ways. In classifying the staphylinid dorylophiles, previous systematists have overlooked this important fact. Six types of petioles and the groups in which they occur are as follows:
Types of Abdominal Petioles

TYPE A (figs. 24, 29, F, 34, F): The sclerites—tergite, sternite, and very slender paratergites and parasternites, if present—of the slender petiolar segments are in generalized positions.

1. *Philacamatus* group (Aleocharinae, Dorylomimini): Four American genera with one, two or three-segmented petioles.


3. *Ecitocryptodes* Seevs of the neotropical *Ecitonidia* subgroup (Aleocharinae, Myrmedoniini, *Dinocoryna* group), with a one-segmented petiole.


5. *Ecitophytes* Wasmann (Staphylininae, Staphylinini), a neotropical genus with a one-segmented petiole.

TYPE B (figs. 20, D, 21): The sclerites of each petiolar segment are fused to form a tube without sutures.


TYPE C (fig. 19, A–E): The petiole is formed solely by the tergite of the second abdominal segment the sides of which are prolonged ventrad to form a partial or complete tube.


TYPE D (fig. 23, A, B, C, E): The petiole is formed by the “sternite” of the second abdominal segment and the attenuated base of the third segment tergite. Inasmuch as the Aleocharinae in general lack a second segment sternite, this petiolar type is of special interest.

9. *Pulicomorpha* group (Aleocharinae, Dorylomimini): Three American genera have this type of petiole.

TYPE E (fig. 36, A–C): The petiole is formed by the basal half of the third abdominal segment; the tergite is very slender proximally,
and the sternite, broad at its apex, tapers strongly to participate in petiole formation.


TYPE F (fig. 25, E): The short petiole is formed in a remarkable manner; the very large metepimera are prolonged ventrally and apparently fused to form a tubular structure with which the abdomen articulates.


SUB-PETIOLAR TYPES: Although not having a petiole in a strict sense, numerous genera of Dorylomimini have ovoidal abdomens which articulate by slender condyles with the thorax and are, as a result, more or less myrmecoid in appearance. Several dorylomimine phyletic series have abdomens of this nature: The *Labidopullus-Leptanillophilus-Mimeciton* series, including about 13 American genera; *Ecitomorpha* and *Ecitophya* of an American series; and the African genus *Dorylogaster* of the *Dorylomimus* group.

**Limuloid Dorylophiles**

A number of non-myrmecoid dorylophiles may be categorized as limuloid. They are characterized by large carapace-like pronota and elytra which tend to cover, and presumably to protect, most of the head, mouthparts, antennae, legs, and even the retractile abdomen. The degree to which these parts are covered is variable. Wasmann considered the possession of a "defense type" body form to be a major factor in the adaptation of limuloid species to life in termite and ant societies. It seems likely that Wasmann's explanation is an oversimplification, and that many limuloid species are too well integrated with the society—many are host specific in their relations—to be dependent solely on form to provide protection. In the course of their evolution it is probable that many species acquired a true physiological adjustment to the integrating mechanisms of the colony. The limuloid, or fusiform groups of dorylophilous Staphylinidae, are as follows: (1) Tribe Vatesini (Tachyporinae) with one genus and many species in the Neotropical Region; (2) Tribe Pygostenini (Aleocharinae) with several fusiform genera in Africa; (3) Tribe Phyllodinardini (Aleocharinae) with one African genus; (4) Tribe Trilobitideini (Aleocharinae) with one African genus.
Regressive Specializations

Regressive specializations are a recurrent feature in a number of phyletic series of dorylophiles. These specializations include eyelessness, aptery, elytral fusion, elytral reduction and even complete loss, fusion of cephalic sclerites, extreme fusion of thoracic sclerites, reduction in number of antennal and tarsal segments, and loss of paratergites and parasternites. Eyelessness and aptery are not correlated with a particular body form and occur in generalized, myrmecoid, and limuloid species; more complex regressive modifications are usually features of myrmecoid species. There seems to be a strong correlation between regressive changes and the hypogaeic mode of life characteristic of most doryline ants.

Eyelessness occurs in at least ten different phyletic lines of dorylophilous Aleocharinae and apparently evolved independently in each case. The blind species usually occur with army ants that have strong subterranean tendencies and that are rarely found above ground during the day (e.g., *Dorylus* s.s., *Neivamyrmex, Labidus coecus*). Eyeless species are distributed as follows:

Tribe Dorylomimini:
1. All species of the *Leptanillophilus* group (with *Neivamyrmex* and *Nomamyrmex*) and *Mimeciton* group (with *Labidus*).
2. *Pulicomorpha* Mann of *Pulicomorpha* group (with *Neivamyrmex*).
3. *Mimanomma* Wasmann of the *Mimanomma* group (with *Anomma*).

Tribe Myrmedoniini:
4. *Ecitotyphlus* Borgmeier of the *Tetradonia* group (with *Labidus*).
5. *Typhlonusa* Borgmeier of the *Dinocoryna* group (with *Neivamyrmex*).

Tribe Pygostenini:
6. *Dorylotyphlus* Bernhauer (with *Dorylus* s.s.).
8. *Lydorus* Normand (with *Dorylus*, subgenus *Typhlopone*).
9. *Typhlopolemon* Patrizi (with *Dorylus* s.s.).

Tribe Trilobitideini:
10. *Trilobitideus* Raffray (with *Dorylus* s.s., *Anomma*, and probably *Aenictus*).
Aptery occurs more frequently than eyelessness. Probably the most interesting case involving aptery is that of the phyletic series including the *Leptanillophilus* and *Mimeciton* groups of the American tropics because of accompanying elytral modifications. These range from elytral fusion in the former group to reduction and loss in the latter. The species of *Mimeciton* lack elytra, a condition that may be unique among adult (non-larviform) beetles.

Extreme fusion of cephalic and thoracic sclerites is well illustrated by two independently evolved genera: *Mimeciton* (fig. 26) of the Neotropical Region and *Mimanomma* (fig. 20, D) of equatorial Africa. The sutures of head and thorax are virtually non-existent in both cases.

**The Dorylophilous Tribe Dorylomimini (Aleocharinae): Organization, Phylogeny, and Zoogeography**

**Introduction**

The tribe Dorylomimini was proposed by Wasmann (1916) for three African genera associated with driver ants of the subgenus *Anomma*. In proposing an artificial tribal system for the Aleocharinae, Fenyes (1918–21) was obliged to place Wasmann’s genera in the Hygronomini with a miscellaneous assortment of free-living and termitophilous genera having 4, 4, 4-segmented tarsi. Pointing out that Fenyes’ system obscures all phyletic relationships, I transferred the termitophilous genera from the Hygronomini to the Corotocini in an earlier paper (Seevers, 1957). I now propose to revive Wasmann’s Dorylomimini and to assign additional Old World and American dorylophilous genera to it. As herein constituted, the Dorylomimini contains 33 Ethiopian, Oriental, Neotropical, and Nearctic genera formerly placed in about a dozen aleocharine tribal categories. Several small tribes, some monobasic, have been incorporated in the Dorylomimini, and some genera have been transferred from the heterogeneous Myrmedonini. Over the years classification of dorylophilous genera has progressed in a haphazard fashion, with some authors—Fenyes, Bernhauer, Cameron and others—following the simple expedient of complete reliance on tarsal segmentation for tribal assignment, and other authors proposing a series of new tribes for what they believed to be very distinctive and isolated genera.

The abdomens of dorylophilous Aleocharinae exhibit remarkable diversity and it is far easier to detect striking differences than to
discern patterns of similarity. The characteristics of the abdomen do not seem to provide a reliable basis for tribal assignment in numerous cases, although structural patterns may be noted in some generic groups and phyletic series. So great is the abdominal diversity within the Dorylomimini that it is almost impossible to define a tribal pattern of characters. In no other section of the entire family Staphylinidae is the adaptive plasticity of the staphylinid abdomen shown to better advantage than in the Dorylomimini (see preceding section on morphological specializations and the systematic section on the tribe).

As a group the Dorylomimini have a myrmecoid habitus, but because the abdomen does not provide a set of characters for tribal definition it is necessary to utilize a pattern of thoracic and cephalic characteristics for this purpose. Although the thorax is subject to variation in very specialized genera, it provides the most consistent set of diagnostic characters for the tribe: Pronotum usually elongated, relatively slender, and strongly convex; pronotal sides strongly deflexed, not delimited from the hypomera, and more or less inflexed behind the procoxae; procoxal cavities almost closed by the elongated prosternum, the inflexed pronotum, and the enlarged mesothoracic peritremes (sometimes small, in which cases the pronotal hypomera are more deeply inflexed); mesocoxae widely separated and free, i.e., not set in margined acetabula; metasternum large and inordinately convex; metacoxae distinctively subtriangular or subconical—transverse in a large majority of Aleocharinae—and projecting laterally as well as posteriorly from the body because of the convexity of the metasternum.

In the systematic section of the monograph the dorylomimine genera are organized into ten groups and eight phyletic series (three in the Ethiopian Region, one in the Oriental Region, and three in the New World). Provisional conclusions concerning the phyletic and host relationships of the genera of Dorylomimini are summarized in figure 1. It should be noted that no genus of the tribe is known

Fig. 14. A diagram of the host and phyletic relationships of the Dorylomimini (Aleocharinae). Ection, Nomamyrmex, Labidus, and Netivamyrmez are New World army ant genera of the Ectioni; Aenictus and Dorylus are Old World genera of the Aenictini and Dorylini. Eight phyletic lines within the Dorylomimini are indicated by number: (1) Dorylomimus series; (2) Mimanomma series; (3) Sahlbergius series; (4) Aenictoteras series; (5) Ecitomorpha series; (6) Puliconomorpha series; (7) Philacamatus series; (8) Labidopullus-Leptanillophilus-Mimeciton series. As they have not as yet been recorded with army ants, the host relationships of Jeanneliusa, Sahlbergius, and Parasahlbergius are questioned.
to occur with more than one host genus and only the *Leptanillophilus*
generic group (with a single discordant genus) with more than one
host genus. A large majority, if not all, of the dorylophile species
are evidently host specific, although in a few cases the specificity in-
volves several closely allied host species. It seems clear that a high
degree of host specificity was a major factor throughout the evolu-
tion of the host-guest interrelationships and was essential for the
preservation of the interspecies system (or systems) of Dorylomim-
ini-Dorylinae.

Although I have assembled a number of Old World and American
genera in the Dorylomimini, it is not certain that all of the assign-
ments will prove defensible. In the strictest sense of monophyly,
this classification implies that the Dorylomimini stemmed from a
single aleocharine species which adapted to the social organization of
a single doryline ant species at some remote time. From that event
a dorylomimine-doryline interspecies system could have evolved pro-
vided that the system were maintained through rigorous host speci-
icity, with differentiation of beetle species, genera, and generic
groups correlated with differentiation of host-ant genera and tribes.

The present-day host-guest relationships of dorylomimine genera
suggest that such an evolutionary course may have been followed (if
the tribe is polyphyletic, the several included systems may have
evolved in the above manner from several initial species adaptations
as dorylophiles). A major point at issue in these postulations is the
phylogenetic history of the army ants. Assignment of Old and
New World army ants to a single subfamily, Dorylinae, implies
monophyly, but there are myrmecologists (Brown, 1954) who be-
lieve that the Old and New World army ants evolved independently
and developed similar behavior patterns convergently. However,
Schneirla (1957) postulated that the nomadic behavior patterns of
all army ants are homologous and stemmed from a common ancestral
pattern. If the Dorylini, Aenictini, and Ecitonini share a common
heritage, it seems likely that the separation of Old and New World
components took place early in the evolutionary history of the group,
perhaps in the Mesozoic. Inasmuch as the Old and New World
army ant faunas do not share a single genus or tribe, an ancient
divergence is probable if a common ancestor existed. Because army
ants, with a few exceptions, are tropic-limited organisms, there evi-
dently were few opportunities—if any—for species to pass by way
of an Alaskan or Antarctic bridge under tropical conditions from the
Old World to the Americas or in the opposite direction.
Should it be demonstrated conclusively that the Old and New World army ants did not have a common origin, retention of the tribe Dorylomimini as herein constituted would be indefensible.

The evolutionary implications of independently derived faunal systems of Ecitonini and eciptophiles in the New World, and Dorylini, Aenictini and their dorylophiles and aenictophiles in the Old World, are no less interesting than those of a single system. The convergent evolution of such strikingly similar interspecies systems is a matter of considerable evolutionary interest.

Dorylomimini of the Ethiopian Region

The African Dorylomimini seem to have differentiated along three phyletic lines as indicated by three generic groups: Dorylomimus group with Anomma, Mimanomma group with Dorylus s.s. and Anomma, and Sahlbergius group with undetermined hosts.

Among the Dorylomimini, Dorylomimus is relatively generalized and may serve as a “prototype” in exhibiting the tribal pattern of characters. There is considerable diversification of abdominal structure in the Dorylomimus group; the abdomen is never petiolate although in Dorylogaster (fig. 18, F) it may appear myrmecoid because of its ovoidal form and slender base. The Dorylocratus abdomen is robust and has curiously fimbriated sternites and parasternites (fig. 19, J, K) of undetermined significance. With 17 recorded species Jeanneliusa is the largest genus of the group; although its species have not been recorded with ants (all collected at lights) Jeanneliusa is clearly related to Dorylocratus and must be included in the tribe. The abdomen of Jeanneliusa (fig. 19, G) is singularly modified to receive the wings in repose; the sides of the abdomen are elevated and the dorsum depressed so that the wings—which apparently cannot be folded under the elytra—lie in a concave trough. Most species of the Dorylomimus group, if not all, have foliate setae on the planter surface of the tarsi, as have some species of Pygostenini.

Mimanomma and allied genera constitute a second phyletic series in Africa. Dorylobactrus and Dorylostethus contain several small, slender species with eyes, wings, and non-petiolate abdomens (fig. 20, A, B). Mimanomma, by contrast, one of the most highly specialized dorylophiles (fig. 20, D), is in form not unlike a small phasmid. In addition to its distinctive petiolate abdomen, Mimanomma has numerous characters that may be considered regressive, including eyelessness, aptery, and extreme fusion of sclerites. One of the most
interesting features of the *Mimanomma* group is a specialization of the legs: The femora and tibiae are grooved to receive the tibiae and tarsi, respectively (fig. 20, C). Thus the legs may be folded compactly, an adaptation that could presumably serve to minimize the loss of parts. This adaptation would seem to suggest some unusual behavior on the part of the beetles or their hosts; the beetles might be carried by their hosts during emigrations, for example.

The *Mimanomma* phyletic series illustrates a significant point to be considered in the procedure of classifying dorylophiles. No matter how specialized and bizarre a genus such as *Mimanomma* may be, there is little justification for proposing a special tribe or subfamily for it on these grounds alone. By itself *Mimanomma* is so unusual that its position seems to be very isolated; Wasmann (1912a) erected a subfamily to receive it but soon recognized its alecharine affinities through relationship to the more generalized *Dorylobactrus* and *Dorylostethus*.

A third Ethiopian phyletic series is represented by *Parasahlbergius* and *Sahlbergius*, two genera collected at lights in Liberia and Tanganyika but certainly dorylophilous in habits. Myrmecoid in form, these small beetles have petiolate abdomens of a distinctive type (fig. 19, A, B). The petiole is formed by the tergite of the second abdominal segment; in *Parasahlbergius* it forms a semicylindrical structure, in *Sahlbergius* a complete tube. The remainder of the abdomen is more or less ovoidal in form and articulate with the unique petiole by slender condyles of the third segment.

**Dorylomimini of the Oriental Region**

Of the few aenictophilous staphylinid genera recorded from the Oriental Region, only the Philippine genus *Aenictoteras* is a possible member of the Dorylomimini. This genus (fig. 21) is so distinctive and has such an unusual abdomen that, in the absence of linking forms, definite proof of its relationship to the Dorylomimini is not possible at this time. The isolated position of *Aenictoteras*, however, should be considered with caution; it may be recalled that the equally bizarre African genus *Mimanomma* occupied a seemingly isolated position before its generalized relatives were discovered.

The thoracic characters of *Aenictoteras* conforms to the pattern that distinguishes the Dorylomimini as defined in this monograph. *Aenictoteras* does not belong to the Myrmedoniini in which it is placed in current catalogues. The abdomen of *Aenictoteras* is unique in several respects. The two-segmented petiole is formed by the
third and fourth abdominal segments; the sclerites of each segment have fused to form a cylinder without sutures—as in the African *Mimanomma*. From the fifth segment a distinctive tube projects forward; when the abdomen is recurved over the thorax, the tube is probably directed caudally. The apex of the tube seems to be closed by a membrane, and it has not been ascertained whether or not the function of the tube is secretory.

*Dorylomimini of the New World*

It is my opinion at this time that the evolution of the American dorylomimine fauna progressed along four major lines; the *Ecitomorpha* group differentiated in colonies of the large epigaic Ecitons, the *Pulicomorpha* and *Philacamatus* groups with *Neivamyrnex*, and the *Labidopullus-Leptanillophilus-Mimeciton* phyletic series with *Labidus*, *Neivamyrnex*, and *Nomamyrmex*. Myrmecoidy, accompanied by the development of petiolate and subpetiolate abdomens—frequently by different means—evolved in parallel fashion in each of these phyletic lines.

*Ecitomorpha* and *Ecitophya*, although specialized to run in the files of their epigaic hosts, are more generalized in many ways than the other genera of American dorylomimines. In important respects these genera appear to be counterparts of the African *Dorylomimus*. They bear a general resemblance to their hosts in coloration, surface sculpture, antennal form, in their slender heads and pronota, long appendages, and ellipsoidal, subpetiolate abdomens. The species appear to be well suited for an epigaic, nomadic life; they are agile, rapid runners, have large eyes and functional wings.

*Probeyeria*, *Beyeria*, and *Pulicomorpha* represent a phyletic series associated with *Neivamyrnex* in southwestern United States (at least as far north as northern Kansas) and Mexico. *Probeyeria* and *Beyeria* are especially noteworthy for the distinctive manner in which the petiole is formed (fig. 23, A, C, E) by the “second segment sternite”—a sclerite not characteristic of the Aleocharinae—and the attenuated third segment tergite. The second sternite attains a remarkable size in *Beyeria*. It is understandable how a second segment sternite could justifiably “reappear” in some physogastric termitophiles to aid in the support of the large membranous abdomens (Seevers, 1957), but its presence in this group is an enigma. Apart from the distinctive abdomen, the genera *Probeyeria* and *Beyeria* are relatively generalized ecitophiles possessing eyes and functional wings (they are attracted to lights). *Pulicomorpha*, however, is eyeless
and apterous; its single recorded species is a minute, pale form occurring with a minute, pale Neivamyrmex in Baja, California.

The Philacamatini group comprises four genera that share a pattern of petiole formation yet differing in the number of segments that contribute to the petiole. The structure of the individual petiolar segments is the same; each segment is exceptionally slender but retains generalized sclerite relationships (paratergites and paratergites if present are very slender). The genera differ in that Philacamatini (fig. 24, A) has a one-segmented petiole, Crematoxenus (fig. 24, D) and Cryptomimus (fig. 24, B) have two-segmented petioles, and Diploeciton (fig. 24, C) has a three-segmented petiole. The non-petiolar segments form an ovoidal "gaster" in these genera, and although the number of segments that contribute to it varies, its general appearance remains about the same. Current catalogues (Blackwelder, 1944; Borgmeier, 1949) segregate the four genera of this group into three tribes (Philacamatini, Crematoxenini, and Myrmedoniini) and completely obscure any possible relationship that they may have. Although the abdomens of the members of this group differ chiefly in the number of segments involved in the petiole and "gaster," it seems unlikely that additional segments were added to the petiole in step-like sequence but probably developed through parallel evolution. Cephalic and thoracic differences indicate that Crematoxenus and Cryptomimus could not have evolved from a Philacamatini-like ancestor, nor Diploeciton from any of the other genera. One of the most puzzling features of the group is a long, anteriorly-directed filiform process on the underside of the Diploeciton abdomen (fig. 24, C), formed by combined prolongations of the third and fourth sternites. As we have no evidence that this process has special glandular openings, its function is problematical. The occurrence of this distinctive structure might perhaps be dismissed as fortuitous were it not for the fact that a recently discovered new genus, Ecitotima Seevers (fig. 36, F), of the tribe Myrmedoniini, has an almost identical process. The convergent evolution of this unusual structure poses an intriguing problem.

In my opinion a fourth phyletic series of American Dorylomimini comprises the Labidopullus, Leptanillophilus, and Mimeciton generic groups. Despite the fact that current catalogues divide these groups in a variety of ways—usually into the tribes Leptanillophilini and Mimecitonini (Borgmeier, 1949)—it seems unmistakable that they stemmed from the same ancestral stock. Borgmeier (1958) left Labidopullus unassigned, being unable to fit it into any tribe. The
species of this series are small in size, more or less myrmecoid, and noteworthy for regressive specializations. The myrmecoid abdomen, with minor exceptions, is uniform in structure and appearance: Ovoidal to ellipsoidal, subpetiolate in having the third segment very slender at base and articulating by condyles with second tergite and metasternum, lacking paratergites and parasternites, and with overlapping tergites and sternites on the side.

The Leptanillophilus and Mimeciton generic groups contain many of the most highly specialized members of the American Dorylomimini, and have many regressive specializations. Labidopullus Borgmeier is certainly the most generalized member of the phyletic series and exhibits none of the regressive specializations that characterize the other groups. It is of special interest in forming a link between generalized Dorylomimini and the two very specialized groups of the series. The Leptanillophilus group is characterized by eyelessness, aptery, ten-segmented antennae, fused elytra, and some
unusual body forms. The *Mimeciton* group is also eyeless and apterous, and has greatly reduced elytra or lacks them entirely (*Mimeciton*). Complete fusion of sclerites of the head and thorax is a common feature of many species and sutures (e.g., the gular sutures) are often absent. Bizarre body forms, such as that of *Labidominimus* (fig. 27, A, B), are a feature of the *Mimeciton* group.

The dichotomy resulting in the two principal groups of this series was apparently correlated with the differentiation of their host genera: The *Mimeciton* group is restricted to *Labidus* societies and the *Leptanillophilus* group to the societies of *Neivamyrnex* and *Nomamyrnex*. The generalized *Labidopullus* is associated with *Labidus*. One may surmise that the common ancestral stock for this series occurred in an early period of the history of the American army ant societies, possibly before the existing genera of Ecitonini had differentiated. Isolation of stocks of this series in the subsequently differentiating *Labidus* and *Neivamyrnex* may have provided a basis for the evolution of the *Leptanillophilus* and *Mimeciton* groups. The occurrence of *Ecitophanes* with *Nomamyrnex* presents a problem, but since *Ecitophanes* is closely allied to *Ecitomerus*, a *Neivamyrnex* guest, this association may have resulted from a change of host affinity. It seems evident that a high level of host specificity must have been maintained throughout the evolutionary history of this series to account for the present host-guest correlations. But an occasional adaptation to the societies of another species, even of another genus, does not seem unreasonable.

**THE TRIBE MYRMEDEONIINI (ALEOCHARINAEE): CONVERGENT EVOLUTION OF DORYLOPHILOUS GROUPS**

*Tribal Composition*

The tribe Myrmedoniini as defined in this study is a much restricted taxon compared to the Myrmedoniini of current catalogues (see Systematic Section for a characterization of the tribe). Even in a restricted sense, though, the tribe is not exclusively dorylophilous, but contains other types of myrmecophiles as well as termitophiles. In this respect it differs from the exclusively dorylophilous aleocharine tribes (the Pygostenini may be an exception) with which this monograph is concerned.

Most species of Myrmedoniini, if not all, have some association with ant or termite societies. The relationship varies from simple
predation, facultative or obligate, to true integration with the society. The generalized members of the tribe, species of Drusilla and Zyras s.l. for instance, may be persecuted predators living near ant and termite colonies or in sparsely populated sections of the nest. Some species of Myrmedoniini have been able to attain true integration with their hosts and to establish the basis for enduring interspecies systems. Some of these independently evolved systems of Myrmedoniini are associated with:

1. Ants of the subfamily Formicinae (*Formica, Camponotus*).
   a. Subtribe Lomechusina: *Lomechusa, Lomechusoides* and *Xenodus* in the Palaearctic, Nearctic and Ethiopian Regions.

2. Termites of the subfamily Nasutitermitinae.
   a. Subtribe Termitozyrina: *Termitozyras, Termitosymbia, etc*, in the Neotropical Region.

3. Army ants of the subfamily Dorylinae.
   b. *Tetradonia* group in Neotropical and Nearctic Regions.
   c. *Dinocoryna* group in Neotropical and Nearctic Regions.
   d. *Ecitosius* group in Neotropical Region.
   e. *Aenictonia* group in Ethiopian and Oriental Regions.
   f. *Ocyplanus* group in Ethiopian Region.
   g. *Myrmechusa* group in Ethiopian Region.
   h. *Aenictobia* group in Oriental Region.
   i. *Aenictophila* group in Oriental Region.

The Lomechusina are noteworthy for the presence of tufts of golden glandular hairs (trichomes) on the abdomen, and for their obligate association with formicine ants. The Termitozyrina (Seev, 1957) includes several limuloid genera of termitophiles and one especially interesting physogastric genus, *Termitosymbia*, the only such genus in the Myrmedoniini.

The Dorylophilous Components of the Tribe

The Myrmedoniini associated with army ants undoubtedly constitute a number of independently evolved groups. It is not easy to determine whether or not each of the groups represents an independent adaptation to army-ant societies, but a summary of my tentative conclusions in schematized in figure 16 (the *Ecitosius* group recently discovered in Costa Rica with *Neivamyrmex* is not included).
Fig. 16. Host and phyletic relationships of the dorylophilous Myrmedoniini (Aleocharinae). The diagram is designed to indicate that dorylophily evolved independently a number of times within the Myrmedoniini, and that other groups of myrmecophilous and termitophilous groups exist as well.
There is no conclusive evidence of a close relationship between the Old and New World dorylophilous groups, although the possibility of a link between the Philippine *Aenictobia* and the American *Ecitopora* group should not be ignored. Most Old and New World groups are clearly of independent origin.

The dorylophilous *Myrmedoniini* do not display anything like the morphological diversity that makes the Dorylomimini so outstanding, yet do show some of the same adaptations. Only three genera are known to have petiolate abdomens although others have a myrmecoid habitus; only two cases of eyelessness indicate evolutionary regression. Two genera with petiolate abdomens are members of the American *Dinocoryna* group, yet apparently developed petioles independently: *Ecitocryptodes* with a one-segmented petiole is associated with *Neivamyrmex; Ecitocryptus*, with a two-segmented petiole, is a member of a small group of species living with *Noma*-*myrmex*. The genus *Ecitosisus*, a member of a group of *Neivamyrmex* guests, has a petiole structurally different from those of the other two cases. *Ecitotima* (fig. 36, F) is remarkable in having a distinctive abdominal process structurally similar to that of *Diploeciton* (fig. 24, C) of the Dorylomimini (see discussion of that tribe).

The American fauna of dorylophilous *Myrmedoniini* seemingly consists of four principal phyletic series that originated from different stocks within the tribe. *Ecitopora* and allied genera are relatively generalized and seem to be morphologically specialized only in bearing close resemblance to their hosts in coloration, surface sculpture, and antennal form. The genera of the *Ecitopora* group occur with all genera of Ecitonini, but one must not infer from this that the species have numerous hosts; many species are host specific. The *Tetradonia* group is characterized by relatively slender bodies, exceptionally long antennae and legs, and large eyes. They seem to be adapted, in most instances, for an epigaeic life with such hosts as *Eciton* and *Labidus praedator*. It may be significant that the only known blind member, *Ecitotyphlus*, occurs with the hypogaeic species, *Labidus coecus*.

Inasmuch as Dr. David Kistner is making a comprehensive study of the African dorylophile fauna, I shall make few comments about it here. It is my impression that the several groups of myrmedonine dorylophiles show few morphological specializations for this mode of life. Many of the dorylophiles are related to, or belong to, the vast "Zyras complex" that numbers hundreds of species in Africa and Asia. The taxonomy of this complex will require much refinement.
to be meaningful. So far the only known link between the Ethiopian and Oriental myrmedoniine faunas is *Aenictonia*, with the first Oriental species recorded from Thailand later in the monograph.

In addition to *Aenictonia*, the poorly studied Oriental aenictophile fauna is known to have two myrmedoniine genera, *Aenictobia* and *Aenictophilus*. As each is more or less isolated morphologically, I have placed each in a separate group. *Aenictobia* may be allied to the American *Ecitophiletus* group but the matter is conjectural at this time. A new Thailand genus, *Aenictophilus* (fig. 30, D), has several interesting features; its abdomen has the two basal segments narrower than the others and is perhaps incipiently petiolate; and the fourth sternite has deep impressions accompanied by an unusual vestiture of fine setae. *Aenictophilus* resembles the American genus *Ecitophiletus* of the *Dinocoryna* series in some interesting respects but it is doubtful if these connote close relationship.

**The Old-World Tribe Pygostenini (Aleocharinae)**

The largest tribe of Old-World dorylophiles, the Pygostenini, was thoroughly revised by Kistner (1958), who recognized 19 genera and 121 species. Inasmuch as Kistner considered the classification, phylogeny, and host relationships of the genera and species of the tribe in detail, interested readers are referred to his monograph. After establishing the fact that the Pygostenini are Aleocharinae, Kistner noted that in the three principal phyletic series there was an evolutionary trend for the development of special body forms, while in secondary lines regressive changes occurred repeatedly. Some pygostenines retain a more or less generalized aleocharine form, others are fusiform, and some distinctively attenuated. A correlation between body form and mode of life was not established. It is interesting to note that there is no indication of the evolution of myrmecoid species with petiolate abdomens in the Pygostenini. The principal regressive specializations in the Pygostenini are eyelessness and aptery, both correlated with life in the hypogaeic societies of *Dorylus* s.s.. Pygostenini have been recorded with *Dorylus* s.s., *Dorylus* (*Anomma*), *Dorylus* (*Typhlopone*), and *Aenictus*. A large majority of the pygostenine species are Ethiopian, although some occur in the Palaeartic Region of northern Africa and Asia Minor, and one curious genus, *Aenictoxenus*, is associated with *Aenictus* in the Philippines. A puzzling ecological feature of the tribe is the association of an Oriental genus, *Odontoxenus*, with fungus-growing termites (*Odontotermes*).
The Neotropical Ecitophilous Tribe Ecitogastrini (Aleocharinae)

Ecitogaster, with five species living with Labidus praedator, is the sole representative of this seemingly isolated tribe, and occurs from Brazil to Mexico. I have been unable to relate it to any dorylophilous or free-living group. In important respects it bears a close resemblance to certain genera of Old World Pygostenini, but the similarities are probably the result of convergence. At my request, Dr. Kistner examined Ecitogaster and concluded that it should not be classed with the Pygostenini, although conceding that it might have a remote ancestral relationship. Three factors seem to make it unlikely that Ecitogaster and the Pygostenini stemmed from common ancestral stock: Ecitogaster, itself very specialized, resembles most closely a highly specialized genus of pygostenines, Sympolemon, rather than the generalized members of that tribe; Ecitogaster occurs with a single species of neotropical ants (Labidus praedator); and the aedeagus and terminal abdominal sclerites do not conform well with the pygostenine pattern of characters. If Ecitogaster is related to the Old World tribe, a large number of linking forms must have disappeared during the evolutionary history of the genus.

The Neotropical Ecitophilous Tribe Ecitocharini (Aleocharinae)

The American tribe Ecitocharini and the African tribe Deremini that follows are proposed as new taxa in the Systematic Section. The genera of these tribes are currently catalogued as Myrmedoniini but they do not belong to that tribe in its restricted sense (the characters that differentiate these tribes from the Myrmedoniini s.s. are given elsewhere). The Ecitocharini and Deremini may be most closely related to the Athetini but that tribe is poorly delimited and ill-defined. The fact that these two tribes are discussed together does not imply that I consider them to have had a common origin. They do have many similar characteristics, especially with respect to integumental features.

Except for the myrmecoid Ecitodaemon Reichensperger, the Ecitocharini have a generalized body form. The cephalic, thoracic, and abdominal ornamentations and modifications that are a noteworthy feature of the Ecitocharini are well illustrated by the species of Ecitozena Wasmann (fig. 31); included are sulci, carinae, and a
variety of eminences. Inasmuch as integumental specializations occur so much more frequently among dorylophilous Staphylinidae than among non-inquilines, they probably have had some adaptive value. Carinae, sulci, impressions, tubercles and other eminences feature the aleocharine tribes Ecitocharini, Deremini, some Myrmedoniini, Phyllodinardine, and Trilobitideini, as well as the groups of dorylophilous Paederinae.

With its petiolate abdomen, Ecitodaemon is especially noteworthy, and provides another example of the strong selection pressure for myrmecoidy that must have existed during the evolution of the dorylophilous fauna.

The four genera and ten species of Ecitocharini were collected with a few species of Eciton, indicating a strong host specificity.

THE ETHIOPIAN TRIBE DEREMINI (ALEOCHARINAE)

As indicated in the previous section, it seems necessary to remove this group from the Myrmedoniini, s.l., and to establish a new taxon for it. Difficult to differentiate from the Athetini at present, the species are recognized by their habitus and by their dorylophily. The Deremini are very small, slender, somewhat attenuated species that exhibit a variety of integumental specializations. It is likely that all species of Deremini occur with doryline ants even though many of the 75 or more described species were collected only at lights. The six genera are recorded as guests of Dorylus (Anomma) and Dorylus s.s.

ECITOPHILOUS PAEDERINAE, STAPHYLININAE, AND TACHYPORINAE

These staphylinid subfamilies have contributed interesting species to the ecitophilous fauna of the American tropics, but seem to have no Old World counterparts.

PAEDERINAE: Although the ecitophilous Paederinae do have unusual features, they are not so modified structurally as to be clearly recognizable as inquilines. The nine genera of known obligate ecitophiles appear to have developed from three different paederine stocks and I am placing them in the Mimophites, Ecitonides and Ecitomedon groups. The group and host relationships of the ecitophilous Paederinae are illustrated in figure 17. It is interesting to note that the three independently derived groups have essentially
FIG. 17. A diagram of the host relationships of the New World ecitophilous Paederinae.

the same host patterns with a large majority of the species occurring with Labidus. It is especially noteworthy that ten genera and 22 species of Paederinae are recorded from the societies of Labidus praedator (seven genera and ten species of the Ecitonides group, nine species of Mimophites, and two genera and three species of the Ecitomedon group). Labidus praedator is widely distributed from Mexico to Argentina and is almost surely polytypic. Isolation of populations of this host have probably provided numerous opportunities for speciation of the guests isolated with them. Labidus praedator doubtless has more species of ecitophilous Staphylinidae of all groups than any other American species of army ants. A comprehensive study of the various populations of Labidus praedator and their remarkable ecitophile fauna should be a fruitful project. Some of the Paederinae such as Mimophites, Bolbophites, Labido-
phites, and Synecitonides have long slender bodies and exceptionally long appendages but none has a petiolate or myrmecoid abdomen. Ecitotropis and Ecitosaurus are short, compact species with short, stout legs; they may perhaps be considered sub-limuloid. A characteristic feature of almost all seven genera of the Ecitonides group is an unusual ornamentation of tubercles, carinae, and sulci (fig. 34).

**STAPHYLININAE:** There are two principal generic groups of ecitophilous Staphylininae: The Ecitolycus group in the Quediini, and the Ecitophytes group in the Staphylinini. The former has no noteworthy adaptive features, but the latter contains the remarkable myrmecoid genus Ecitophytes. In a tribe as conservative in form as the Staphylinini, Ecitophytes (fig. 34, E) is outstanding for its petiolate abdomen and aleocharine facies. Understandably, Wasmann assigned this genus to the Aleocharinae as a relative of Ecitophyta, but it does not belong to that subfamily as its aedeagus clearly reveals. Proxenobius and Xenobius, more generalized relatives of Ecitophytes, are also unusual members of the Staphylinini but do not have either a myrmecoid facies or a petiolate abdomen.

**TACHYPORINAE:** The limuloid genus Vatesus of the monobasic tribe Vatesini, with more than 25 species, is an important and almost ubiquitous component of the Neotropical ecitophilous fauna. The occurrence of the genus from Argentina to Vera Cruz in Mexico, and its association with four genera of Ecitonini (and possibly Cheliomyrmex as well) attest to the ancient origin of the Vatesini. As suggested by the present pattern of host relationships, Vatesus has maintained apparently an excellent record for host specificity during its evolution. Although some species of Vatesus occur with several hosts, others are restricted to societies of one host. Species groups are usually restricted to one or two host genera and there is a definite host pattern throughout the genus. In general form Vatesus does not differ greatly from some free-living tachyporines, such as Coproporus and Tachyporus. Designated by Wasmann as one of the “defense-type” myrmecophiles, Vatesus has an exceptionally large, carapace-like pronotum and large, strongly deflexed elytra. The head is almost completely covered by the pronotum and its vital parts are unexposed; the legs and retractile abdomen may also be covered by the pronotum and elytra. It appears that Vatesus is now a well-integrated and tolerated inquiline, but this may not have been the case during the early evolutionary history of the genus when it became associated with army ants.
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Table 1.—Host Relationships of the Independently Derived Groups of Dorylophilous Staphylinidae
SYSTEMATIC SECTION

GENERAE OF DORYLOPHILOUS STAPHYLINIDAE

The following summary is designed to indicate the status of generic names proposed for dorylophilous Staphylinidae and show the categories to which I am assigning the valid genera. The tribal or subfamily positions of almost one-half of the genera are changed in this monograph. Unless otherwise indicated, tribal categories are in the Aleocharinae.

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<th>Present position</th>
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Acamatoreras Reichensperger
(synonym of Diploeconton Wasmann)

Acamatoxenus Mann
(new synonym of Beyeria Fenyes)

Acamatusina Bruch
(synonym of Leptanillophilus Holmgren)

Acamatusinella Bruch
Dorylomimini

Acanthodonia Bruch
(synonym of Tetradoria Wasmann)

Acanthonia Wasmann
(synonym of Gapia Blackwelder)

Aenictobia Seevers
Myrmedoniini

Aenicientonia Wasmann
Myrmedoniini

Aenicienthiphila, new genus
Myrmedoniini

Aenictoteras Wheeler
Dorylomimini

Aenictotyphlus Patrizi
(synonym of Lydorus Normand)

Aenictozenus Seevers
Pygostenini

Aneptopleura Aeniceps Patrizi
Myrmedoniini

Aenicientonidius Fagel
Oxytelinae

Anisopsis Fauvel
Oxytelinae

Anisopods Fauvel
Oxytelinae

Anommatocera Wasmann
(subgenus of Aenicientonia Wasmann)
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FIELDIANA: ZOOLOGY, VOLUME 47

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Subfamily ALEOCHARINAE

A KEY TO OLD WORLD TRIBES WITH DORYLOPHILOUS GENERA

1. Species strongly compressed dorso-ventrally and limuloid in form (fig. 33, D, I) .......................................................... 2
   Species not compressed dorso-ventrally and not limuloid in form (fusiform in some Pygostenini) .................................. 3

2. Dorsum with numerous tubercles and carinae (fig. 33, D); eyeless; antennae deeply recessed in head (fig. 33, F) .......... Trilobitideini
   Dorsum smooth but with numerous distinctive setae (fig. 33, I); eyes present; antennae not recessed ........................................ Phyllodinardini

3. Antennae compactly organized; their segments contiguous so that the pedicels are not visible ...................................... Pygosteni
   Antennae more loosely organized; the segmental pedicels visible .................................... 4

4. Metacoxae transverse (generalized aleocharine type); metasternum not unusually convex; mesocoxae set in margined acetabula; meso- and metasternal processes broad and margined laterally; galea and lacinia exceptionally long (length of lacinia greater than distance from base of maxilla to lacinia) ...
   Myrmedoniini

Metacoxae elongated and either subtriangular, subconical, or spindle-shaped; metasternum strongly convex; mesocoxae free, not set in margined acetabula; meso- and metasternal processes moderately broad but not distinctly delimited laterally; galea and lacinia only moderate in length (length of lacinia not greater than distance from base of maxillae to lacinia) .................. Dorylomimini

A KEY TO NEW WORLD TRIBES WITH DORYLOPHILOUS GENERA

1. Mesocoxae narrowly separated; mesosternal process longer than metasterna process ................................................. Ecitocharini
   Mesocoxae broadly separated; metasternal process longer than mesosternal process ....................... 2

2. Metacoxae elongated and subtriangular, subconical, or spindle-shaped; metasternum strongly convex; mesocoxae free, not set in margined acetabula; meso- and metasternal processes moderately broad but indistinctly delimited laterally; galea and lacinia moderately long (length of lacinia not greater than distance from base of maxilla to lacinia) ....... Dorylomimini

Metacoxae transverse (generalized aleocharine type); metasternum not strongly convex; mesocoxae broadly separated and the broad meso- and metasternal processes margined laterally; galea and lacinia usually exceptionally long .... 3

3. Tarsi 4, 5, 5-segmented; galea and lacinia long (length of lacinia longer than distance from base of maxilla to lacinia); ninth tergite not deeply incised ...
   Myrmedoniini

Tarsi 4, 4, 4-segmented; galea and lacinia moderately long; ninth tergite deeply incised to form two strongly sclerotized processes (fig. 82, D) ...... Ecitogastrini

Remarks.—The above key may not separate satisfactorily some of the most highly specialized Myrmedoniiini from the Dorylomimini. Development of a myrmecoid body form in some Myrmedoniiini has brought about some structural changes paralleling those of the Dorylomimini. The comparatively long galea and lacinia of the myrmedoniine maxilla may provide the best diagnostic character.
Tribe DORYLOMIMINI


ETHIOPIAN REGION

DORYLOMIMUS Group
Dorylomimini, Wasmann, 1916; Hygronomini, Corotocae (in part), Fenyes, 1918; Dorylogastrini (for Dorylogaster), Wasmann, 1916; Fenyes, 1918.

Dorylocratus Wasmann..................... Dorylus (Anomma)
Dorylogaster Wasmann..................... Dorylus (Anomma)
Dorylomimus Wasmann..................... Dorylus (Anomma)
Dorylonannus Wasmann..................... Dorylus (Anomma)
Jeanneliusa Bernhauer.................... Host unknown

MIMANOMMA Group
Mimanommatinae, Wasmann, 1912; Bernhauer and Scheerpeltz, 1926.

Dorylobactrus Wasmann..................... Dorylus (Anomma)
Dorylostelthus Brauns...................... Dorylus s.s.
Mimanomma Wasmann....................... Dorylus (Anomma)

SAHLBERGIUS Group
Myrmedoniini (in part)

Parasahlbergius, new genus................ Host unknown
Sahlbergius Bernhauer..................... Host unknown

ORIENTAL REGION

AENICTOTERAS Group
Myrmedoniini (in part), Wheeler, 1932.

Aenictoteras Wheeler..................... Aenictus

NEOTROPICAL and NEARCTIC REGIONS

ECITOMORPHA Group
Myrmedoniini, Myrmedoninae (in part), Fenyes, 1918; Bernhauer and Scheerpeltz, 1926; Blackwelder, 1944; Athetini (in part), Borgmeier, 1949.

Ecitomorpha Wasmann...................... Eciton
Ecitophya Wasmann......................... Eciton

PULICOMORPHA Group
Pulicomorphini, Mann, 1924; Pulicomorphinae, Sanderson, 1943; Aleocharini, Caloderae (in part), Fenyes, 1918; Bernhauer and Scheerpeltz, 1926.

Beyeria Fenyes............................. Neivamyrmex
Probeyeria, new genus..................... Neivamyrmex
Pulicomorpha Mann......................... Neivamyrmex

PHILACAMATUS Group
Philacamatini, Bruch, 1933; Blackwelder, 1944; Borgmeier, 1949; Crematoxenini, Mann, 1921; Blackwelder, 1944; Borgmeier, 1949; Myrmedoniini, Falagriae (in part), Blackwelder, 1944; Athetini (in part), Borgmeier, 1949.
Crematoxenus Mann .......................... Neivamyrmex
Cryptomimus Reichensperger .................. Neivamyrmex
Diploeciton Wasmann .......................... Neivamyrmex
Philacamatus Bruch .......................... Neivamyrmex

LABIDOPULLUS Group
Incertae sedis, Borgmeier, 1958.
Labidopullus Borgmeier ....................... Labidus

LEPTANILLOPHILUS Group
Leptanillophilini, Fenyes, 1918; Bernhauer and Scheerpeltz, 1926; Blackwelder, 1944; Borgmeier, 1949.
Acamatusinella Bruch .......................... Neivamyrmex
Ecitomerus Borgmeier .......................... Neivamyrmex
Ecitophanes Borgmeier .......................... Nomamyrmex
Ecitosoma Borgmeier .......................... Neivamyrmex
Leptanillophilus Holmgren ..................... Neivamyrmex
Mimacamatus Bruch ............................ Neivamyrmex

MIMECITON Group
Mimecitonini, Wasmann, 1916; Bernhauer and Scheerpeltz, 1926; Blackwelder, 1944; Borgmeier, 1949; Hygronomini, Mimonillae, Bernhauer and Scheerpeltz, 1926; Blackwelder, 1944.
Labidoglobus Reichensperger ................... Labidus
Labidomimus Wasmann .......................... Labidus
Labidosphaerula Reichensperger ................... Labidus
Mimeciton Wasmann ............................. Labidus
Mimonilla Wasmann ............................. Labidus
Paramimeciton Reichensperger ................... Labidus

Wasmann (1916) proposed the tribe Dorylomomini for four genera of African dorylophiles but the category has never appeared in subsequent catalogues (Fenyes, 1918–21; Bernhauer and Scheerpeltz, 1926). I now revive and expand the tribe to include 33 Old and New World genera scattered through a dozen of more tribal and subfamily categories in catalogues currently used (Fenyes, 1918–21; Bernhauer and Scheerpeltz, 1926; Scheerpeltz, 1933 and 1934; Blackwelder, 1944; and Borgmeier, 1949). Categories to which genera had been previously assigned follow:

Hygronomini, Corotocae: Dorylonannus, Dorylocratus, Dorylomimus, and Jeanneliusa.
Doryloganstrini: Dorylogaster.
Pulicomorphini (or Pulicomorphinae): Pulicomorpha, and Beyeria.
Philacamatini: Philacamatus.
Crematoxenini: Crematoxenus, Cryptomimus.

Mimecitonini: *Mimeciton, Labidoglobus, Labidosphaerula, Paramimeciton, Mimonilla,* and *Labidominus.*

Hygronomini, Mimonillae: *Mimonilla, Labidominus.*


Myrmedoniini, Falagriae: *Diploeciton.*

Aleocharini, Caloderae: *Beyeria.*

Aleocharinae (incertae sedis): *Acamatoxenus, Labidopullus.*

Mimanommatinae: *Mimanomma.*

Few attempts have been made to justify the tribal assignments outlined above, and the classification as a whole has developed haphazardly. The assignments have the weaknesses of obscuring generic relationships, segregating closely allied genera in different tribes, and erroneously placing many specialized dorylophiles in large tribes with unrelated free-living genera, and even with unrelated termitophiles. For instance, there has been no justification—except that all genera concerned have 4, 4, 4-segmented tarsi—for grouping *Dorylomimus* and relatives, certain specialized termitophiles and miscellaneous free-living genera in the Hygronomini.

The grouping of 33 genera from several zoogeographic realms in a single pantropical tribe may imply a monophyletic origin, perhaps from a single dorylphilous species. The wisdom of this proposal may be questioned, considering the fact that it has not been proven beyond doubt that the subfamily Dorylinae is a monophyletic group. As nearly as possible, I have tried to keep host relationships and zoogeographic data in the background in preparing my classification and to use only morphological data for my conclusions. In an assemblage as morphologically diversified as the 33 genera assigned to the Dorylomimini, it might not be difficult to justify the elevation of many generic groups to tribal rank on the basis of abdominal differences. But I do not believe that the ten generic groups represent ten independent adaptations to life in army-ant societies. My investigations have stressed the discovery of morphological patterns, and I have concluded that there is a tribal pattern of thoracic characters in particular. Existence of the pattern does not necessarily connate close relationship and does not rule out the possibility of convergent development.
Because of the inordinately large number of specialized genera, it is difficult to characterize the tribe Dorylomimini so as to include all the members. The thorax provides a community of characters that seem to me to differentiate the tribe, although it must be recognized that all genera do not necessarily have to conform to the pattern in all respects. Morphological generalizations may be summarized as follows:

**PROTHORAX.**—The prothorax is essentially a heavily sclerotized, compact, sub-cylindrical tube. The pronotum is usually elongated, relatively slender, and very convex; its deflexed sides are not delimited from the vertical hypomera and are often somewhat inflexed behind the procoxae. The prosternum is exceptionally large (for the Aleocharinae) and extends caudal between the procoxae; more often that not it is contiguous with, or fused to, enlarged mesothoracic peritremes. The size and degree of sclerotization of the spiracle-bearing peritremes are not uniform and apparently do not conform to a phyletic pattern (as examples, the peritremes are small and feebly sclerotized in *Probeyeria, Beyeria,* and *Diploeciton;* they are large and contiguous with the prosternum in *Ecitomorpha, Ecitophyia,* and *Dorylocratus,* and are large and fused to the prosternum in *Dorylomimus* and genera of the *Mimeciton* group). The procoxal cavities are almost "closed," as a rule, by the approximation of the prosternum, large peritremes, and inflexed pronotal sides, or (in the event that the peritremes are small) by an exceptionally long prosternum and deeply inflexed pronotal sides.

**MESO-METATHORAX.**—The ventral side of these regions and the coxae provide a distinctive pattern of characters: The "free" mesocoxae are not set in mesocoxal acetabula because these are very shallow and unmargined; the mesocoxae are moderately widely separated and the meso- and metasternal processes between them are feebly delimited; the metasternum is moderately to very strongly convex and, as a result, the caudal margin on each side is more nearly vertical than horizontal in many cases so that the hind coxae tend to project somewhat laterad as well as caudal from the metathorax; the metacoxae are sub-conical, spindle-shaped, or even subglobose (in contrast to the transverse type that is so characteristic of the Aleocharinae).

The elytra are generalized in most genera, but in the *Leptanil-lophilus* group are fused together, and in the *Mimeciton* group are vestigial or absent. Functional wings are present in some genera (e.g., *Jeanneliusa* and *Parasahlbergius* in the Ethiopian Region, and
Probeyeria, Beyeria, and Dinocoryna in the New World), and are absent in many others (e.g., Mimanomma, Pulicomorpha, Leptanil-lopilus group genera, and Mimeciton group genera). In the Mimanomma and Mimeciton phyletic series the sclerites of the mesothorax and metathorax have undergone extensive fusion in some genera, and in some cases the mesothoracic tube formed by sclerite fusion is attenuated and articulates by condyles with the semi-tubular prothorax.

LEGs.—In many generic groups the legs are inordinately long by aleocharine standards. Coxal form, freedom, and position seemingly aid in lengthening the legs—the procoxae are long and spindle-shaped, the free mesocoxae are not set in deep acetabula, and the metacoxae are elongated and project laterally from the body to some degree. The tarsi are either 4, 5, 5-segmented or 4, 4, 4-segmented (both conditions are found in both the Old and New Worlds).

SPECIALIZATIONS FOR EXUDATION.—Trichomes are not present, and exodatory mechanisms, if present, are not obvious.

HEAD.—Although variable in form the head capsule is relatively generalized and has few impressions or ornamentations. The clypeus is usually deflexed so that the antennae are inserted under an arcade. The base of the head is constricted, forming a neck which articulates by a condylar surface with the semitubular apex of the pronotum; the “ball and socket” articulation (if it is really that) may provide the head with exceptional mobility. Infra-orbital carinae are absent. About two-thirds of the genera have medium-sized to large eyes, and and the others are eyeless (blindness evolved independently in three phyletic lines, at least). 11-segmented antennae are the rule but members of several American groups have 10-segmented antennae. Antennal form is variable; long antennae are more common than short, compact ones; in some instances, the antennae are rather similar in form to those of their hosts (e.g., Ecitomorpha). The gular region is generalized except in the Mimeciton group which has united gular sutures or lacks them. The mouthparts tend to be generalized. The length of the galea and lacinia (from the level of the palpal articulation) is not greater than the distance from the base of the maxilla to the same level. The maxillary sinuses are small. The mandibles are well developed.

ABDOMEN.—The abdomen may be characterized as myrmecoid except in a few genera (Doryloctates and Jeanneliusa), and is either petiolate, sub-petiolate, or non-petiolate. Strikingly different methods of petiole formation are discussed in an earlier section (evolu-
tionary considerations) and will be considered in the subsequent sections on the generic groups.

**DORYLOMIMUS Group**

This group contains five genera associated with African driver ants (*Anomma*). Judging from abdominal peculiarities, evolution in this phyletic series proceeded along three lines, represented by *Dorylomimus* and *Dorylonannus, Dorylocratus* and *Janneliusa*, and *Dorylogaster*. The abdomen of *Dorylomimus* is non-petiolate, slightly scaphoidal in form, and generalized in the sense that all sclerites are present in generalized positions. The abdomen of *Dorylogaster* is ellipsoidal and sub-petiolate, i.e., the third segment tapers to a very slender base. The abdomen of *Dorylocratus* is very robust and non-myrmecoid and characterized by unusual modifications of the sternite and parasternites (fig. 19, J, K). *Janneliusa* has the abdominal dorsum depressed and groove-like presumably to receive the wings in repose (evidently they cannot be folded under the elytra). In all genera the legs are long, the tarsi are 4, 4, 4-segmented, and the tarsi bear foliate setae on their plantar surfaces. The pronotum has a pair of distinctive apical impressions.

**Dorylomimus** Wasmann. Figure 18, A–E.


Habitus as in fig. 18, A. Head elongated, its sides converging to a short, narrow neck. Eyes large, reniform. Gula (fig. 18, B) long and slender. Antennae geniculate; scape about one-half the length of segments 2–11 combined; many segments elongated. Pronotum elongated, dorsum with a pair of apical impressions. Prosternum prolonged between procoxae and fused to the large peritremes (fig. 18, C); procoxal cavities closed by prosternum, peritremes, and inflexed hypomera. Elytra shorter than pronotum. Wings present. Legs very long; tarsi 4, 4, 4-segmented. Abdomen scaphoidal; tergites and sternites moderately to strongly convex; dorsum with a deep trough along each side the paratergites and parasternites oblique. Length, 2–4 mm.

**SPECIES OF DORYLOMIMUS WASMANN**


Fig. 18. *Dorylomimus kohli* Wasmann: A, lateral view; B, head, ventral view; C, prothorax, ventral view; D, mesometathorax; E, aedeagus, lateral view; *Dorylogaster longipes* Wasmann: F, lateral view; G, hind tarsus, lateral and dorsal views.
at St. Gabriel, Congo; and Dorylus (Anomma) nigricans sjoestedti Emery, at Gross Batanga, Cameroons. *New synonym*.

**Remarks.**—Wasmann’s (1917) key to the species does not satisfactorily separate *laticeps* from *kohli*, or *brevicornis* from *breviceps*. After examination of the types it seems likely to me that only two valid species are represented in the Wasmann collection.

**Dorylonannus** Wasmann


The following characteristics distinguish this genus from *Dorylomimus*: small size (1.8 mm. in length); head slightly transverse; eyes extremely large; antennal scape less than one-half the length of segments 2–11 combined; most antennal segments short and transverse; pronotum one-sixth broader than long; pronotum strongly constricted at middle, at which point it is only two-thirds the maximum width; hind legs long and stout; claws of hind tarsi unequal in size.

**SPECIES OF DORYLONANNUS WASMANN**


**Dorylogaster** Wasmann. Figure 18, F, G.


*Dorylogaster* is easily distinguished from the other genera of this group by its ellipsoidal abdomen (fig. 18, F). In addition, the antennae are very long, with all segments elongated; the antennal scape is relatively short, only one-sixth as long as segments 2–11 combined; the gula is very narrow; the pronotum is very feebly constricted at middle; and the coxae are extremely long, the fore and middle coxae being longer than the pronotum. Length, 2 mm.

**Remarks.**—The tarsi of *Dorylogaster* are very unusual. Reported by Wasmann to be one-segmented, they are actually four-segmented, although incompletely so. The types of Wasmann’s three species (the only collected specimens until recently) have incomplete tarsi, the three distal segments having been broken off. Recently collected specimens kindly sent to me for study by Dr. David Kistner have complete tarsi as shown in fig. 18, G. The fourth segment is extremely slender and fragile; the thicker proximal portion is constricted (feebly so in many instances) at two points, and is evidently composed of three partially fused segments. Lacking the fourth seg-
ment and having the constrictions feebly indicated, a tarsus may easily be interpreted as a one-segmented structure. The tarsi have numerous foliate setae on their plantar surface.

**SPECIES OF DORYLOGASTER WASMANN**


**Remarks.**—In the Wasmann collection the three named species are represented only by the types. The types are very similar in structure and doubtfully representative of three species; Wasmann's key does not adequately differentiate the species. The status of the names can be determined only through study of considerable additional material.

**Dorylocratus** Wasmann. Figure 19, I, K.


*Dorylocratus* is distinguished from the other genera of the group by its relatively large size and robust form, its voluminous abdomen, and by distinctive abdominal specializations.

Head one-sixth broader than long; clypeus in same plane with vertex so that the antennal fossae open dorsad; basal angles of head somewhat delimited as prominent eminences due to the presence of oblique impressions extending medio-caudad from the eyes to the basal margin; neck narrow, less than one-third as broad as head. Eyes very large, reniform. Antennae geniculate; the very long scape one-half as long as segments 2–11 combined; segments 2–10 decreasing in length and very slightly incrassate. Gular sutures fused for a moderate distance at base, and diverging slightly to the exceptionally short submentum. Mentum large, its sides and apex continuously arcuate, and its surface depressed between the very large maxillae. Mandibles large and strong. Second and third maxillary palpi-meres somewhat compressed. Pronotum one-sixth broader than long, much broader at apex than at base; sides strongly sinuate to the arcuate base. Pronotum with the two deep apical impressions typical of the group. Elytra generalized; wings present. Meso-metasternum exceptionally short. Legs very long; the coxae, and especially the hind ones, extremely long. Tarsi with numerous foliate setae. Abdomen broad and voluminous; the sternites prolonged over the dorsum (figs. 19, J, K); apical margins of the sternites fimbriated; the parasternites with knob-like processes. Judging from the position of the spiracles, the para-tergites are fused to the tergites. Length, 6 mm., width, 3 mm.
SPECIES OF DORYLOCRATUS WASMANN


Jeanneliusa Bernhauer. Figure 19, G, H.


Allied to Dorylocratus, the species of this genus are smaller, more slender, and less robust; the abdomen is distinctive in its semitubular form, and in lacking the specializations of the abdominal sternites.

Habitus as in fig. 19, G. Head variable in form; subequal in length and width or longer than broad; dorsum uniformly convex or with a shallow vertexal impression (in at least one species). Eyes large; reniform with a caudal emargination or rarely oval. Antennae variable in length; scape equal to segments 2–5 combined or segments 2–7 combined; segment 3 sometimes elongated, 4–10 usually short, cylindric, subequal. Pronotum variable in form; broader than long or longer than broad; side margins vary from feebly sinuate to strongly bisinuate; dorsum with a pair of apical impressions as a rule, but these may be absent. Inner margins of elytra often widely divergent in apical half. Wings in repose resting in the semitubular abdomen (fig. 19, G); presumably never folded beneath elytra. Legs long; tarsi 4, 4, 4-segmented, three basal segments of pro- and mesotarsi with leaf-like setae on plantar surface. Abdomen semi-tubular in cross-section; dorsum depressed, and sternites visible from above; sternites and parasternites not modified as in Dorylocratus.

Remarks.—Although eighteen species of Jeanneliusa are now recorded, there is no direct evidence concerning their mode of life. With the probable exception of the apterous species, overlaeti Fagel, all known species were attracted to lights at the time of capture. Various workers (Bernhauer and Jeannel, 1936, Silvestri, 1946, Patrizi, 1951, and Fagel, 1956, 1959, 1962) have surmised that Jeanneliusa is either termitophilous or myrmecophilous, but there are no records of its association with social insects. The fact that Jeanneliusa is clearly related to Dorylocratus and the Dorylomimus group provides strong indirect evidence that the hosts of the species are Dorylus (Anomma). Patrizi searched colonies of Anomma for this genus at Addis Ababa where he collected Jeanneliusa giaquintoi at lights, but without success. Patrizi attempted, with little success, to keep Jeanneliusa in moist chambers; he did note that during the interval of survival they never folded the wings under the elytra.

Fagel (1962) recently reported an apterous species, overlaeti, from the Congo. Perhaps the most interesting feature of this species,
aside from the aptery, is its excessively developed abdomen, a condition Fagel surmised might be one of incipient physogastry. Unfortunately, there was no record of the circumstances of the capture of this species.

**SPECIES OF JEANNELIUSA BERNHAUER**


**ANGOLA:** Dundo.

*arambourgi* Bernhauer, 1935, Rev. Franc. Ent., 2, p. 218, fig. 5. **KENYA:** Mt. Elgon.


**CONGO:** Elisabethville. **ANGOLA:** Dundo.


*conspicua* Silvestri, 1946, Boll. Lab. Agr. Portici, 6, p. 54, figs. 1–4. **ITALIAN SOMALIA:** Genale.


**ANGOLA:** Dundo.


*humilis* Fagel, 1962, Publ. Cult. Co. Diam. Angola, 58, p. 31, figs. 6, 14, 21g

**ANGOLA:** Lake Calundo.


*liberiae*, n. sp. **LIBERIA:** Suakoko.


**ANGOLA:** Dundo.


**ANGOLA:** Dundo.

*overlaetii* Fagel, 1962, Publ. Cult. Co. Diam. Angola, 58, p. 36, fig. 3. **CONGO:** Luluia; Sandoa.


**Jeanneliusa liberiae**, new species. Figure 19, H.

This small species is evidently most closely related to the Angolan species, *machadoi* Fagel; its length is slightly below the generic range of 2.4 mm. (*machadoi* Fagel) to 6.5 mm. (*giaquintoi* Patrizi). It shares with *machadoi* two distinctive features: the head is relatively long and slender (one-half longer than broad), and the pronotum is strongly constricted behind the middle. This species differs from *machadoi* in the form of the pronotum and in the relatively shorter second and third antennal segments.

Coloration flavo-testaceous. Head, pronotum, elytra, and most abdominal sclerites microreticulate. Head, pronotum, and elytra with a moderately dense
vestiture of short, fine, pale hairs. Sternites with a moderate pubescence and scattered fine, pale setae. Head (fig. 19, H) one-half longer than broad, excluding labrum and neck; vertex with a median eminence between antennae, and with a slight to moderate impression between eyes (some specimens with an eminence medial to each eye behind antennal fossa); sides of head converging gradually behind eyes to the moderately broad neck. Antennae with segments of the following relative length: 60 : 16 : 14 : 10 : 9 : 8 : 8 : 8 : 8 : 24. Antennal scape subequal to segments 2–6 combined; segment 2 slender, segment 3 a little broader, segments 4–10 subequal in width, subcylindrical. Eyes large (L : 29, W : 10); reniform, with a moderately deep caudal emargination; eye length subequal to distance from base of head; eye width about one-fourth head width; in lateral view, eyes occupy a major part of apical half of head. Pronotum (fig. 19, H) one-third longer than broad; broadest subapically; strongly constricted at middle so that the side margins are very strongly bisinuate; moderately broad at base; surface with two apical impressions (typical of the genus), and two smaller basal impressions. Inner margins of elytra diverging apically. Wings resting in semi-tubular abdomen in repose. Abdomen typical of the genus. Legs elongated; hind leg with following proportions: femur (122), tibia (95), tarsi (128), tarsal segments (52, 28, 22, 26). Legs moderately densely setose; protibiae with fine hairs in two comb-like rows near apex; pro- and mesotibiae with a pair of short apical spines; metatibiae with two longer, stronger spines; pro- and mesocoxae with leaf-like setae (see Patrizi, 1951, fig. 6).

Type from Suakoko, Liberia, collected December 28, 1951, by Mr. Blickenstaff, presumably at light; in collection of United States National Museum. Seven paratypes, same data as type, collected December 28, 1951–January 5, 1952; in United States National Museum and Chicago Natural History Museum.

SAHLBERGIUS Group

Clearly related to the Dorylomimus group through similarities in cephalic and thoracic structure, Sahlbergius and a new genus, Parasahlbergius, are placed in a distinct group on the basis of their distinctive petiolate abdomen (figs. 19, A, B), and their 4, 5, 5-segmented tarsi. The abdominal petiole is unique in that only the second segment tergite is involved in its formation. In Sahlbergius the second tergite is in the form of a complete tube, with only a slight ventral

Fig. 19. Sahlbergius mirabilis Bernhauer: A, lateral view; D, hind coxae, second tergite (petiole), and third sternite, ventral view; E, abdomen, dorsal view. Parasahlbergius liberiae, n. sp.: B, lateral view; C, second and third abdominal segments, and hind coxa, dorsal view; F, head, pronotum, and elytron, dorsal view. Jeanneliusa conspicua Silvestri: G, dorsal view. Jeanneliusa liberiae, n. sp.: H, head and pronotum. DoryLocratus rex Wasmann: I, pronotum; J, abdomen, lateral view. K, fourth and fifth abdominal segments, dorsal view to show modifications of sternites and parastermites, paratergites probably fused to tergites.
fissure to indicate the approximation of its ventrally-prolonged lateral margins. An intermediate condition prevails in *Parasahlbergius* in that the second tergite is semitubular. The tergite and sternite of the third segment taper strongly to basal condyles by which they articulate with the petiole. As a result of the development of a petiolate abdomen in this group, the hind coxae are rendered visible from above (figs. 19, C, E)—a distinctive feature—and are revealed to have small to conspicuous dorsal spurs.

Only two specimens of this interesting group have been collected, presumably both at lights. In view of their obvious affinities with the *Dorylomimus* group, there can be little doubt that *Sahlbergius* and *Parasahlbergius* are dorylophiles.

*Sahlbergius* Bernhauer. Figure 19, A, D, E.


Habitus as in fig. 19, A. Coloration of *mirabilis* pale yellow; its integuments smooth, shining, and very sparsely punctate; its vestiture consists of sparsely arranged long setae, chiefly on pronotum and sternites. Head two-fifths broader than long; dorsum feebly convex. Eyes moderately large, protruding somewhat from side of head; their posterior margin slightly indented. Pronotum one-fifth longer than broad; somewhat hour-glass shaped; broadest in apical half; very strongly constricted in basal half, at narrowest point slightly less than two-fifths maximum width; apex bisinuate, apical angles slightly rounded; base V-shaped. Elytral margins arcuate; apices almost straight. Abdomen (fig. 19, E) presumably subovate in form (the terminal segments of the type specimen are so telescoped that the exact form of the abdomen is not apparent). Abdomen petiolate, the second tergite forming a cylindrical sclerite with a narrow slit on its ventral surface (fig. 19, D). Third abdominal segment strongly constricted at base, its tergite and sternite articulating by condyles with the tubular petiole. Legs long and slender; tarsi 4, 5, 5-segmented. Hind coxae (fig. 19, E) visible from above; each with a slight, dorsally-directed spine. Length, 2 mm.

**SPECIES OF SAHLBERGIUS BERNHAUER**


*Parasahlbergius* new genus. Figure 19, B, C, F.

Type species: *Parasahlbergius liberiae* new species.

This genus may be distinguished from *Sahlbergius* by the following characters: Second tergite relatively generalized, not forming a complete tube; the large reniform eyes even with the surface of the head, not protruding; head more slender, only one-sixth broader than long; head globose in form, pronotum longer and more slender, two-
fifths longer than broad, pronotum less deeply constricted in basal half, the width at the narrowest point is two-thirds the maximum width; the presence of a strong dorsal denticle on hind coxae.

Habitus as in fig. 19, B. Head convex, subglobular; dorsum without impressions. Eyes extremely large, reniform, their surface even with that of the head. Antennal fossae relatively close together, the clypeus between them strongly deflexed and acutely carinate. Neck very slender. Antennae (fig. 19, B) geniculate, moderately long, segments 4–10 slightly transverse and slightly incrasate. Ventral surface of head generalized. Maxillary palpi small. Pronotum (fig. 19, F) two-fifths longer than broad; broadest subapically; constricted in basal half, so that the narrowest point is two-thirds the maximum width; dorsum with two shallow apical impressions; apical margin slightly bisinuate; apex continuously arcuate with the strongly bisinuate side margins, the apical angles obsolete; base arcuate. Prosternum very large, extending between procoxae to meet the very large, heavily sclerotized peritremes. Meso- and metasternal relations typical of the tribe; metasternum strongly convex. Hind coxae subtrigangular in ventral view; on their dorsal surface they bear a strong dorsal process visible in lateral and dorsal views (figs. 19, B, C). Elytra elongated; side margins arcuate. Wings present. Legs long and slender; femora swollen apically; tibiae uniformly slender; tarsi 4, 5, 5-segmented. Abdomen subovate; the third segment tergite and sternite tapering very strongly at base, and the former articulating by a condyle with the petiole formed by the second tergite. Tergites 3–6 moderately convex. Parasternites and paratergites probably present but difficult to discern in type specimen. Terminal tergites with a series of hook-like setae.

**Parasahlbergius liberiae** new species. Figure 19, B, C, F.

Coloration light rufo-testaceous. Head slightly less than one-sixth broader than long, excluding neck. Head smooth, shining; very sparsely punctulate and setulose; with several setae medial to each eye. Antennal segments with the following relative lengths: 28 : 5 : 13 : 8 : 8 : 7 : 8 : 8 : 6 : 22; segments 2–10 slightly incrassate. Pronotum shining, without reticulation; punctuation moderately coarse and dense, more so in basal half. Elytra with moderately dense, coarse punctuation in basal third; apical two-thirds almost impunctate. Abdominal sclerites subglabrous; tergites 3–6 with an apical row of a dozen or more long, fine, curved setae. Stermites with a moderate vestiture of medium-length fine setae (widely distributed on third sternite but nearly restricted to apical row otherwise). Length, 2 mm.

*Type* from Suakoko, Liberia; collected December 30, 1951, by Mr. Blickenstaff; presumably at light (no indication on data labels); in collection of United States National Museum. No paratypes.

**MIMANOMMA** Group

This small Ethiopian group contains the minute phasmoid species, *Mimanomma spectrum* (fig. 20, D), and two less specialized genera, *Dorylobactrus* and *Dorylostethus* (fig. 20, A, B). *Mimanomma* is per-
haps the most bizarre genus of the Dorylomimini, combining, as it does, a myrmecoid character—a petiolate abdomen—with an extreme combination of retrogressive characters—eyelessness, aptery, elytral fusion, and extensive merger of sclerites of both the head and thorax. The less specialized genera do not share with Mimanomma the above combination of characters, but any doubt of relationship is dispelled if the legs of the three genera are compared. The outer surface of
the femora and the inner surface of the tibiae are deeply sulcate (fig. 20, C) to receive the tibiae and tarsi, respectively. This arrangement would seemingly enable the legs to be very compactly folded, and I have wondered whether or not this is an adaptation to facilitate the carrying of the beetles by their hosts during emigration. It seems, though, from the report of the Rev. George Schwab (Mann, 1924) that Mimanomma walks slowly, at least at times, in the files of Anomma.

Wasmann, far more strongly convinced than Wheeler or Mann that Mimanomma has an ant-like appearance, apparently believed that ant mimicry could not have much adaptive significance beyond a certain point, and proposed the theory of hypertely—a view that mimicry can be greatly exaggerated and useless. Mann (1922) proposed the interesting hypothesis that inquilines with long slender bodies, or even those with limuloid forms, might be well adapted to move about through the great mass of ants in a bivouac.

Dorylostethus Brauns. Figure 20, B.


Habitus as in fig. 20, B. Head elongated; moderately constricted behind eyes. Gula slender; mentum moderately large; maxillae small and slender; maxillary sinuses very small. Antennae 11-segmented; with a long, stout scape and a long terminal segments, but unusually short intermediate segments. Prosternum prolonged between procoxae to fuse with mesothoracic peritremes. Elytra separate and movable. Wings present. Metasternum very large and convex. Coxae relatively short for the Dorylomimini. Legs with femoral and tibial sulci as in Mimanomma. Tarsi 4, 5, 5-segmented. Abdomen as in fig. 20, B; with a stout second tergite to which the third tergite articulates by a slender condyle.

SPECIES OF DORYLOSTETHUS BRAUNs


Remarks.—I find no important basis for retaining Bernhauer's genus Dorylusina, the type species of which is closely related to

Dorylobactrus Wasmann. Figure 20, A.


Dorylobactrus differs from Dorylostethus in the greater convexity of the tergites (fig. 20, A), and in not having the head constricted at the middle.

SPECIES OF DORYLOBACTRUS WASMANN


Mimanomma Wasmann. Figure 20, C, D.


The features of this genus (fig. 20, D) are so distinctive that they scarcely require elaboration. The extremely slender tubular body is unlike that of any genus in the Aleocharinae. By extreme consolidation and elimination of sclerites, the head, thorax, and abdominal petiole are virtually without sutures. The head is tubular, and the gular and other sutures are absent. The mouthparts are minute. The eyes are absent. The antennae are moderately long and moderately incrassate. Most thoracic sutures are eliminated by fusion of sutures. The elytra are fused and immobile. The abdomen has a two-segmented petiole and an ellipsoidal "gaster." The petiolar segments (third and fourth) are tubular and without sutures (comparable only to the Philippine Aenictoteras).

SPECIES OF MIMANOMMA WASMANN


AENICTOTERAS Group

The Philippine genus Aenictoteras Wheeler is difficult to classify at this time. This is due, in part, to our scant knowledge of the Oriental dorylophile fauna and of the inquilines associated with Aenictus. In the absence of intermediate forms linking Aenictoteras to either the African or American faunas, we can only speculate about its possible relationships. Because of its very bizarre abdomen, there is a strong temptation to place Aenictoteras in a mono-
basic tribe and await further evidence. This approach, however, only serves to emphasize the unusual nature of the *Aenictoteras* abdomen, and ignores whatever similarities this genus may have to other Aleocharinae. As I have stressed elsewhere in the paper, the abdomens of dorylophilous Staphylinidae are unreliable for determining systematic position. The abdomen of army ant guests was apparently subjected to very strong selection pressure to assume a “myrmecoid form” and numerous types have emerged. In view of this fact, I have relied almost entirely on thoracic and cephalic characters for tribal placement.

When viewed in the above light, *Aenictoteras* conforms very well to the pattern of characters upon which the tribe Dorylomimini is based. To place the genus elsewhere is to ignore possible relationships that may link the dorylophile faunas of the Old and New Worlds.
Aenictoteras Wheeler. Figure 21.


Habitus as in fig. 21. Head one-half longer than broad; moderately compressed; sides converging strongly toward base; the apex two-thirds broader than base; dorsum strongly impressed between the antennal fossae. Eyes moderate in size. Antennae 11-segmented; the stout clavate scape three times as long as broad; segments 2–10 slender, cylindrical; segments 2 and 3 elongated, 4–10 shorter, feebly incrassate. Gula long and narrow; mentum bilobed. Pronotum one-half longer than broad; more slender than head; sides subparallel basally, converging in front to the narrow apex; basal border straight. The slender convex elytra with apices produced as acuminate processes. Wings present. Mesosternum very short; metasternum very large and exceptionally convex. Coxae of only moderate length; mesocoxae comparatively small, ovoidal, situated along sides of metasternum (due to great convexity of the latter). Legs long and slender. Tarsi 4, 5, 5-segmented. Abdomen with a petiole consisting of two slender, sub-fusiform tubes without sutures; these tubes formed by the fused sclerites of the third and fourth segments. Fifth and subsequent abdominal segments enlarged to form an ellipsoidal, somewhat compressed "gaster." The fifth segment, which articulates with the petiole, with a remarkable caudally-directed tube formed by the prolongation of the base of the sternite. The truncated apex of this tube bears a circlet of hairs. Fifth and sixth tergites with strong apical tuberosities.

Remarks.—Wheeler (1932) commented at some length on various features of *Aenictoteras* and on the mimicry problem. He admitted that there is a resemblance between *Aenictoteras* and its hosts, especially in color, sculpture, pilosity, and superficial body form, but he pointed out that numerous differences in detailed structure exist. Wheeler states that there is nothing ant-like about the head, the swollen metasternum, the too long and too slender abdominal petiole, and the several processes on the "gaster." As it is not my intention to discuss the mimicry problem, I shall not comment on Wheeler's ideas. However, some of Wheeler's statements on morphological structures of *Aenictoteras* require correction.

Wheeler's illustration of the *Aenictoteras* abdomen is superficial and does not correctly interpret the sclerites. In his figure the dorsal tuberosities are not delimited from the sternites and give the impression that they are derived from these sclerites. Furthermore, the tuberosities are incorrectly placed on the morphological sixth and seventh segments (fourth and fifth visible segments of Wheeler) rather than on the fifth and sixth morphological tergites. Wheeler attempts to homologize the tuberosities with superficially similar processes on the abdomen of the American genus *Nototaphra* Casey (a genus of the tribe Myrmedoniini near *Zyrras* Stephens). As the tuberosities of *Nototaphra* are on the morphological fourth and fifth
segments, and as that genus and Aenictoteras are specialized forms of entirely different phyletic series, Wheeler's attempt to draw homologies seems unwarranted.

SPECIES OF AENICTOTERAS WHEELER
chapmani Wheeler, 1932, Soc. Ent. France, Livre Cent., 1932, p. 303, figs. 1, 2
Host: Aenictus martini Forel. PHILIPPINES: Dumaguete, Negros Oriental.

NEW-WORLD DORYLOMIMINII
(Subtribe MIMECITONINA)

A PROVISIONAL KEY TO THE NEW-WORLD GENERA

1. Eyes present........................................................................................................ 2
   Eyes absent........................................................................................................ 10

2. Abdomen strongly petiolate—the petiole formed by one or more entire, slender segments (3–5); the side margins of each petiolar segment almost parallel (fig. 24, A–D); second sternite never present........................................................................... 3
   Abdomen petiolate or not; but the petiole, if present, never formed by entire segments; second sternite present or absent.................................................. 6

3. Petiole one-segmented; basal antennal segment distinctly discoidal (fig. 24, A). Philacatamus Bruch
   Petiole two or three-segmented; basal antennal segment generalized.............. 4

4. Abdominal petiole three-segmented; sternites of segments three and four strongly produced in combination to form a moderate to rather long filiform process under the thorax (fig. 24, C) ........................................... Diploeciton Wasmann
   Abdominal petiole two-segmented; abdomen without process .................... 5

5. Head form distinctive (fig. 24, D); eyes small; distal petiolar segment (fourth) longer than basal segment (third) ........................................... Crematosexus Mann
   Head slender, not as above (fig. 24, B); eyes large; distal petiolar segment only about one-half as long as the basal one ....... Cryptominimus Reichensperger

6. Abdomen petiolate (petiole short in Probeyeria); a second segment "sternite" present; petiole formed by a combination of second sternite and the attenuated basal part of the third tergite (fig. 23, A, B, C, E, F, J) ........................................... 7
   Abdomen not petiolate (the third segment is constricted at the base in Labidopullus, fig. 25, A); second segment "sternite" absent ........................................... 8

7. Second segment sternite large and caudally prolonged beneath the attenuated basal part of the third tergite to form the convex ventral part of the petiole (fig. 23, C, E, F, J) ........................................................................... Beyeria Fenyes
   Second sternite small and not prolonged beneath third segment, which is moderately constricted at base (fig. 23, A, B, H).

Probeyeria Seevens, n. g.

8. Size small (1.75 mm. in length); tarsi 4, 4, 4-segmented; head and pronotum broader than long; appendages moderate in length; gula broad; paratergites and parasternites absent; abdomen strongly constricted at base (fig. 25, A). Labidopullus Borgmeier
   Size moderate (4–5 mm. in length); tarsi 4, 5, 5-segmented; head and pronotum elongated; appendages elongated (extremely so in Ecitophya); gula slender; paratergites and parasternites present; abdomen moderately broad at base........................................... 9
9. Mentum bilobed (fig. 22, B); head (excluding labrum and neck) more than twice as long as broad; antennae very long—more than six times (up to seven and one-half) as long as the width of the head; four terminal segments of antennae not much broader than the preceding segments; eyes small, only one-sixth as long as head; gula slender throughout, its sutures not converging strongly in front; body more attenuated and appendages more elongated (fig. 22, A) .......... Ecitophya Wasmann

Mentum not bilobed; head less than twice as long as broad; antennae about five times as long as head width; antennal segments 8–11 broader than the preceding, the antennae somewhat clavate; gula moderately broad at base and its sutures converging more than in the above species; body less attenuated and appendages only moderately long .......... Ecitomorpha Wasmann

10. Antennae 11-segmented .................................................. 11
Antennae 10-segmented .................................................. 15

11. Tarsi 4, 5, 5-segmented; body form as in fig. 23, D; elytra generalized although somewhat separated basally; second “sternite” present. Pulicomorpha Mann

Tarsi 4, 4, 4-segmented; body form not as above; elytra vestigial or absent; second sternite absent ............................................. 12

12. Mesothorax (fig. 27, F, A) tapering basally to a strong condyle for articulation with the semi-tubular base of the pronotum; terminal segments modified as in fig. 27, A, G; sclerites of the seventh and eighth segments heavily sclerotized and pigmented ............................................. 13
Mesothorax not attenuated as above (fig. 26, E, I); terminal segments not modified ......................................................... 14

13. Mesosternum remarkably elongated and “petiole-like” (fig. 27, A); pronotum extremely large and cordiform .......... Labidomimus Reichensperger
Mesosternum much less elongated (fig. 27, E, F); pronotum subglobose. Mimomilla Wasmann

14. Elytra absent (fig. 26, E, A); the fused meso-metathorax without sutures in dorsal view (may be mistaken for fused elytra); pronotum in lateral view as in fig. 26, G ................................. Mimeciton Wasmann (s.s.)
Elytra vestigial, and meso-metathorax distinctive (fig. 26, I); pronotum in lateral view as in fig. 26, F ................................. Labidosphaerula Reichensperger

15. Elytra vestigial or absent .................................................. 16
Elytra present (usually fused at suture) .................................. 18

16. Elytra absent; meso-metathorax without sutures in dorsal view (fig. 26, E). Mimeciton (Pseudomimeciton) Wasmann
Elytra vestigial; meso-metathorax as in fig. 26, J .......................... 17

17. Abdomen globose; terminal segments of abdomen moderately strongly sclerotized and pigmented ................................. Labidoglobus Reichensperger
Abdomen ovate; terminal segments of abdomen not unusually sclerotized or pigmented ......................................................... Paramimeciton Reichensperger

18. Base of abdomen with a pair of distinctive tuberosities, probably on second tergite (fig. 25, B, C) .................................. Leptanillophilus Holmgren
Abdomen without tuberosities ............................................... 19

19. Metepimera much enlarged and apparently fused ventrally to form a tube-like petiole to receive the abdomen (fig. 25, E) ............ Mimacatus Bruch
Metepimera moderate in size and not as above ................................ 20

20. Pronotum exceptionally large (fig. 25, D) in relation to size of head and elytra; coxae small and globose .......... Ectosoma Borgmeier
Pronotum moderately large; coxae robust .................................. 21
21. Form robust; moderately large species (4.2–5.6 mm. in length); rufopiceous; antennae robust, fusiform, its segments contiguous so that the pedicels are not visible; abdomen robust, and bearing a row of dark setae at base of third sternite (fig. 25, F, G) ................................................. Ecitophanes Borgmeier

Form frail; small species (2.1–2.5 mm. in length); testaceous; antennae frail, non-fusiform, its segments not contiguous and the pedicels visible; abdomen not robust, and without row of dark setae at base of third sternite. 

Ecitomerus Borgmeier

Remarks.—Acamatusinella Bruch was not available for study and is not included in the above key.

ECITOMORPHA Group

This group includes the largest species of New World Dorylmimini; they occur in the large epigaec societies of Eciton and appear well adapted to run in the files of these ants. Although highly specialized, they are less so than many of the American Dorylmimini and are perhaps counterparts of the Old World Dorylomimus. Adjusted as they are to the epigaec army-ant behavior pattern, they do not show the regressive specializations of many guests of Neivamyrmex and Labidus.

Ecitomorpha Wasmann. Figure 22, C–F.


Habitus similar to that of Ecitophya as illustrated in fig. 22, A, except that the body is less attenuated and the appendages shorter. Integuments granulose in appearance due to a fine-meshed reticulation. Head elongated, its sides converging basally. Eyes moderate in size. Antennae moderate in length and somewhat clavate due to enlargement of the four terminal segments. Gular sutures moderately widely separated at base and converging strongly in front. Mentum emarginate but not bilobed; ligula bilobed; mandibles small; galea and lacinia moderate in length. Pronotum elongated and more or less hexagonal in outline above; broadest in apical half; dorsum with a moderately deep median furrow and, as a rule, a shallow lateral impression on each side. Prosternum carinate (fig. 22, C); prolonged between procoxae and contiguous with, but not fused to, the very large united peritremes (fig. 22, C). Meso- and metasternum (fig. 22, D) with the generalized tribal characteristics. Legs very long; tarsi 4, 5, 5-segmented. Abdomen ovoidal; sclerites generalized in their relationships; tergites moderately broad and convex; sternites very large and strongly convex; paratergites and parاستernites broad. Female abdomen more voluminous than that of male. Third sternite with a moderately deep pit on each side. Aedeagus as in fig. 22, E, F.

Remarks.—Species identification is very difficult in this genus and Ecitophya at the present time. I have examined a large number of specimens from Costa Rica, Panama, Colombia, British Guiana, Bolivia, and Brazil and am unable to differentiate the four named spe-
Fig. 22. *Ecitophya bicolor* Reichensperger: A, lateral view; B, head, ventral view. *Ecilomorpha nevermanni* Reichensperger: C, prothorax, ventral view; D, mesometathorax, ventral view; E, median lobe of aedeagus; F, paramere of aedeagus.
cies. Whether or not it is possible to distinguish *melanotica* and *nevermanni* from *arachnoides* must be determined by careful study. The antennal and pronotal characters suggested by Reichensperger (1935) do not seem to apply to large series. I have not examined in detail the aedeagi and spermathecae of many specimens so it is possible that these structures may provide diagnostic features. *E. breviceps*, a smaller species, is probably valid. According to all available records, *Ecitomorpha* occurs only in societies of *Eciton burchelli*, a species that ranges from Mexico to southern Brazil. Doubtless a polytypic species, the societies of *burchelli* have been inadequately studied from the standpoint of subspeciation. It will be interesting to know whether or not *Ecitomorpha* has undergone much speciation in societies of this wide-ranging host.

**SPECIES OF ECITOMORPHA WASMANN**


**Ecitophya** Wasmann. Figure 22, A, B.


*Ecitophya* is distinguished from *Ecitomorpha* by the characters listed in the key to the American genera of Dorylomimini. The five named species of *Ecitophya* are difficult to differentiate and some may not be valid. For instance, I have not been able to distinguish *bicolor* from *simulans*, both of which were collected with *Eciton burchelli*, even after examining more than one hundred specimens from Costa Rica, Panama, and Brazil. Reichensperger’s (1933) key to the species does not seem to me to be workable. Some of the species (consecta, gracillima, and rapazaæ) are based on very few specimens and require larger series for detailed study. The fact that *Ecitophya* occurs with several species of *Eciton*—in contrast to *Ecitomorpha*—may indicate that isolation with different hosts provided more opportunities for speciation than in the case of the latter.
SPECIES OF ECITOPHYA WASMANN


simulans Wasmann, 1889, Deut. Ent. Zeitschr., 1889, p. 187 (Ecitomorpha); 1890, Tijds. Ent., 33, p. 87; 1900, Zool. Jahrb. Syst., 14, p. 224, pl. 1, figs. 2, 2a-d; 1925, Ameisenmimikry, p. 120, fig. 3a-b; Reichensperger, 1933, Rev. de Ent., 3, p. 184, figs. 9, 13, 16, 18. Host: *Eciton burchelli* Westwood. BRAZIL: Blumenau.

PULICOMORPHA Group

This small group comprises three Nearctic genera associated with *Neivamyrmex* in the southern United States and Mexico. The group is most noteworthy for its unusual petiolar structure involving a sclerite not typical of the Aleocharinae, a sclerite that has to be called a second segment sternite because of its position. Some subfamilies of Staphylinidae have second sternites but the subfamily Aleocharinae is not numbered among them, except for some rare termitophilous Corotocini with large membranous abdomens (Severs, 1959) and the members of this group. The second sternite is inconspicuous in *Pulicomorpha*—a genus that does not have a petiolate abdomen in a strict sense—and not very large in *Probeyeria* (fig. 23, A) which has a short petiole. It is in *Beyeria* that the second sternite attains its large size and in association with the attenuated basal part of the third tergite form a conspicuous petiole. *Probeyeria* and *Beyeria* have eyes and are winged, but *Pulicomorpha* is eyeless and apterous.

Pulicomorpha Mann. Figure 23, D.


Habitus as in fig. 23, D. Head subquadrate; the short neck almost one-half as broad as head; vertex impression absent. Eyes absent. Antennae moderate in length, feebly incrassate, most segments transverse. Pronotum strongly convex, broadest near apex, pronotal sides converging strongly to the narrow, arcuate
SEEVERS: STAPHYLINID BEETLES

base (fig. 23). Prosternum moderate in size; mesothoracic peritremes small, feebly sclerotized. Metasternum small; metepimeras short. Elytral inner margins separated for some distance basally but contiguous apically. Wings absent. Tarsi 4, 5, 5-segmented. Abdomen somewhat spindle-shaped; not distinctly petiolate although third segment narrows at base to articulate with the second segment. Second tergite broad and moderately long; second sternite with a broad, stout basal condyle for metathoracic articulation and an acetabulum for reception of the third sternite. Paratergites and parasternites moderate in size.

Remarks.—Mann recorded one pale, minute species of this genus from Lower California and noted that individuals of two sizes were found in a single colony of the host ants. The larger forms are moderately stout; the smaller ones are relatively slender. The two types are rather similar in structure and differ chiefly in certain proportions. Elytra of the smaller individuals are about two-thirds as broad as long; those of the others are subequal in length and width. Whether or not this is a sex difference is not known.

SPECIES OF PULICOMORPHA MANN

Probeyeria, new genus. Figure 23, A, B, H.

Type species: Probeyeria pulex Sanderson (Beyeria).

Allied to Beyeria, this genus is distinguished by a less specialized abdominal petiole: the second segment sternite is relatively small and not prolonged caudad beneath the attenuated third segment tergite.

Habitus as in fig. 23, A. Head one-fourth to one-third longer than broad, excluding labrum and neck; sides converging behind eyes to the neck which is about two-fifths as broad as head; neck with an occipital condyle. Antennal fossae narrowly separated, opening cephalad. Vertex with a crater-like impression medial to eyes, the impression continued onto the clypeus. Eyes moderate in size (about one-third as long as head), coarsely faceted. Antennae moderately robust, with three basal segments elongated and subclavate; basal segment shorter than the two following segments combined; segments 4–10 obtapezoidal, usually transverse (except fourth); 4–10 slightly incrasate.

Pronotum strongly convex, its sides deflexed; broadest at base, sides straight in basal three-fifths, then converging strongly to the narrow apex (little more than one-half the basal width). Prosternum large, carinate; mesothoracic peritremes very small (fig. 23, H). Metasternum very large, convex; metepimeras abbreviated. Elytra elongated; apex emarginate. Wings present. Legs very long; coxae somewhat spindle-shaped. Tarsi 4, 5, 5-segmented. Abdomen ovoidal, with a one-segmented petiole composed of the second segment tergite and sternite (figs. 23, A, B); the robust second tergite with a strong basal condyle (for metathoracic articulation), and an apical socket to receive the third tergite; second sternite in
the form of a half-cylinder, with apical acetabula to receive a pair of third sternite condyles.

**SPECIES OF PROBEYERIA SEEVERS, n. gen.**


Host: *Neivamyrmex opacithorax* Emery (Arizona, Kansas). 

**Remarks.**—The original series of *pulex* was collected at lights and it was only recently that *Neivamyrmex* was established as its host. The Arizona and Kansas specimens are darker and larger than the type specimens of *pulex* and may differ slightly in other respects, but the proposal of another species category seems unwarranted at this time.

**Beyeria** Fenyes. Figure 23, C, E, F, G, I, J.


*Beyeria* is noteworthy for its distinctive abdominal petiole (figs. 23, C, E) which is composed of the second tergite and a remarkably elongated second sternite that embraces the elongated and attenuated base of the third tergite (and the very slender paratergites and parasternites, if present).

**Remarks.**—The original series of *Beyeria vespa* Fenyes was collected at light and the author apparently did not suspect its ecitophilous habits. Furthermore, having incorrectly determined its tarsal formula to be 5, 5, 5, Fenyes placed *Beyeria* in the tribe Aleocharini. When Mann described *Acamatoxenus suavis* in 1925, there was little reason for him to suspect its affinities with *Beyeria*. Mann did not attempt to place *Acamatoxenus* in a tribe and it has appeared in catalogues (Blackwelder, 1944, Borgmeier, 1949) in the category "Incertae sedis." It is my opinion that the differences between *Beyeria vespa* and *Acamatoxenus suavis* are largely quantitative—difference in length of the second sternite and degree of attenuation of the third tergite—and that they should be included in the same genus.

In 1943, Sanderson brought out the relationship between *Beyeria* and *Pulicomorpha* and deduced that the former has ecitophilous habits. He proposed that these genera be placed in a separate subfamily, Pulicomorphinae, but I believe that this would isolate them too much from the Aleocharinae.
FIG. 23. **Probeyeria pulex** Sanderson: A, lateral view; B, second and third abdominal segments, dorsal view; H, head and prothorax, ventral view. **Beyeria vespa** Fenyes: C, abdomen, lateral view; F, second and third abdominal segments, dorsal view; G, mesometathorax, ventral view; I, prothorax, ventral view. **Beyeria (=Acamatoxenus) suavis** Mann: E, abdomen, lateral view; J, second and third abdominal segments, dorsal view. **Pulicomorpha coecum** Mann: D, dorsal view.

215
FIELDIANA: ZOOLOGY, VOLUME 47

SPECIES OF BAYERIA FENYES


PHILACAMATUS Group

The four neotropical genera which I now propose to group together are segregated in these tribes—Philacamatini, Crematoxenini, and Myrmedoniini—in the currently adopted aleocharine classification (Blackwelder, 1944, Borgmeier, 1949). In my opinion undue emphasis has been given to what appear to be striking differences and not enough stress on characteristics in common. The outstanding feature of the group is the development of a myrmecoid abdomen. The genera differ in the number of segments involved in the petiole, but the petiolar structure is basically the same for each individual segment. Philacamatus has a one-segmented petiole, Crematoxenus and Cryptomimus have two-segmented petioles, and Diploeciton has a three-segmented petiole. The non-petiolar segments in all cases form an ellipsoidal “gaster” that is very similar in appearance even though fewer segments compose it in some genera. There can be no doubt that this is a group of bizarre genera: in addition to the differences mentioned above, Philacamatus has a unique antennal scape, a dorso-ventrally compressed head, and an unusual pronotum, Crematoxenus has a strongly convex head, and Diploeciton has a distinctive filiform process on the ventral surface of the petiole (fig. 24, C).

Philacamatus Bruch. Figure 24, A.


Habitus as in fig. 24, A. The very much elongated head compressed dorso-ventrally; broadest behind eyes; vertex with a median impression; basal border emarginate. Antennae distinctive (fig. 24, A); basal segment a large concave disk; other segments robust, cylindrical. Pronotum convex; sides bisinate, apical margin bisinate; dorsum with a small impression. Metasternum moderately long, strongly convex. Middle and hind coxae comparative short. Third abdominal segment forming a one-segmented petiole; the tergite is less than two-fifths as broad as long, the cylindrical sternite strongly convex and the paratergites and/or parasternites very slender.

SPECIES OF PHILACAMATUS BRUCH

bosqi Bruch, 1933, Rev. de Ent., 3, 209, figs. 1–10, pl. 2, figs. 1–2; Borgmeier, 1949 Rev. de Ent., 20, pl. 7, fig. 1. Host: Neivamyrmex pseudops Forel. ARGENTINA: Tucuman.
Crematoxenus Mann. Figure 11, D.

Crematoxenus Mann, 1921, Proc. U. S. Nat. Mus., 59, p. 547. Type species:
Crematoxenus aenigma Mann.

Crematoxenus and the following genus, Cryptomimus, are the only American genera of Dorylomimini with two-segmented petioles. From Cryptomimus, this genus may be distinguished by its distinctive head form and small eyes, and by having the distal petiolar segment longer than the proximal one.

Habitus as in fig. 24, D. Head very strongly convex distally and tapering strongly to the slender neck. Eyes small. Antennae geniculate, segments elongated, segments 3–10 moderately incassate. Third and fourth abdominal segments modified to form a two-segmented petiole; each segment constructed as the single petiolar segment of Philacamon. Fifth and distal segments enlarged as a subellipsoidal "gaster." Legs long and slender (fig. 24, D).

SPECIES OF CREMATOXENUS MANN


Cryptomimus Reichensperger. Figure 24, B.

Cryptomimus Reichensperger, 1926, Zool. Anz., 69, p. 114. Type species:
Cryptomimus handlirschi Reichensperger.

Habitus as in fig. 24, B. Head longer than broad; somewhat compressed dorso-ventrally; more or less uniform in thickness except for the neck. Eyes very large and protuberant, moderately coarsely faceted. Antennae moderately long, relatively slender, segments elongated, slightly incassate. Pronotum longer than broad, broadest subapically, deeply constricted in basal two-thirds, side margins strongly bisinuate; dorsum with a median impression. Metepimera produced as slender apical processes. Two-segmented abdominal petiole as in Crematoxenus, except that proximal segment (third) is about twice as long as distal (fourth). The fifth and distal abdominal segments form a subglobose "gaster." Legs moderately long and slender; procoxae slender and spindle-shaped; mesocoxae short; hind coxae moderately long.

SPECIES OF CRYPTOMIMUS REICHENSPERGER


Remarks.—The two sympatric species of this genus may be distinguished as follows:

1. Pronotum one-half longer than broad; strongly constricted in basal half, the side margins strongly bisinuate; width at narrowest point about two-thirds maximum width. Elytra relatively slender; their maximum width is four-fifths sutural.
length (sutural length—60, maximum width—48, apical width—32); proximal petiolar segment strongly constricted at base, and strongly impressed on sides adjacent to metacoxae. .............................................................. wasmanni

Pronotum one-third longer than broad; less strongly constricted in basal two-thirds; width at narrowest point five-sixths maximum width; side margins in basal two-thirds almost parallel except near base. Elytra relatively broad; maximum width one-sixth greater than sutural length (sutural length—60, maximum width—70, apical width—55); basal petiolar segment much less strongly constricted and impressed .............................................................. handlirschi

Diploeciton Wasmann. Figure 24, C.


Head broadest at eye level; sides converging to the neck which is about half as broad as head; vertex broadly impressed between eyes. Antennae geniculate; long slender, feebly incrassate; all segments elongated. Pronotum elongated; broadest in apical half; very strongly constricted behind procoxae. Elytra large, strongly convex. Legs very long; hind coxae unusually long and robust (fig. 24, C). Abdominal petiole (fig. 24, C) three-segmented (third, fourth, and fifth segments). Petiole with a moderately long to very long cylindrical process derived from the third and fourth sternites conjointly. Sixth and distal segments enlarged as a "gaster"; sixth sternite bearing an articular condyle for petiole.

SPECIES OF _DIPLOECITON_ WASMANN


The filiform process protruding from the ventral surface of the petiole is the most noteworthy feature of _Diploeciton_. When the abdomen is recurved over the foreparts, this process may be directed caudal, but its function in this position is conjectural. Analogous structures occur in _Ecitotima_ (Myrmedonini) and _Aenictoteras_ (Dorylomimini). That of the former genus is almost identical in structure with the process of _Diploeciton_, but that of the latter is considerably different and has a membranous covering over an apical aperture.

Fig. 24. _Philacamatus bosgi_ Bruch: A, lateral view; abdominal segments numbered. _Cryptomimus wasmanni_ Reichensperger: B, lateral view. _Diploeciton nevermanni_ Reichensperger: C, lateral view. _Crematozenus aenigma_ Mann: D, lateral view.
LABIDOPULLUS Group

When Borgmeier described the genus *Labidopullus* in 1958 he did not attempt to place it in a tribe. He noted the striking similarity in abdominal structure between this genus and the *Mimeciton* group, but was puzzled by the differences in the head and thorax.

It seems to me that *Labidopullus* belongs to the Dorylomimini and that it bears a moderately close relationship to the *Leptanillophilus-Mimeciton* phyletic series. Inasmuch as it does not exhibit the regressive characters so characteristic of the above groups, *Labidopullus* probably stemmed from the same generalized stock from which they were derived. With this in mind, I am placing *Labidopullus* in a separate group of the *Labidopullus-Leptanillophilus-Mimeciton* series.

In the structure of head, pronotum, and elytra, the presence of eyes and wings, and the clearly delimited sclerites of head and thorax, *Labidopullus* is a relatively generalized dorylomimine. Its subpetioloate "myrmecoid" abdomen, absence of paratergites and parasternites, and 4-4-4 segmented tarsi are specializations characteristic of the phyletic series. The abdomen, with the third segment strongly tapered at the base, is very similar to that of the *Leptanillophilus* and *Mimeciton* groups. The antennae, missing from the type specimen, are probably 11-segmented.

*Labidopullus* seems to be of unusual interest in linking the highly specialized *Leptanillophilus* and *Mimeciton* groups with the more generalized Dorylomimini.

**Labidopullus** Borgmeier. Figure 25, A.


Habitus as in fig. 25, A. Head about one-tenth broader than long; sides parallel, base transverse, basal angles rectangular, slightly rounded; vertex with a shallow median impression. Eyes large. Antennae incomplete in type (probably 11-segmented); segments 3 and 4 transverse (suggesting antennae of moderate length). Gula broad and well-defined. Pronotum short, only three-fourths as long as head; slightly transverse; broadest subapically, sides sinuate; dorsum with a tiny, moderately deep pit in basal half. Elytra elongated, two-thirds longer than pronotum; apex emarginate so that the metepimera and second tergite are visible from above. Sclerites of meso- and metathorax delimited; metepimera conspicuous, metasternum large. Hind coxae very large. Wings present. Abdomen strongly constricted at base, the sclerites of the third segment tapering to a slender base. Paratergites and parasternites absent. Length, 1.75 mm.
SPECIES OF LABIDOPULLUS BORGMEIER
spininodis Emery. COLOMBIA: Putumayo, Umbria. Type deposited in
Chicago Natural History Museum by Dr. Thomas Borgmeier.

LEPTANILLOPHILUS Group

This relatively homogeneous group of six genera occurs chiefly with Neivamyrmex and only the genus Ecitophanes is known to be
associated with Nomamyrmex. Together with the more generalized
genus Labidopullus and the more specialized Mimeciton group, they
seem to form a phyletic series within the Dorylomimini. This series
is especially noteworthy for regressive changes in body structure.

The Leptonillophilus group is characterized by 10-segmented anten-
nae, 4, 4, 4-segmented tarsi, absence of eyes, apery, fusion of
elytra, and an ovoidal abdomen that lacks paratergites and para-
sternites. In the three groups that constitute this series the abdo-
men is basically quite similar, and although superficially myrmecoid,
is rarely distinctly petiolate.

The known representatives of this group may be only a small
fraction of the existing species; the ecitophile faunas of relatively
few species of the large host genus Neivamyrmex have been investi-
gated. It is anticipated, therefore, that the present generic align-
ments may require modification in the future.

Although evolutionary changes within the group do not for the
most part appear to be noteworthy, one modification merits attention. The metepimera of Mimacamatus longiceps (the only species
of the genus examined) are enlarged and apparently fused ventrad
(fig. 25, E). The resulting tube-like sclerite receives the base of the
abdomen and appears distinctly petiolate.

Leptanillophilus Holmgren. Figure 25, B, C.

Leptanillophilus Holmgren, 1908, Zool. Anz., 33, p. 340. Type species: Lept-
anillophilus similis Holmgren.

Acamatusina Bruch, 1930, Physis, 10, p. 18; Bruch, 1933, Rev. Ent., 3 (=Lep-
anillophilus Holmgren). Type species: Acamatusina inopinata Bruch.

Leptanillophilus is distinguished from the other genera of the
group by a pair of distinctive tuberosities on the second abdominal
tergite (fig. 25); otherwise it conforms well to the group structural
pattern and has no especially noteworthy features.
SPECIES OF *LEPTANILLOPHILUS* HOMGREN


**Ecitosoma** Borgmeier. Figure 25, D.

*Ecitosoma* Borgmeier, 1939, Rev. de Ent., 10, p. 458. Type species: *Ecitosoma lamellatum* Borgmeier.

This genus is distinguished by its exceptionally large pronotum (fig. 25, D), short head, and distinctive coxae. The coxae are globose and less massive than in the other genera, and the procoxae articulate by a long, slender basal pedicel. The abdomen is globose. Length, 2.5 mm.

**SPECIES OF ECITOSOMA BORGMEIER**

*lamellatum* Borgmeier, 1939, Rev. de Ent., 10, p. 458, figs. 1–3. Type deposited in Chicago Natural History Museum by Dr. T. Borgmeier. Host: *Neivamyrmex antillanum* Forel. COSTA RICA: San José.

**Mimacamatus** Bruch. Figure 25, E.

*Mimacamatus* Bruch, 1933, Rev. de Ent., 3, p. 16. Type species: *Mimacama tus mirabilis* Bruch.

*Synacamatus* Bruch, 1933, Physis, 11, p. 351 (without description). Type species: *Synacamatus fraterculus* Bruch (*Mimacamat us*).


My concept of this genus is based on an examination of *M. longiceps* Borgmeier. Pselaphid-like in habitus, its most noteworthy feature is the remarkable enlargement of the metepimera and the fusion of these sclerites ventrad (fig. 25). The tube thus formed obscures the second tergite and seems to form an articulating pediole to receive the third abdominal segment. The coxae of this species are very robust. The abdomen is ellipsoidal.

Length, 2.5 mm., slender.

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SPECIES OF MIMACAMATUS BRUCH

*fraterculus* Bruch, 1933, Rev. de Ent., 3, p. 20, figs. 22–27, pl. 1, fig. 2; Borgmeier, 1939, Rev. de Ent., 10, p. 458; 1949, Rev. de Ent., 20, p. 124, pl. IV, fig. 4. Host: *Neivamyrmex hetschkoi* Mayr (=*Neivamyrmex raptans* rebellatum Santschi). ARGENTINA: Misiones, Loreto.


*mirabilis* Bruch, 1933, Rev. de Ent., 3, p. 18, figs. 12–21, pl. 1, fig. 1; Borgmeier, 1939, Rev. de Ent., 10, p. 459. Host: *Neivamyrmex hetschkoi* Mayr. ARGENTINA: Misiones; Loreto.

Ecitophanes Borgmeier. Figure 25, F, G.


This genus and the following genus, *Ecitomerus*, are closely allied. *Ecitophanes* is somewhat larger and more robust than the other genera of the series and has a distinctive habitus (fig. 25, G). It is differentiated from *Ecitomerus* by dark rufo-piceous coloration; robust form; larger size (4.2–5.6 mm. in length); robust antennae having segments 2–10 fusiform (intermediate segments broadest) and the segments telescoped so that the pedicels are not visible; exceptionally strong mandibles; and a row of dark setae at the base of third segment (fig. 25, G). The thorax is rather similar in both genera (fig. 25, F), the coxae are robust and similar in form, and the abdomen is ant-like in form. The legs are robust, the tarsi strong and the tarsal segments strongly compressed. The legs have dense clusters of white silky hairs on underside of profemora near base, on protibiae near apex, and on an oval area at apex of meso- and metatibiae.

SPECIES OF ECITOPHANES BORGMEIER


Ecitomerus Borgmeier


*Ecitomerus* is most closely related to *Ecitophanes* from which it may be distinguished by its less robust form, testaceous coloration, smaller size (2.1–2.5 mm.), frail non-fusiform antennae with visible pedicels (segments 3–10 are slightly incrassate, and the terminal segment is the longest and broadest), moderately robust mandibles, and the absence of a row of setae at base of third abdominal segment.
The form of the head, pronotum, meso-metathorax, and abdomen is similar in the two genera. The coxae are very strong in both cases, and the legs are similar, although those of Ecitomerus are less robust and the tarsi are frail.

SPECIES OF ECITOMERUS BORGMEIER

*impressifrons* Borgmeier, 1933, V. Congr. Int. Ent., 1932, p. 371, figs. 1–16, pl. 20, figs. 1–6, pl. 21, fig. 1; 1939, Rev. Ent., 10, p. 458. Host: *Neivamyrmex densepunctatum* Borgmeier. BRAZIL: Rio de Janeiro; Itatiaya.

**Acamatusinella** Bruch


This genus was not available.

SPECIES OF ACAMATUSINELLA BRUCH

*globuliventris* Bruch, 1931, Rev. Ent., 1, p. 16, figs. 1–8. Host: *Neivamyrmex pertyi* Schuckard. ARGENTINA: Córdoba; Alta Gracia.

**MIMECITON** Group

The evolution of this interesting group of minute aleocharines presumably occurred only in association with the host genus *Labidus*. Evidently derived from the same stock as the *Leptanillophilus* group, *Mimeciton* and allies share with that group such regressive changes as eyelessness, aptery, reduction of tarsal segmentation to 4, 4, 4, loss of paratergites and parasternites, and fusion of some mesothoracic sclerites. After divergence from the *Leptanillophilus* group, the elytra were reduced to vestiges or lost, the gular sutures fused and in some cases disappeared, and further fusion of thoracic sclerites occurred.

The principal group characteristics are as follows: Head elongated or slightly transverse; antennal fossae opening cephalad; gular sutures united or absent; submentum fused to postgenae; eyes absent; antennae 11-segmented or 10-segmented; the scape often very long; pronotum strongly convex, variable in form; sternonotal sutures absent; prosternum large and carinate and usually fused with the large peritremes; thorax with few sutures; mesothorax with a tendency to elongation and attenuation; most sclerites of the meso- and metasternum fused and individually delimited; elytra vestigial or absent; wingless; legs very long; coxae subcylindrical; tarsi 4, 4, 4-segmented; abdomen ovoidal; the third segment much constricted at base and with condylar surfaces; paratergites and parasternites absent.
Mimeciton Wasmann.  Figure 26, A–E, G.


*Mimeciton* is easily recognized by its distinctive metathorax and the absence of elytra (fig. 26, A, E).

Head and pronotum slender; elongated; their lateral margins parallel; pronotum with shallowly impressed sides and in some cases a transversely impressed dorsum. Antennae not clavate; scape subequal in length to head; segments 3–9 elongated except in *pulex*; 11-segmented, or 10-segmented in *Pseudomimeciton* (due to obvious fusion of the two terminal segments). Metathorax distinctive; elytra absent. Abdomen ovoidal; terminal segments unmodified.

Remarks.—Two names, *Pseudomimeciton* Heikertinger based on *zikani* Wasmann, and *Metamimeciton* Reichensperger based on *antennatum* Mann, were proposed for species of *Mimeciton* that have 10-segmented antennae. If it is desirable to acknowledge this distinction by subgeneric rank, the former name should have priority, although it has been customary to use the latter.

**SPECIES OF MIMECITON WASMANN**


gigas Reichensperger, 1936, Rev. de Ent., 6, p. 231, figs. 3–4, pl. 1, fig. 4. COSTA RICA: La Caja. Host: *Labidus coecus* Latreille.


**A KEY TO THE SPECIES OF MIMECITON**

1. Antennae 10-segmented (fusion of segments 10 and 11 incomplete in some cases) ........................................ Subgenus *Pseudomimeciton* (2)
Antennae 11-segmented .................................................. 3
2. Second antennal segment relatively long (scape only two and one-half times as long as second); third antennal segment less than one-fourth as long as second .................................................. antennatum
Second antennal segment relatively short (scape four and one-half times as long as second); third antennal segment two-thirds as long as second. ...zikani
3. Antennal segments, except the subquadrate tenth, elongated ............ gigas
Antennae segments 3–10 transverse ................................... pulex

Paramimeciton Reichensperger. Figure 26, H, J.


Reichensperger proposed Paramimeciton as a subgenus of Mimeciton, but it seems to me that it is more closely allied to Labidosphaerula and deserves generic rank. It differs from Mimeciton in having a relatively short antennal scape, a different form of meso-metathorax (fig. 26, J), vestiges of the elytra, and a different form of pronotum (lateral view, fig. 26, H). In these respects, Labidosphaerula also differs from Mimeciton.

Head elongated; antennal fossae narrowly separated by a sharp carina. Eyes absent. Antennae 10-segmented (line of fusion between tenth and eleventh segments obvious); relative lengths of segments as follows: 38 : 16 : 9 : 8 : 8 : 8 : 8 : 9 : 10 : 30; scape two-thirds as long as head, clavate; segments 3–9 transverse, 2–10 incrassate. Prosternum feebly prolonged as a spine between procoxae. Abdomen ovate, third segment very slenderly petiolate at base; terminal segments not modified. Tarsi very strongly compressed and heavily sclerotized; hind tibiae (but not the others) also compressed. Hind tibiae longer than tarsi; relative lengths—tibiae (140), tarsi (126), tarsal segments (54, 24, 20, 28).

SPECIES OF PARAMIMECITON REICHENSPERGER

Labidosphaerula Reichensperger. Figure 26, F, I.


Labidosphaerula has much in common with Paramimeciton and is retained as a distinct genus with some reservations. This genus differs from the latter in having 11-segmented antennae, scape only one-half as long as head and not clavate, meso-metathoracic differences (figs. 26, I, J), globose abdomen, hind tarsi longer than hind tibiae, tarsi only moderately compressed and feebly sclerotized, antennal fossae farther apart and not separated by a sharp carina.
Head two-fifths longer than broad, excluding neck. Antenna 11-segmented; scape one-half as long as head, not clavate; segments of these relative lengths: 20 : 7 : 5 : 5 : 5 : 5 : 6 : 9 : 10 : 6; segments 3–10 transverse, strongly incrassate; 11 very small, conical. Elytra vestigial; the broad metathorax distinctive (fig. 26, 1). Abdomen globose, terminal segments not modified; third segment with very slender articulating condyles. Tarsi moderately compressed, feebly sclerotized; hind tibiae shorter than tarsi; relative lengths as follows: tibiae (74), tarsi (80), tarsal segments (30 : 16 : 14 : 20).

SPECIES OF LABIDOSPHAERULA REICHENSPERGER


Labidoglobus Reichensperger

Labidoglobus Reichensperger, 1933, Rev. de Ent., 3, p. 179. Type species: Labidoglobus nevermanni Reichensperger.

The relationships of this genus are puzzling. Reichensperger compared and contrasted Labidoglobus and Labidosphaerula, and the two genera appear to be moderately closely related. On the other hand, the seventh tergite and sternite are moderately heavily sclerotized and pigmented in what seems to be an incipient Mimonilla condition. In other ways, Labidoglobus does not resemble the Mimonilla-Labidomimus series very closely.

From Labidosphaerula, this genus may be differentiated by the 10-segmented antennae, clavate scape, modified hind tibiae, and modified seventh abdominal sclerites. As revealed in Reichensperger’s figures, the mouthparts differ as follows: in Labidoglobus, mandibles relatively stout, apex broader and more blunt, teeth absent or very minute, maxillary palpi with third segment subequal in length to the exceptionally large second segment, fourth segment shorter than third, third labial palpomere shorter than second; in Labidosphaerula, mandibles less stout, apex slender, sharp, with a row of acute teeth; maxillary palpi with third segment considerably longer than second, fourth segment a little longer than third; third labial palpomere much longer than second.

Head, pronotum, and meso-metathorax essentially as in Labidosphaerula. Antennae 10-segmented; scape clavate, its apex almost twice as broad as second segment; segments 3–9 transverse. Elytra extremely small. Anterior tibiae slender at base and rather abruptly broader in apical two-thirds; hind tibiae with a broad, shallow concavity on outer surface (tibiae appear constricted). Sclerites of seventh abdominal segment more heavily sclerotized and more darkly pigmented than in the foregoing genera. Tarsi not compressed. Hind legs with the following proportions: tibia (78), tarsi (72), tarsal segments (34 : 12 : 8 : 18).
Fig. 27. Labidomimus incertus Reichensperger: A, lateral view; B, head and pronotum, dorsal view. Mimonilla ecitonis Wasmann: C, prothorax, ventral view; D, mesometathorax, ventral view; E, pronotum, dorsal view; F, mesometathorax and second tergite, dorsal view; G, abdomen, lateral view.

SPECIES OF LABIDOGLOBUS REICHENSPERGER

Mimonilla Wasmann. Figure 27, C–G.


The mesothorax of this and the following genus is specialized for articulation with the pronotum. A second notable feature is the unusual modification of the terminal abdominal sclerites.
Head slightly transverse; sides parallel in front, and broadly rounded at base. Antennae 11-segmented; scape moderately long, not clavate, although expanded a little distally; scape longer than segments 2, 3, and 4 combined; segment 2 a little longer than 3; segments 3–10 transverse; compactly arranged; their pedicels not visible; segment 11 conical, a trifle longer than 10. Pronotum broader than long; very strongly convex, globose in form. Mesothorax (fig. 27, F) tapering apically to a moderately broad condyle for articulation with the close-fitting pronotum. Vestigial elytra present. Metathorax as in fig. 27, F. Abdomen with heavily sclerotized and pigmented seventh and eighth segment sclerites (fig. 27, G).

**SPECIES OF MIMONILLA WASMANN**


**Labidomimus** Wasmann. Figure 27, A, B.


This bizarre genus scarcely requires characterization.

Habitus as in fig. 27, A. The distinctive head (fig. 27, B) subequal in length and width; its sides converging strongly to the narrow neck; dorso-ventrally compressed to a moderate degree. Antennae 11-segmented; comparatively short and compact; scape short and moderately stout, longer than the three following segments combined. Segments 3–10 short, transverse. The unique cordiform pronotum (fig. 27, B) extremely convex; its sides inflexed slightly near base. The slender, attenuated mesothorax petiolate in form (fig. 27, A), with an apical condyle for pronotal articulation. Elytra vestigial. Seventh and eighth abdominal segments as in fig. 27, A.

**SPECIES OF LABIDOMIMUS WASMANN**


*petiolatus* Wasmann, 1923, Tijds. Ent., 66, p. lxiii; 1925, Ameisenmimikry, p. 126, pl. 2, fig. 6a, b. Host: *Labidus coecus* Latreille. BRAZIL: Minas Gerais; Passa Quatro.
Tribe MYRMEDONIINI, s.s.

In the restricted sense of this monograph, the tribe Myrmedoniini includes the large Drusilla-Zyras complex and several groups of myrmecophilous and termitophilous genera (see section on Evolutionary Considerations and fig. 16). The vast artificial tribe Myrmedoniini of all catalogues and treatises in current use (Fenyes, 1918–21, Bernhauer and Scheerpeltz, 1926, Cameron, 1939, Blackwelder, 1944) must be subdivided into categories based on more than one character—the 4, 5, 5 tarsal formula. The large Atheta complex, for instance, does not belong in the Myrmedoniini. In this monograph and an earlier one (Seevers, 1957), I have initiated a program of transferring genera to other categories, but the task will require additional studies.

The Myrmedoniini may be differentiated by the following combination of characters:

—The maxillae are distinctive: the galea and lacinia are elongated (often appreciably), the length of the lacinia is greater than distance from base of maxilla to the lacinia.

—The mesocoxae are widely separated and are set in well-defined, margined acetabula.

—The broad metasternal process between the coxae is much longer than the broad, short mesosternal process.

—The maxillary sinuses are frequently, but not necessarily, somewhat more extensive than the cardos that rest in them.

—The metasternum is only slightly or moderately convex, and the transverse metacoxae are of the generalized aleocharine type (except in certain myrmecoid genera).

—The tarsi are 4, 5, 5-segmented.

—The aedeagus has distinctive features of importance; recent studies have convinced me that this is true but I am not yet prepared to report my conclusions.

In the most specialized eicitophilous genera (e.g., Ecitosius, Ecitocryptus, Ecitocryptodes) some of the structures with characters of diagnostic value have been modified in such a way that they resemble the same structures in the Dorylomimini, the tribe with which certain myrmedoniines may be confused. The convergence evidently resulted from the evolution of myrmecoid body types.

The New World eicitophilous Myrmedoniini exhibit greater morphological diversification than their Ethiopian tribal relatives. Sev-
eral American groups contain myrmecoid genera—some with petiolate abdomens—and several include eyeless species. The African myrmedoniine guests are, more often than not, generalized forms derived from, or similar to, the Zyras s.l. complex. Our limited knowledge of the genera living with *Aenictus* suggests that the myrmedoniine aenictophiles are inclined to be diversified.

**A PROVISIONAL KEY TO THE GENERA OF NEW-WORLD ECITOPHILOUS MYRMEDONIINI**

1. Eyes absent .................................................. 2
   Eyes present .................................................. 3

2. Head circular in outline (fig. 28, G), subequal in length and width; pronotum one-sixth longer than broad; sternites with fine short hairs; body very slender in form; 2 mm. in length (Costa Rica with *Labidius*).
   *Ecitotyphlus* Borgmeier
   Head one-half broader than long; pronotum three-fifths broader than long; sternites with a vestiture of long fine setae; body moderately broad; 2 mm. in length (Costa Rica with *Neivamyrmex*). ............................... *Typhlonusa* Borgmeier

3. Head with three strong carinae that form an inverted Y, a tubercle above each eye, a supra-orbital carina, and a vertical postgenal carina; pronotum with two undulating carinae (North Carolina–Texas; Brazil with *Neivamyrmex*). ............................... *Ectoxenida* Wasmann
   Head and pronotum not carinate as above ........................................ 4

4. Abdomen with a distinctive filiform process (fig. 36, F) extending cephalad beneath the thorax (Costa Rica with *Neivamyrmex*). ............................... *Ecitotima* Seevers, n.g.
   Abdomen without an abdominal process .................. 5

5. Abdomen with a very slender one or two-segmented petiole (fig. 29, F) formed by the entire third segment or the third and fourth segments ................. 6
   Abdomen non-petiolate in most genera, but if a petiole is present it is formed by the proximal half of the third segment ........................................ 7

6. Petiole one-segmented; body very small and slender, 2–2.2 mm. in length; fig. 29, F (Brazil with *Neivamyrmex*). ............................... *Ecitocryptodes* Seevers, n.g.
   Petiole two-segmented; body more robust, 4.2 mm. in length (Brazil with *Nomamyrmex*). ............................... *Ecitocryptus* Borgmeier

7. Myrmecoid in form; the abdominal petiole formed by the proximal half of the third segment, with the tergite and sternite tapering strongly from the broad apex of the segment (fig. 36, A–C); integuments with a distinctive rugose sculpture (figs. 36, A, C; 37, H). Costa Rica with *Neivamyrmex*.
   *Ecitotius* Seevers, n.g.
   Abdomen not petiolate; integumental sculpture otherwise ......................... 8

8. Pronotum with a very deep median sulcus (fig. 29, E, H, J) ....................... 9
   Pronotum frequently with other types of impressions, but without a deep median sulcus (with a moderately deep cross-shaped impression in *Ecitopeleta*) ............................................. 14

9. Body attenuated (fig. 29, I); pronotum, elytra, meso- and metasternum, abdomen (segments four and five exceptionally long), antennae, and legs exceptionally long; pronotal sulcus with sloping rather than vertical sides; meso- and metaternal processes exceptionally slender for the tribe; coxae distinctive—the mesoacetabula elongated and not set in margined acetabula; metacoxae sub-triangular ........................................... 10
Body not attenuated (fig. 29, E, H, J); pronotal sulcus more slender and more clearly defined; meso- and metasternal processes moderately broad; coxae typical of the tribe.........................11

10. Eyes extremely large (fig. 29, I); pronotum slightly broader than long; elytral suture longer than pronotum; third sternite with deep oval impressions to receive hind coxae (Brazil with Neivamyrmex)..............Ectitophiletus Borgmeier

Eyes moderate in size; pronotum one-fifth longer than broad; elytral suture shorter than pronotum; third sternite without impressions (Argentina and Costa Rica with Neivamyrmex).........................Dromacamatus Bruch

11. Abdomen robust, sub-ellipsoidal in form; sternites very strongly convex, the tergites moderately so; relatively large species, 4–7 mm. in length....................12

Abdomen more generalized (except for the constricted basal segments in Gallardoia); small species, 3 mm. in length..........................13

12. Tergites of segments 3, 4 and 5 deeply impressed at base; sternites of segments 3 and 4 somewhat constricted at base; paratergites of segments 3–5 extended as triangular processes above tergal impressions (Brazil with Nomamyrmex).................................Ectitophiletus Borgmeier

Tergites only feebly impressed and sternites not constricted; paratergites not as above (Bolivia, Brazil, and Panama with Nomamyrmex)........................................Wasmannina Mann

13. Third and fourth sternites constricted at base (fig. 29, G)—the side margins of third segment parallel in argentinus Bruch, but not in bucki, n.sp.; fourth tergite strongly impressed at base (fig. 29, H). Argentina and Brazil with Neivamyrmex.....................................................Gallardoia Bruch

Third and fourth sternites not constricted at base; fourth tergite not impressed (fig. 29, E). Southern United States (Arkansas to Colorado and Arizona with Neivamyrmex)..................................................Ecitonidia Wasmann

14. Abdomen claviform (fig. 28, I), broadest at apex of fifth segment; fifth and sixth tergites elongated; head and pronotum slender (fig. 28, H), the latter with a slender base; size small, 3 mm. in length. (Brazil with Labidus and other genera)..................................................Ecitonilla Wasmann

Abdomen not claviform, not broadest at apex of fifth segment.......................15

15. Genera as a group with the following combination of characters (individual genera may not have all the traits): Integuments smooth, not reticulated (except Palagonilla) or reticulation obsolescent; head slender to moderately transverse (Tetradonia); relatively long slender neck present; pronotum slender to moderately transverse (Tetradonia); pronotum not impressed; eyes medium-sized to very large; general habitus long and slender; antennae and legs long to extremely long (fig. 28, A–F)..................................................16

Habitus more generalized; integuments usually densely reticulated (except in some Dinocoryna), head usually transverse, rarely subquadrate; neck relatively short, broad, and inconspicuous; pronotum almost always transverse, and frequently with impressions; eyes moderate in size; antennae not unusually long, their segments usually cylindrical and not elongated; legs of moderate length..........................................................21

16. Pronotum transverse; antennae moderately long, only about two and one-half times longer than width of head; legs moderate in length (fig. 28, A)......17

Pronotum subquadrate to elongated; antennae extremely long, the length four to six times the width of head (see measurements in section of Tetradonia group); legs extremely long........................................19

17. Elytra one-fourth broader than the slender abdomen; fourth antennal segments not more than one-half as long as any other segment (Brazil with Labidus).................................Labidilla Borgmeier

Elytra not broader than abdomen; fourth antennal segment nearly as long as any of segments 5–9..........................................................18
18. Integuments with numerous fine umbilicate punctures (Brazil with Eciton).  
Ecitonophrura Wasmann  
Integuments sparsely punctate (except elytra in some species); numerous  
species from Argentina to Texas with several host genera.  
Tetradonia Wasmann

19. Antennae extremely long, about six times as long as width of head; seventh  
tergite with numerous parallel striations; proportions of antennal segments  
and the parts of the legs distinctive (see Tetradonia section). Brazil with  
Labidus.  
Dromeciton Fauvel  
Antennae about four times as long as width of head; seventh tergite not striated; proportions of antennal segments and parts of legs listed in Tetradonia  
section.  

20. Head distinctly impressed (fig. 28, C, D); clypeus relatively broad between  
antennal insertions; head form distinctive; pronotal sides strongly bisinuate;  
asal segment of hind tarsi at least two and one-half times as long as second  
segment (Argentina, Bolivia, Mexico with Labidus).  
Labidoculex Reichensperger 
Head very faintly impressed (fig. 28, F); clypeus narrow between antennal  
insertions; head form distinctive; pronotal sides moderately bisinuate; basal  
segment of hind tarsi little longer than second (Costa Rica with Labidus).  
Palagonilla Reichensperger

21. Antennae robust (in relation to body size), the segments cylindrical and  
compactly arranged (the pedicels invisible); sternites bristling with long fine  
setae; integuments reticulated or not, but the surface does not appear  
granulose from a close-meshed, raised reticulation; size small, 1.8-3 mm.  
in length.  
Ecitonophrura Borgmeier  
Antennae robust or not, the segments cylindrical to compressed terminal seg-  
ments), but not so compactly arranged so as to obscure the pedicels; stern-  
ites not bristling with long fine setae; integuments (except in Microdonia  
and perhaps other genera) with a granulose-appearing surface sculpture  
resulting from a fine-meshed raised reticulation; moderate and small-sized  
species, 4-5 mm. in length.  

22. Pronotum longer than broad, its median sulcus in the form of an inverted drop  
(rather feeble in antennalis), the apex arcuate and sides subparallel (Panama  
and Costa Rica with Neivamyrmex)  
Echitoglossa Borgmeier  
Pronotum subquadrate to broader than long; median sulcus absent, shallow  
or moderately deep (not formed as above); apex of pronotum bisinuate, the  
sides not subparallel.  

23. Pronotum with a very shallow or a broad deep median concavity, and a  
shallow to moderately deep impression on each side (Brazil and Costa Rica  
with Neivamyrmex)  
Echitophrura Reichensperger  
Pronotum not impressed or with a single shallow to moderately deep median  
impression (Florida, North Carolina, Kansas, and Arizona, with Neiva-  
myrmex)  
Dinocorynus Casey

24. Eighth tergite denticulate (fig. 29, Q, R)  
Eighth tergite not denticulate (a pair of incurved spines may be present in  
some species of Echitopora)  

25. Pronotum cordiform, subequal in length and width; dorsum with a strong  
impression not unlike the form of an inverted cross; arcuate pronotal apex  
narrow, only little more than one-half the maximum pronotal width (Brazil  
with Nomamyrmex)  
Echitopella Borgmeier  
Pronotum at least one-sixth broader than long; dorsum with very shallow to  
conspicuous lateral impressions, but no median impression; pronotal form  
not as above.  

26. Each elytron with a conspicuous impression; metasternal process exception-  
ally slender for the tribe (fig. 29, K); pronotal impressions moderately deep
(in the form of parentheses enclosing a median flattened area); antennae distinctive (fig. 37, D); tenth tergite not incised (fig. 29, M); sutural length of elytra only three-fourths pronotal length; outer apical angles of elytra not prolonged (Costa Rica with Neivamyrmex)…… Ecitana Seevers, n.g.

Elytra without impressions; metasternal process broad (fig. 29, L); pronotal impressions very shallow to moderately deep (not formed as above); antennae not as above (fig. 37, E); sutural length equal to pronotal length; tenth tergite deeply incised in Ecitodonia………………………………...27

27. Head, pronotum, and elytra with numerous large “rosette type” umbilicate punctures; head and pronotum one-third broader than long; pronotal impressions moderately deep; apices of elytra strongly bisinuate and outer apical angles prolonged (Brazil with Nomamyrmex)…… Ecitodiscus Borgmeier

Head, pronotum, and elytra with or without small umbilicate punctures, but not the “rosette type”; head and pronotum one-sixth broader than long; pronotal impressions very shallow; elytral apices scarcely sinuate and the outer apical angles not prolonged; tenth tergite incised (fig. 29, N). (Brazil and Costa Rica with Eciton)…………………………………… Ecitodonia Seevers, n.g.

28. Integuments with a microsculpture of a fine-meshed reticulation and numerous fine, asperate punctures—with the appearance of granulation; eighth tergite with a pair of incurved spines in both sexes of some species; body moderately broad and convex; length 3-4 mm. (Brazil, Bolivia, and Costa Rica with Eciton, as a rule)…………………………… Ecitopora Wasmann

Integuments of head and pronotum reticulated or not, but not as above and not granulose in appearance; eighth tegite never bearing spines; body slender and somewhat dorso-ventrally compressed; length, 2-3 mm……………...29

29 Vertex not impressed; pronotum with a shallow submarginal impression on each side; antennae longer and less compact (segments 3-10 moderately broad and slightly incrassate; 2-3 mm. in length (Kansas, Texas, Arizona, Mexico, Costa Rica with Neivamyrmex)…………………Microdonia Casey

Remarks.—Zyras s.l., Ecitonia Wasmann, Ecitopolites Borgmeier, and Ecitocerus Borgmeier are not included in the above key.

NEW WORLD ECITOPHILOUS GROUPS

The hosts and number of guest species with each are indicated.

DRUSILLA Group
Zyras Stephens, s.l. Host: Eciton, Neivamyrmex

ECITOPORA Group
Ecitana, new genus Neivamyrmex (1)
Ecitocerus Borgmeier Nomamyrmex (1)
Ecitodiscus Borgmeier Nomamyrmex (1)
Ecitodonia, new genus Eciton (2)
Ecitonia Wasmann Nomamyrmex (1), Labidus (1), and
Ecitonopella Borgmeier Neivamyrmex (1)
Ecitophila Wasmann Nomamyrmex (1)
Ecitopolites Borgmeier Labidus (1)
Ecitopora Wasmann Eciton (1), Nomamyrmex (1)
Ecitozenidia Wasmann Eciton (6), Nomamyrmex (1)
Microdonia Casey Neivamyrmex (4)

Neivamyrmex (4), Labidus?
TETRADONIA Group

- *Dromeciton* Fauvel
- *Ecitonilla* Borgmeier
- *Ecitotyphlus* Borgmeier
- *Falagonilla* Reichensperger
- *Labidilla* Borgmeier
- *Labidoculex* Reichensperger
- *Scotodonia* Wasmann
- *Tetradonia* Wasmann

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<tr>
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<td><em>Neivamyrmex</em> (2)</td>
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<tr>
<td><em>Ecitotima</em>, new genus</td>
<td><em>Neivamyrmex</em> (1)</td>
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DINOCORYNA Group

- *Dinocoryna* Casey
- *Dromacamatus* Bruch
- *Ectocryptodes*, new genus
- *Ectocryptus* Borgmeier
- *Ectognosia* Wasmann
- *Ectophiletus* Borgmeier
- *Ectophrura* Reichensperger
- *Ectoplectus* Borgmeier
- *Gallardoia* Bruch
- *Typhlonusa* Borgmeier
- *Wasamnina* Mann

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ECITOSIUS Group

- *Ecitosius*, new genus
- *Ecitotima*, new genus
DRUSILLA Group

Drusilla Leach (=Myrmedonia Erichson), the type genus of the Myrmedonini (the tribal name may be derived from a synonym), is Palaearctic in distribution and does not occur with army ants. The single South American species of Drusilla recorded with army ants belongs to Tetrads. 

Zyras Stephens


More than 500 species of Zyras s.l. have been recorded throughout the world but in my opinion most of them are not congeneric with the Palaearctic haworthi. The taxonomic state of the vast "Zyras complex" is one of great confusion and the proposal of more than 50 subgenera has not helped clarify matters very much. Blackwelder's catalogue (1944) records 69 species of Neotropical Zyras, and Borgmeier (1949) lists six of these as ecitophilous species. The New World species of "Zyras" associated with army ants are found chiefly in the rubbish heaps of Eciton; at least those collected by Rettenmeyer in Panama were generally in this material.

ECITOPHILOUS SPECIES OF ZYRAS STEPHENS, S.L.


ECITOPORA Group

Even though it is difficult at this time to satisfactorily delimit Ecitopora and its allied genera from the large Zyras s.l. complex (the neotropical species of which must, in my opinion, be assigned to genera other than Zyras s.s.), there is little doubt that they constitute a group of obligate ecitophiles. In contrast to a large majority of genera of other groups of New World ecitophilous Myrmedonini,
the members of the Ecitopora group are relatively generalized in form and exhibit few specializations (Ecitoxentidia is an exception). Inasmuch as many of the genera of this group are not well defined nor delimited, a thorough study is needed. Studies of the male and female genitalia should help to resolve some of the problems of generic assignment. A few genera of the Ecitopora group are not included in the tribal generic key.

Ecitopora Wasmann


Ecitopora may be distinguished from Zyros s.l. by its granulose-appearing microsculpture (finely reticulate and asperate). Characters to differentiate this genus from others of the tribe are given in the generic key.

Ecitopora was the first genus of ecitophilous Myrmedoniini to be described yet, over the years, species were assigned to it chiefly on the basis of general resemblance to Ecitopora opaca Wasmann. In order to reduce the heterogeneity, I transferred E. tenella Wasmann, E. laticollis Brues, and E. nitidiventris Brues to Microdonia Casey in an earlier paper (Seevers, 1959). I now propose to transfer E. major Wasmann to a new genus, Ecitodonia. It will probably be advisable to remove E. setosa Borgmeier from this genus, too. Four nomina nuda were listed by Wasmann but not validated: bicolor (in Reichensperger, 1935), nigrita Wasmann, 1925, quadricollis (in Reichensperger, 1935), and zikani Wasmann, 1925.

Integuments with a fine-meshed reticulation and numerous fine, asperate punctures with a short, fine pubescence. Head broader than long; neck more than one-half as broad as head; vertex usually moderately impressed; infraorbital carinae absent. Eyes finely faceted; small to moderately large. Antennal length two and one-half to three and one-half times the width of head; segments 4–10 transverse and incrasate in some species; in other species, segments 4–6 elongated and 7–10 subquadrate. Pronotum one-fifth to one-fourth broader than long; pronotum broadest in apical half, its sides bisinuate, and base and apex arcuate; dorsum shallowly impressed in the middle and on each side; the dorsum abruptly deflexed laterally and the hypomera completely visible from the side. Abdomen generalized in form; eighth tergite with or without a pair of prominent incurved spines (present in opaca, brevicornis, fernandi and probably others). Length, 3–4 mm.

Remarks.—Reichensperger (1935, p. 214) implied that the incurved spines of the eighth tergite occur in the male of all species, but they occur in both sexes of some species.
SPECIES OF ECITOPORA WASMANN


ECITODISCUS Subgroup

Ecitodiscus Borgmeier, Ecitopelta Borgmeier, Ecitodonia n.g., and Ecitana n.g. are distinguished from the other genera of the Ecitopora group by their denticulate eighth tergite.

Ecitodiscus Borgmeier


Coloration light reddish-brown. Head, pronotum, and elytra with numerous large, "rosette type" umbilicate punctures (my term for those umbilicate punctures with a central seta and a series of fine radiating lines); intervals finely reticulated. Umbilicate punctures of head larger and less numerous than those of pronotum and elytra (punctures of the latter very numerous; the narrow intervals almost without reticulation). Abdomen shining; reticulation obsolescent. Head one-third broader than long; vertex shallowly impressed. Eyes very large and convex, occupying almost the entire side of head (distance of eye from base of head less than one-fourth eye length). Three basal antennal segments elongated; segments 4-10 transverse, subcylindrical and slightly compressed. Pronotum one-third broader than long; broad subapically, the sides arcuate but scarcely sinuate; apex slightly bisinuate; base moderately arcuate, basal angles rounded. Pronotum with a long, moderately deep submarginal impression on each side. Length of elytral suture subequal to pronotal length; elytral apices strongly bisinuate—conspicuously emarginate near the prolonged outer angles; elytra not impressed. Meso- and metasternal processes broad. Eighth tergite denticulate. Length, 5 mm.

SPECIES OF ECITODISCUS BORGMEIER

Ecitopelta Borgmeier


Among other differences, this genus is distinguished from _Ecitodiscus_ by the presence of a neck, pronotal shape, and distinctive pronotal impressions.

Head one-fifth broader than long; neck only about one-third as broad as head and with a stout occipital condyle. Eyes moderate in size. Antennae much as in _Ecitodiscus_. Integuments reticulated and with some rosette-type umbilical punctures, but these are not as numerous nor as large as in the preceding genus. Pronotum somewhat cordiform, subequal in length and width; the arcuate apex only little more than one-half maximum pronotal width; sides converging very strongly laterally and the hypomera completely visible from the side. Abdomen generalized toward the arcuate base with which it is continuously rounded. Pronotal dorsum with a strong impression which in form is not unlike an inverted cross. Abdomen broadest at third segment, tapering to a slender apex; eighth tergite denticulate; tergites 3–6 reticulated, 7 and 8 glabrous. Length, 4 mm.

**SPECIES OF ECITOPELTA BORGMEIER**

_reticulata_ Borgmeier, 1949, Rev. Ent., 20, p. 140; figs. 69–77, pl. 2, fig. 2 (photograph). Host: _Nomamyrmex schlechtendali_ Mayr. BRAZIL: Goiás; Campinas.

Ecitodonia, new genus. Figures 29, L, N, P, Q; and 37 A, B, E.

Type species: _Ecitodonia major_ Wasmann (_Ecitopora_).

_Ecitodonia_ may be differentiated from _Ecitodiscus_ by the absence of rosette-type umbilical punctures, strong abdominal reticulation, a narrower head, only one-sixth broader than long, very shallow pronotal impressions, and feebly emarginate elytral apices of which the outer angles are not prolonged. From the other genera, _Ecitodonia_ is distinguished by the characters in the key to the myrme- doniine genera.

Head, pronotum, and elytra with a fine-meshed, raised reticulation—the integuments have a granulose appearance much as in _Ecitopora_; rosette-type umbilicate punctures absent. Abdomen with a medium-coarse reticulation, and a moderate number of shallow, elongated impressions bearing a recumbent seta at the base. Head one-fifth broader than long, its vertex shallowly concave. Antennae (fig. 37, E) with three elongated basal segments; segments 4–10 subcyllindrical and moderately compressed; apical half of terminal segment strongly impressed. Eyes moderate in size. Pronotum one-sixth broader than long, its basal angles distinct; dorsum with very shallow impressions. Elytral apices feebly bisinuate, and its angles not prolonged. Meso- and metasternal processes broad (fig., 29 L)—typical of the tribe. Eighth tergite denticulate. Tenth tergite deeply incised (fig. 29, P). Aedeagus (median lobe and parameres) as in fig. 37, A, B. Length, 4–5.5 mm.
Ecitodonia setigera, new species. Figures 29, L, N, P, Q and 37 B, E.

Head and pronotum without umbilicate punctures; vertexal impression relatively short and narrow and extending on to the deflexed clypeus; antennal segments with the following relative lengths: 30 : 16 : 18 : 12 : 14 : 14 : 16 : 16 : 17 : 17 : 38; head, pronotum, and elytra with erect setae; spermatheca distinctive (fig. 29, P); aedeagus distinctive (fig. 37, B) setigera, n. sp.

Head and pronotum with small umbilicate punctures scattered throughout the fine reticulation; vertexal impression more extensive and confined to the vertex; antennal segments with the following relative lengths: 46 : 16 : 28 : 16 : 14 : 14 : 14 : 13 : 13 : 13 : 44; head, pronotum, and elytra without erect setae; spermatheca distinctive; aedeagus distinctive (fig. 37, A) setigera, n. sp.

Head, pronotum, and elytra piceous, remainder of body light brown. Head, pronotum, and elytra with a uniform fine-meshed, raised reticulation; umbilicate punctures absent. Head sparsely setose, the setae short and pale except for a few longer darker setae on occipital and clypeal regions. Pronotum with a sparse covering of pale recumbent setae and about 24 erect black setae in irregular longitudinal rows (most numerous in medial and submarginal rows; elytra with scattered erect and semi-recumbent setae. Abdominal sclerites moderately densely clothed with medium-length recumbent hairs, and a few longer setae, chiefly on apical margins. Length, 4-5.5 mm.

Type from Monteverde, Costa Rica (10°29' N, 84°50' W), at 1400 meters elevation, collected February 9, 1963, by Roger D. Akre. Host: Eciton burchelli Westwood (colony E-299). In Chicago Natural History Museum.

Paratypes.—50 specimens, from type locality, collected from three colonies of Eciton burchelli Westwood (E-299, E-305, E-351), February 9–April 30, 1963, by Roger D. Akre. 32 specimens, collected from two colonies (E-299, E-305), February 9–20, by C. W. and M. E. Rettenmeyer. Some paratypes retained in Chicago Natural History Museum and some returned to R. D. Akre and C. W. Rettenmeyer.

Other material.—5 specimens, Hamburg Farm, Costa Rica, collected in July, 1936, by Fred Nevermann, with Eciton burchelli Westwood (label designation only), in Bernhauer collection, Chicago Natural History Museum.

Ecitana, new genus. Figures 29, K, M, O, R and 37, C, D.

Type species: Ecitana biimpressa, new species.
Distinguished from related genera by the diagnostic characters of the key to the myrmedoniine genera. Its most noteworthy distinctive characters are: the exceptionally slender meso- and metasternal processes, conspicuous elytral impressions (absent in all related genera), elytral sutural length only three-fourths pronotal length, antennal segments 5–10 relatively short (fig. 37, D), elytra apices not bisinuate, tenth tergite not incised (fig. 29, M), spermatheca distinctive (fig. 29, O).

Head with rosette type umbilicate punctures that are smaller, more numerous, and more densely arranged than in Ecitodiscus, and with the narrow intervals more strongly elevated than in the latter genus—as a result, the integuments have a very coarse texture that even obscures the umbilicate punctures of the pronotum. Abdominal integuments smooth, the reticulation obsolescent. Head one-third broader than long. Eyes moderate in size; eye length only slightly greater than distance of eye from base of head. Vertex broadly and shallowly impressed. Antennae as in fig. 37, D. Pronotum one-sixth broader than long; similar in form to that of Ecitodiscus; dorsum with two conspicuous impressions forming “parentheses” enclosing a median flat area. Elytral sutural length about three-fourths pronotal length; elytral apices not bisinuate (slightly arcuate and not emarginate laterally). Each elytron with a conspicuous lateral impression that is narrow behind the humerus but gradually broader and shallower toward apex. Metasternal process slender (fig. 29, K). Eighth tergite denticulate (fig. 29, R). Tenth tergite not incised (fig. 29, M). Spermatheca distinctive (fig. 29, O); aedeagus as in fig. 37, C.

Ecitana biimpressa, new species. Figures 29, K, M, O, R and 37, C, D.

Dorsum piceous, apex of abdomen pale; underside reddish-brown, legs light brown. Head, pronotum, and elytra with very short hairs associated with umbilicate punctures. Tergites with a dense covering of short, fine, pale recumbent hairs (more dense on eighth tergite). Tergites 2–6 with an apical row of about 12 moderately long, fine apically-directed setae. Sternites with a dense clothing of fine pubescence and scattered erect and semi-erect setae. Legs without noteworthy features; hind tarsi with segments 1–3 decreasing in length, 3 and 4 subequal, 5 a little longer than 4. Length, 4.5–5 mm.


Paratypes.—153, from same colony as type, collected from February 1–22, 1963 (67 by R. D. Akre, and 86 by C. W. and M. E. Rettenmeyer). Some are retained in Chicago Natural History Museum and the others have been returned to R. D. Akre and C. W. Rettenmeyer.
MICRODONIA Subgroup

Microdonia Casey and Ecitophila Wasmann are genera of minute species (2–3 mm. in length) related to Ecitopora but not easily differentiated from the latter. Their slender, sub-depressed form and different microsculpture are of diagnostic importance, and their eighth tergite never has spines. Microdonia is primarily a Nearctic genus associated with Neivamyrmex, although it is known to extend as far south as Costa Rica, while Ecitopora is a Neotropical genus occurring with Eciton. The single Brazilian species of Ecitophila was recorded with Labidus.

Microdonia Casey


In an earlier paper (Seevers, 1959), I called attention to the eicitophilous habits of this genus, of which Casey was apparently not aware, and transferred several species to it from Ecitopora.

Head transverse, broadest behind eyes because of the arcuate postgenae; basal angles obsolete; dorsum not impressed. Eyes moderate in size, finely faceted. Antennae geniculate, scape short, segments 3–10 transverse, slightly incrassate. Pronotum transverse; sides almost straight in occipitalis to slightly arcuate in kansana; dorsum with a shallow elongated submarginal impression on each half, the impressions connected at times by a feeble basal impression. Elytra generalized, their apices feebly bisinuate. Abdomen generalized, long and slender; third tergite slightly impressed. Integuments reticulated or not; head and pronotum usually with small umbilicate punctures. Abdomen pubescent or glabrous. Length, 2.5–3 mm.; width, 0.7–0.8 mm.

SPECIES OF MICRODONIA CASEY

kansana Seevers, 1959, Coleopt. Bull., 13, p. 69, figs. 6, 7. Host: Neivamyrmex nigrescens Cresson (of type); and Neivamyrmex opacithorax Emery. KANSAS: Lawrence.

Remarks.—A syntype of Ecitopora nitidiventris Brues was recently located by Dr. Thomas Borgmeier in the Museum of Comparative Zoology and sent to me for study. This species was not available when I prepared my 1959 report and was left in Ecitopora. It is now clear that the specimens determined in 1959 as sulcatula Borgmeier belong to nitidiventris Brues, and that the host of this species is primarily Neivamyrmex opacithorax Emery. Brues cited Labidus coecus Latreille as the host of nitidiventris, an association that has never been confirmed.

The available specimen of nitidiventris Brues bears a hand written label, probably of Brues, with the statement “Ecitopora nitidiventris Brues (mss.), type, Austin, Texas,” a red type label probably added by someone else, and a label “bei Eciton coecum Ltr.” possibly added by Wasmann.

Ecitophila Wasmann


Ecitophila is evidently closely related to Microdonia although this fact has not been reported in the literature. Ecitophila has a vertical impression, slightly different pronotal impressions, and shorter and more compact antennae.

Head about one-fifth broader than long; postgenae swollen; vertex with a shallow, smooth, oval impression. Antennae short and stout; scape very short and stout; segment 2 subquadrate; 3–10 very short and strongly incrassate (segment 4 more than four times as broad as long). Head, pronotum and elytra with a fine-meshed, raised reticulation and short pubescence; abdomen reticulate and pubescent. Pronotum with a medial and two lateral impressions; all seem to be joined near base by a very shallow impression (the medial impression moderately broad and shallow); the lateral ones, restricted to basal two-thirds of disk, oval in outline and relatively deep. Length, 2 mm.

SPECIES OF ECITOPHILA WASMANN


ECITOXENIDIA Subgroup

Because of its distinctive ornamentation of cephalic, pronotal, and elytral carinae and eminences, Ecitoxenidia seems to occupy an isolated position in the Ecitopora group. It may, however, have
evolved from a *Microdonia*-like ancestor and be more closely allied to *Microdonia* than its specialized features would suggest. Except for a Brazilian species, the genus has been recorded only from the southern United States (North Carolina to Texas). The fauna of the host genus, *Neivamyrmex*, has been so poorly investigated throughout most its range that recorded distributions are not very meaningful at this time. In an earlier paper (Seevers, 1959), I reviewed the genus, added several new species, and provided some figures. Although Borgmeier's *Ecitocolax longicornis* differs in head contours from the Nearctic species, I am synonymizing the Brazilian *Ecitocolax* Borgmeier. The type species of *Ecitoxenia*, *brevipes* Brues, was originally placed in Wasmann's *Ecitoxenia* because of general similarity in the ornamentation of head and thorax. In my opinion, the two genera do not belong to the same tribe and later in this monograph *Ecitoxenia* Wasmann is placed in a new tribe, the Ecitocharini.

**Ecitoxenia** Wasmann


Head subequal in length and width; dorsum with three strong carinae that form an inverted Y: a median carina that extends from clypeus to middle of vertex and an oblique carina on each half of the occiput. Vertex with a tubercle above each eye that almost obscures the eyes from dorsal view; from this tubercle a supraorbital carina extends caudad to join a vertical postgenal carina. Antennae variable in length. Pronotum three-fifths to nine-tenths broader than long; dorsum divided by two undulating carinae into three areas—the median area is at a somewhat higher level than the broadly concave lateral areas. Elytra broader than pronotum; their margins elevated and sharply carinate. Head, pronotum and elytra with a coarse, fine-meshed reticulation. Head and pronotum with short, sparse, feebly clavate setae. Elytra moderately clothed with clavate setae. Length, 2.5–3 mm.

**SPECIES OF ECITOXENIDIA WASMANN**


*longicornis* Borgmeier, 1949, Rev. Ent., 20, p. 147, figs. 103–107; pl. 3, fig. 3 (*Ecitocolax*). *New combination.* Host: *Neivamyrmex pilosus* F. Smith. BRAZIL: Espirito Santo: Santa Teresa.
SEEVERS: STAPHYLINID BEETLES

247

GENERAE (ECITOPORA GROUP) OF UNCERTAIN POSITION

Ecitonía Wasmann


Head, excluding neck and labrum about as long as broad; sides converging evenly to the broad neck; dorsum with a faint median impression. Eyes small. Antennae longer than head and pronotum; slender, incrassate; scape shorter than the elongated segments 2 and 3; segments 4–10 transverse, incrassate and increasing in length; 11 subequal to 9 and 10 combined. Pronotum feebly transverse; broadest subapically; sides binicate to base which is five-sixths maximum pronotal width. Pronotum strongly deflexed laterad, the hypomera nearly vertical. Pronotum feebly impressed or not. Elytra generalized. Abdomen broadest at the level of the fifth or sixth segment, narrower basally and apically, the base of third segment less than three-fourths maximum abdominal width. Abdominal tergites of segments 3–5 moderately impressed at base; paratergites and parasternites elevated above dorsum. Eighth tergite not denticulate. Length, 2.5–3.75 mm.

SPECIES OF ECITONÍA WASMANN


Ecitopolites Borgmeier


SPECIES OF ECITOPOLITES BORGMEIER

familiaris Borgmeier, 1949, Rev. Ent., 20, p. 144; figs. 87–96; pl. 3, fig. 4 (photograph). Host: Nomamyrmex schlechtendali Mayr. BRAZIL: Goiás; Campinas.


scopifer Borgmeier, 1949, Rev. Ent., 20, p. 142; figs. 78–86, pl. 3, fig. 2 (photograph). Host: Nomamyrmex schlechtendali Mayr. BRAZIL: Goiás; Campinas.

Ecitocerus Borgmeier

SPECIES OF ECITOCERUS BORGMEIER

*gracilipes* Borgmeier, 1949, Rev. Ent., 20, p. 138; figs. 61-68; pl. 2, fig. 3 (photograph). Host: *Nomamyrmex schlechtendali* Mayr. BRAZIL: Goiás; Campinas.

TETRADONIA Group

This group comprises eight genera of Myrmedoniini that have evolved in a different direction from the *Ecitopora* group. The species of *Tetradonia* and allies tend to have slender, elongated bodies, smooth, shining, non-reticulate integuments, small heads with long, slender necks, medium to very large eyes, and long to extremely long appendages. *Tetradonia* is probably the most generalized genus in the group and is a member of a series involving *Scotodonia, Labidilla, Labidoculex, Falagonilla*, and *Dromeciton*. This series is noteworthy for the progressive lengthening of the antennae and legs. *Ecitonilla* and *Ecitotyphlus* evolved in another direction and the latter is one of the two eyeless genera of Myrmedoniini.

The following figures show the range of variation in the lengths of antennae and legs in the *Tetradonia-Dromeciton* series. Each unit of measurement equals 0.009 mm.

Antennae: Relative Length of Segments

<table>
<thead>
<tr>
<th>Segment:</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dromeciton wagneri</em></td>
<td>55</td>
<td>28</td>
<td>56</td>
<td>34</td>
<td>46</td>
<td>50</td>
<td>42</td>
<td>42</td>
<td>42</td>
<td>35</td>
<td>462</td>
<td></td>
</tr>
<tr>
<td><em>Falagonilla cursor</em></td>
<td>38</td>
<td>18</td>
<td>32</td>
<td>24</td>
<td>22</td>
<td>24</td>
<td>28</td>
<td>26</td>
<td>26</td>
<td>22</td>
<td>28</td>
<td>288</td>
</tr>
<tr>
<td><em>Labidoculex fragilis</em></td>
<td>26</td>
<td>18</td>
<td>20</td>
<td>12</td>
<td>18</td>
<td>17</td>
<td>16</td>
<td>15</td>
<td>14</td>
<td>60</td>
<td>234</td>
<td></td>
</tr>
<tr>
<td><em>Labidoculex antennalis</em> (male)</td>
<td>28</td>
<td>18</td>
<td>20</td>
<td>12</td>
<td>18</td>
<td>17</td>
<td>16</td>
<td>15</td>
<td>14</td>
<td>60</td>
<td>234</td>
<td></td>
</tr>
<tr>
<td><em>Labidoculex antennalis</em> (female)</td>
<td>26</td>
<td>18</td>
<td>20</td>
<td>12</td>
<td>18</td>
<td>17</td>
<td>18</td>
<td>18</td>
<td>16</td>
<td>38</td>
<td>219</td>
<td></td>
</tr>
<tr>
<td><em>Tetradonia marginalis</em></td>
<td>30</td>
<td>16</td>
<td>22</td>
<td>12</td>
<td>14</td>
<td>15</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>18</td>
<td>28</td>
<td>197</td>
</tr>
<tr>
<td><em>Labidilla dentiguttur</em></td>
<td>26</td>
<td>12</td>
<td>16</td>
<td>6</td>
<td>13</td>
<td>14</td>
<td>14</td>
<td>15</td>
<td>16</td>
<td>16</td>
<td>20</td>
<td>168</td>
</tr>
</tbody>
</table>

Ratio—Antennal Length : Head Width (including eyes)

<table>
<thead>
<tr>
<th>Species</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dromeciton wagneri</em></td>
<td>462 : 78 = 6x</td>
</tr>
<tr>
<td><em>Falagonilla cursor</em></td>
<td>388 : 66 = 4.36x</td>
</tr>
<tr>
<td><em>Labidoculex fragilis</em></td>
<td>227 : 65 = 3.5x</td>
</tr>
<tr>
<td><em>Labidoculex antennalis</em> (male)</td>
<td>234 : 56 = 4.2x</td>
</tr>
<tr>
<td><em>Labidoculex antennalis</em> (female)</td>
<td>219 : 56 = 3.9x</td>
</tr>
<tr>
<td><em>Tetradonia marginalis</em></td>
<td>197 : 77 = 2.5x</td>
</tr>
<tr>
<td><em>Labidilla dentiguttur</em></td>
<td>168 : 65 = 2.6x</td>
</tr>
</tbody>
</table>

Hind Legs: Length and Length of Parts

<table>
<thead>
<tr>
<th>Species</th>
<th>L</th>
<th>Fe</th>
<th>Ti</th>
<th>Ta</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dromeciton wagneri</em></td>
<td>729</td>
<td>248</td>
<td>265</td>
<td>216</td>
<td>90</td>
<td>40</td>
<td>32</td>
<td>24</td>
<td>30</td>
</tr>
<tr>
<td><em>Falagonilla cursor</em></td>
<td>527</td>
<td>190</td>
<td>195</td>
<td>142</td>
<td>88</td>
<td>30</td>
<td>26</td>
<td>20</td>
<td>28</td>
</tr>
<tr>
<td><em>Labidoculex fragilis</em></td>
<td>465</td>
<td>150</td>
<td>165</td>
<td>150</td>
<td>66</td>
<td>26</td>
<td>20</td>
<td>16</td>
<td>22</td>
</tr>
<tr>
<td><em>Labidoculex antennalis</em></td>
<td>446</td>
<td>155</td>
<td>160</td>
<td>131</td>
<td>58</td>
<td>20</td>
<td>18</td>
<td>15</td>
<td>20</td>
</tr>
</tbody>
</table>
**Tetradonia** Wasmann. Figure 28, A.


*Acanthodonia* Bruch, 1923, Rev. Mus. La Plata, 27, p. 184; Borgmeier, 1959, Bol. Mus. Nac. (Brasil), n.s., Zool., no. 214, p. 10 (=*Tetradonia*).


Integuments smooth and shining, with almost no surface sculpture; elytra relatively smooth to coarsely rugose (resulting from asperate punctures in irregular rows). Sternite with a conspicuous vestiture of long, coarse black setae. Head about one-half broader than long, excluding neck and labrum; neck less than one-half as broad as head; vertex moderately convex, not impressed; clypeus large, strongly declivous. Eyes large to extremely large; facets medium-sized to coarse. Antennae geniculate; nearly three times as long as head width; almost all segments elongated; moderately incrassate beyond fourth segment; segments 2–4 usually slender, 5–11 more robust, 5–10 obtapezoidal. Pronotum longer than head and subequal in width; pronotum one-fifth broader than long or more; evenly convex, not impressed; broader at apex than base; sides converging and continuously arcuate with base, basal angles not prominent. Elytra elongated, not impressed; outer apical angles not prolonged in *Tetradonia* s.s., or prolonged as spinous processes in the males of *Acanthodonia*. Abdomen at base as broad as elytra; broadest at fourth segment, the seventh segment only two-thirds as broad as fourth; parastermata moderately broad, paratergites slender; seventh tergite with a small median tubercle in some species, or with fine parallel striations in others (*Acanthodonia*); eighth tergite tri-emarginate in many species. Length, 3–5 mm.

Remarks.—Inasmuch as *Acanthodonia* has been distinguished from *Tetradonia* chiefly on the basis of the prolongation of the outer apical angles of the male elytra, I am following Borgmeier’s (1959) recommendation that the two genera be merged. *Acanthodonia* may prove to be a useful subgeneric category; its species are apparently restricted to southern South America while those of *Tetradonia* are more abundant in northern South America and Central America.

It was a surprise to discover that *Chlorotusa megalops* Casey of Texas and Louisiana is closely allied to *Tetradonia marginalis* Reichensperger and that *Chlorotusa* Casey is a synonym. All specimens of *megalops* collected to date were probably attracted to lights, so its ecitophilous habits have not been suspected. As the genus *Eciton*, the host of most neotropical species, has not been recorded in the United States, the host of *megalops* is conjectural; perhaps it is *Labidus*.

**SPECIES OF TETRADONIA WASMANN**


argentina Bruch, 1923, Rev. Mus. La Plata, 27, p. 185, figs. 5–7; Borgmeier, 1931, Rev. Ent., 1, p. 365. Host: Ecton dulcius Forel. ARGENTINA: Córdoba; Alta Gracia (Acanthodonia).

brasiliensis Borgmeier, 1931, Rev. Ent., 1, p. 365, fig. 15. Host: Ecton dulcius Forel. BRAZIL: Goiás; Campinas (Acanthodonia).


Remarks.—Borgmeier (1949, p. 111) placed Astilbus spinipennis Bernhauer (1921a) in Acanthodonia, but, after examination of the type, I cannot agree that it belongs in that group. Bernhauer’s spinipennis probably belongs to a new genus but is not now considered as there is no evidence of its occurrence with army ants.

Labidilla Borgmeier. Figure 28, E.


Borgmeier compared this genus with Zyras, but it is certainly more closely allied to Tetradonia. Labidilla is retained as a distinct genus because Tetradonia is more homogeneous without dentiguttur. Labidilla is essentially a slender Tetradonia and may be differentiated as follows: Elytra one-fourth broader than the slender abdomen; abdomen with a dense vestiture of long, fine, pale setae (coarse, black setae in Tetradonia); fourth antennal segment exceptionally short,
no more than one-half as long as any other segment. The antennal proportions are given in the introduction to the Tetradonia group. Length, 2.5–3 mm.

**SPECIES OF LABIDILLA BORGMEIER**


Scotodonia Wasmann


Except for its integumental sculpture, Scotodonia seems to have the characteristics of a Tetradonia. The integuments bear numerous fine umbilicate punctures similar to those of some genera of the Ecito-pora group.

**SPECIES OF SCOTODONIA WASMANN**

Dromeciton Fauvel. Figure 28, B.


Head smooth, shining, very faintly reticulate and very sparsely punctate and pubescent. Pronotum and elytra shining; with moderately dense, asperate punctation; reticulation obsolescent. Tergites faintly reticulate, impunctate. Head about seven-eighths as long as broad, excluding neck and labrum; vertex slightly convex, scarcely impressed; sides of head converging strongly to the slender neck, which is only one-fourth as broad as head. Eyes large, coarsely faceted; about two-thirds eye length from base of head. Antennae extremely long, six times head width; all segments elongated. Pronotum subequal in length and width; broadest in apical half; sides strongly bisinuate; dorsum with two shallow subbasal impressions. Legs extremely long (see group summary for relative length of parts); hind legs more than two and one-half times abdominal length, one-half longer than antennae, and nine times pronotal width; tibia of each leg longer than femur; hind tarsus four-fifths as long as tibia, very slender; basal segment of hind tarsus more than twice as long as second segment (hind tarsal segments—90:40:32:24:30). Abdomen relatively generalized as in Tetradonia; broadest at fourth segment; tergites flat; third and fourth tergites slightly impressed at base; seventh tergite with numerous parallel striations. Length, 4.5 mm.

**SPECIES OF DROMECITON FAUVEL**
Falagonilla Reichensperger. Figure 28, F.


Reichensperger compared Falagonilla with Falagonia Sharp, but it does not seem to be close to that genus; its affinities are with the Tetradonia group, and with Dromeciton in particular. Although Falagonia may be myrmecophilous, it does not occur with army ants. Reichensperger did refer to Dromeciton (incorrectly as Ecitodromus Fauvel) but only to point out that it also has long legs and antennae.

Falagonilla differs from Dromeciton as follows: shorter appendages (see group summary for comparisons); different proportions of antennal and leg segments, shape of head, position of the smaller, finely-faceted eyes; different pronotal proportions; subovate abdomen with strongly convex tergites; and non-striated seventh tergite.

Head, pronotum, elytra, and abdomen with a fine-meshed reticulation; integuments dull, punctures fine (slightly asperate or not), and pubescence moderate throughout. Head flat, with a shallow median impression; sides of head converging moderately to the relatively broad neck, which is two-fifths as broad as head. Eyes relatively small, finely faceted; more than eye length from base of head. Antennae four and one-third times head width. Pronotum similar to that of Dromeciton but two-fifths longer than broad. Legs long, but relatively shorter than in Dromeciton (see summary elsewhere); hind legs about three times abdominal length, four-fifths longer than antennae, and eight times pronotal width; tibia of fore-legs shorter than femur, but tibiae of other legs longer than femora; hind tarsus less than three-fourths as long as tibia; basal segment of hind tarsus about one-fourth as long as second segment (hind tarsal segments—38 : 30 : 26 : 20 : 28). Abdomen subovate; broadest at fifth segment; tergites strongly convex; tergites 3–5 strongly impressed at base; seventh tergite not striated. Length, 3.75–4 mm.

SPECIES OF FALAGONILLA REICHENSPERGER


Labidoculex Reichensperger. Figure 28, C, D.

Labidoculex Reichensperger, 1936, Rev. Ent., 6, p. 234. Type species: Labidoculex fragilis Reichensperger.

Head a little less than one-fifth broader than long, excluding neck and labrum; clypeus broader between antennae than in the two preceding genera; vertex with a smooth median impression (somewhat foveolate) which narrows as it extends to base where it is bounded by low occipital eminences; neck three-tenths as broad as head. Eyes medium-sized and finely faceted or large with coarse facets. Antennae elongated (see group summary). Pronotal form as in fig. 15, C, D; lateral borders more emarginate near base than in preceding genera; pronotal surface rugulose due to coarse reticulation and a coarse asperate punctuation. Legs very
long (see group summary); tibia of fore and middle legs longer than femur, tibia of hind legs shorter than femur; tarsi extremely slender. Abdomen generalized; broadest at fifth segment, tapering to an acute apex; dorsum flat; seventh tergite not striated. Abdomen smooth, shining; with sparse, inconspicuous pubescence. Length, 3 mm.

**SPECIES OF LABIDOCULEX REICHENSPERGER**

*antennalis* n. sp. Host: not known. **MEXICO:** Vera Cruz; Córdoaba.

*fragilis* Reichensperger, 1939, Rev. Ent., 6, p. 236, figs. 10–11; Borgmeier, 1958, Stud. Ent., 1, p. 230, fig. 4. Host: *Labidus praedator* F. Smith (Brazil and Argentina); *Labidus coecus* Latreille (Misiones, Argentina). **BRAZIL:** S. Catarina; Nova Teutonia. R. de J.; Itatiaia (Borgmeier). **ARGENTINA:** Chaco; Roque Saenz Pena (Borgmeier), and Misiones; Loreto (Borgmeier).

*validus* Borgmeier, 1958, Stud. Ent., 1, p. 230, figs. 5–6. Host: not known, probably *Labidus praedator sedulus*. **BOLIVIA:** Chaparé (2,000 meters); Yungas del Palmar.

**Labidoculex antennalis**, new species. Figure 28, D.

This species may be distinguished by form of head (fig. 28, D); extent of vertexal impression and its reticulation; finely faceted, moderate-sized eyes; sexually dimorphic antennae (see summary chart, p. 248), and proportions of hind tarsal segments.

Head form distinctive; vertexal impression shallow, not extensive, and with a relatively narrow area smooth and free from reticulation (in *fragilis*, the deeper fovea-like vertexal impression and its occipital continuation are smooth and free from the coarse reticulation of the head in general). Eyes finely faceted, moderate in size, and some distance from base (in *fragilis*, eyes coarsely faceted, very large, and close to base). Antennae sexually dimorphic; those of female similar to *fragilis*. Male antennae with segments 5–10 decreasing in length, but with terminal segment equal to segments 7–10 combined, and four times length of segment 10. In *fragilis*, antennae of both sexes with segments 5–10 subequal in length, and with terminal segment only as long as segments 9 and 10 combined and twice length of segment 10. First two segments of hind tarsus relatively short, tarsus only five-sixths as long as hind femur (in *fragilis*, hind tarsus equals hind femur in length). Length, 3 mm.

**Type** from Córdoba, Vera Cruz, Mexico, probably collected by A. Fenyes, but with host and date of collection unknown, in California Academy of Sciences. Three paratypes, in above institution and Chicago Natural History Museum. Host almost certainly a species of *Labidus*.

**Ecitonilla** Wasmann. Figure 28, H, I.


*Ecitonilla* and the following genus, *Ecitotyphlus*, are placed in this generic group with some reservations, nevertheless, they conform to
the general pattern of group characters. Their evolution was in a different direction from that of the preceding genera, and was not featured by extreme elongation of the appendages and by large eye size. The abdomens of these genera, which are appreciably narrowed at base and have deeply impressed tergites (and to a lesser extent sternites), are probably their most distinctive feature.

Head slightly (up to one-sixth) longer than broad; dorsum convex, not impressed; slightly arcuate sides converge to a prominent neck that is more than two-fifths as broad as head. Eyes small, finely faceted, only one-fifth as long as head. Antennae moderately long and stout almost three times head width); clavate scape subequal to two following segments combined; segments 4–10 transverse; proportions of antennal segments of socia and claviventris as follows: 22 : 12 : 10 : 8 : 10 : 11 : 11 : 11 : 11 : 20. Pronotum one-fifth longer than broad; broadest in apical half; sides sinuate to arcuate base, which is almost three-fourths as broad as maximum pronotal width. Pronotal disk flat, not impressed; dorsum deflexed laterad and not delimited from hypomera; base strongly margined. Elytra one-sixth longer than pronotum (sutural length is five-sixths pronotal length), subequal in width; lateral margins converge to apex which is only three-fourths maximum elytral width. Abdomen narrow at base; segments 5 and 6 somewhat broader and longer than other segments; segments 3–5 narrower at base than apex, segments 6–8 broader at base than apex. Tergites 3–5 deeply impressed at base, and with apical half strongly convex; sternites 3–5 impressed at base. Proportions of hind legs as follows: femur (86), tibia (84), tarsi (12, 8, 8, 7, 14). Length, 3 mm.

**SPECIES OF ECITONILLA WASMANN**


**Ecitotyphlus** Borgmeier. Figure 28, G.


*Ecitotyphlus* is distinguished from *Ecitonilla* by these features: absence of eyes, aptery, reduction in size of elytra (five-sixths as long as pronotum), absence of neck, shorter antennae (length only twice head width); abdominal segments 4 and 5 subequal in size, wider than 3 and 6 but not markedly so.

Head equal in length and width, almost circular in outline; dorsum evenly convex, not impressed; base straight, neck (if present) not visible from above;
antennae relatively apart. Eyes absent. Antennae relatively short (about twice head width), scape short, subequal to segments 2 and 3 combined; segments 3–10 transverse, incassate; relative lengths of segments: 16 : 9 : 6 : 5 : 5 : 5 : 6 : 6 : 6 : 12. Pronotum one-sixth longer than broad, narrower than head; broadest in apical half; sides converge to base which is about three-fifths maximum pronotal width. Pronotum convex, hypomera not delimited, dorsum slightly flattened but not impressed. Elytra abbreviated, shorter than pronotum, sutural length about three-fifths pronotal length; elytral apices conjointly emarginate. Apterous. Abdomen broadest at level of fourth and fifth segments, third segment broader at apex than base; 6 and 7 narrower at apex than base. Tergites 3–5 moderately deeply impressed at base; tergites convex; sternites 3 and 4 slightly impressed at base. Integuments with a vestiture of fine pale short hairs. Proportions of hind leg as follows: femur (50), tibia (46), tarsi (9, 6, 4, 5, 10). Length, 2 mm.; very slender.

**SPECIES OF ECITOTYPHLUS BORGMEIER**


**DINOCORYNA Group**

This is a newly organized group of a dozen genera of small species associated with *Neivamyrmex* and *Nomamyrmex*. Four subgroups seem to represent different phyletic series:

**DINOCORYNA series, with Neivamyrmex.**

*Dinocoryna* Casey (6 species in the United States).
*Typhlonusa* Borgmeier (1 species in Costa Rica).
*Ecitophrura* Reichensperger (2 species in Costa Rica and Brazil).
*Ecitoglossa* Borgmeier (4 species in Central America).

**ECITONIDIA series, with Neivamyrmex.**

*Ecitonidia* Wasmann (1 species in the United States).
*Gallardoia* Bruch (2 species in Argentina and Brazil).
*Ecitocryptodes*, n. gen. (1 species in Brazil).

**ECITOPHILETUS series, with Neivamyrmex.**

*Ecitophiletus* Borgmeier (1 species in Brazil).
*Dromacamatus* Bruch (2 species in Argentina and Costa Rica).

**WASMAWNINA series, with Nomamyrmex.**

*Wasmannina* Mann (3 species in Brazil, Bolivia, and Panama).
*Ecitoplectus* Borgmeier (1 species in Brazil).
*Ecitocryptus* Borgmeier (1 species in Brazil).
Dinocoryna is probably the most generalized genus of the group and the Dinocoryna and Ecitonidia series could have been derived from it. The positions of the other two series are not clear.

The most remarkable members of the Dinocoryna group are those with a myrmecoid facies and petiolate abdomen. I can only conclude that these interesting adaptive features evolved twice within this group—Ecitocryptus, with a two-segmented petiole, apparently stemmed from an Ecitoplectus-like ancestor in societies of Noma-myrmex, and Ecitocryptodes, with a one-segmented petiole, from a Gallerdoa-like ancestor in Neivamyrmex societies.

Dinocoryna Casey. Figure 29, A, B.


Dinocoryna is widely distributed in the southern United States and probably in northern Mexico as well. It may be replaced in the tropics by genera such as Ecitoglossa, Ecitophrura, and Typhlonusa.

Head subquadrate to one-fourth broader than long; lateral margins behind eyes arcuate or straight; neck one-half to three-fifths as broad as head; vertex not impressed except in carolinensis. Eyes variable in size and convexity (distance from base of head varying from three-fourths eye length to one and one-third eye length). Antennae robust; segments 4–10 cylindrical, slightly transverse, and almost uniform in size; segments compactly arranged (pedicels invisible). Head punctation variable, with fine to coarse umbilicate punctures or “rosette” umbilical punctures. Pronotum one-fifth broader than long or less; apex feebly to strongly bisinuate. Pronotum either not impressed, or with a broad shallow or narrower deeper impression. Elytra generalized. Abdomen generalized, as broad as elytra at base and tapering to an acute apex; with a conspicuous vestiture of long fine hairs, especially on the sternites. Legs long, usually without noteworthy features; in tibalis with compressed hind tibiae and tarsi. Length, 1.8–3 mm.

SPECIES OF DINOCORYNA CASEY

akrai, n. sp. Host: Neivamyrmex carolinensis Emery. KANSAS: Riley Co.


A KEY TO THE SPECIES OF DINOCORYNA CASEY

1. Head with a shallow impression medial to each eye; eyes one and three-fourths eye length from base of head; head, pronotum, and elytra with very coarse "rosette type" umbilicate punctures.......................... carolinensis
   Head not impressed; eyes less than the above distance from base of head; head, pronotum, and elytra with fine to coarse (non-rosette) umbilicate punctures..................................................2
2. Pronotum without median impression; head subequal in length and width;..................3
   Pronotum with a median impression; head one-tenth to two-fifths broader than long; hind tibiae never compressed.................................4
3. Hind tibiae almost as broad as femora and strongly compressed; pronotum one-fourth broader than long..........................tibialis
   Hind tibiae cylindrical; pronotum one-sixth broader than long................akrei
4. Pronotal apex strongly bisinuate; pronotum at least two-fifths broader than long; head at least one-fifth broader than long........................................bisanuata
   Pronotal apex feebly bisinuate; pronotum about one-third broader than long; head less than one-fifth broader than long..............................5
5. Antennal segments 4–10 slightly transverse, nearly uniform in size, not increasing in length or width distally............................arizonensis
   Antennal segments 4–10 increasing in length and width, the tenth about one-third longer and broader than fourth segment..........................schmitti

Dinocoryna akrei, new species.

Probably most closely related to tibialis from which it is differentiated by the characters of the key.

Light chocolate-brown; antennae and legs paler. Head subequal in length and width (including eyes). Head not impressed; clypeus in front of antennal level convex medially; occipital border emarginate medially; sides almost parallel behind eyes. Eyes moderately large and convex, about one and one-sixth eye length from base of head. Integuments not reticulated. Head with coarse setigerous umbilicate punctures (often slightly elongated), each half of vertex with about 16, and the sides of head with an additional 10 or more, more closely arranged. Antennae typical of the genus; robust, segments 4–10 transverse but not incrassate. Pronotum about one-sixth broader than long; without a median impression; apex moderately bisinuate; pronotum broadest in front of middle, the sides converging basally and continuous with the rounded basal angles and arcuate base. Pronotum with sparsely arranged, coarsely umbilicate punctures (20–25 smaller, more densely arranged punctures near apical border, and each half of remainder of dorsum with about 20–25 punctures). Pronotum with relatively few long erect setae (one near each basal angle). Elytra distinctive in its smoothness and paucity of setigerous punctures (elytra, metasternum and sides of thorax almost impunctate and glabrous). Tergites 3–5 with moderately dense punctuation and short recumbent hairs. Punctuation of sixth tergite sparser, and that of stergites 7 and 8 almost absent. Tergites with relatively few long erect setae; sterna with the usual vestiture of long fine setae. Length, 1.8 mm.
Type from Riley County, Kansas, collected April 17, 1962, by Roger D. Akre. Host: Neivamyrmex carolinensis Emery (colony E-273).


Typhlonusa Borgmeier


Typhlonusa opacicornis is essentially an eyeless species of Dinocoryna and might well be placed in that genus. In the key to the species of Dinocoryna, this species is closest to D. bisinuata from which it may be distinguished by these characters: absence of eyes, more transverse head and pronotum, shorter elytra, distinctive pronotal form, less compact antennae, and a more acutely tapered abdomen.

Head one-half broader than long; clypeus deflexed; sides of head strongly arcuate. Eyes absent. Antennae about as long as head, pronotum, and elytra combined; segments 4–10 subcylindrical but not compactly arranged, their pedicels visible; segments 4–10 slightly transverse and slightly incrassate. Pronotum three-fifths broader than long; dorsum with a very shallow, moderately broad impression; apex bisinuate; pronotum broadest near apex, the sides converging strongly and almost arcuate with the base; basal angles obsolescent. Elytra subequal in length to pronotum, their sutural length only about two-thirds pronotal length. Abdomen as wide at base as elytra, tapering to a slender apex. Integuments smooth, shining, without reticulation; punctures fine and sparse. Sternites with a vestiture of long, fine setae. Length, 2 mm.

SPECIES OF TYPHLONUSA BORGMEIER


Ecitoglossa Borgmeier. Figure 29, C.


Borgmeier (1958) did not attempt to place Ecitoglossa but there is no doubt that it is closely related to Dinocoryna. This is a Neotropical genus recorded from Costa Rica and Panama, while Dinocoryna
is Nearctic in distribution. The following diagnostic characters separate the two genera:

Pronotum longer than broad, its median sulcus in the form of an inverted drop; pronotal apex arcuate, and its sides subparallel. .................. *Ecitoglossa*

Pronotum broader than long, its median impression shallow and not drop-shaped; pronotal apex bisinuate, its sides not subparallel. .................. *Dinocoryna*

Head subequal in length and width or slightly longer than broad, with a broad, moderately long neck; clypeus carinate; dorsum with a shallow impression: sides subparallel (somewhat arcuate in *antennalis*); base slightly to moderately deeply emarginate. Eyes small to very large (one-fourth to one-half as long as head); distance from base of head variable—less than eye length to three times eye length. Antennae geniculate, robust, segments 4–10 cylindrical, slightly incrassate. Pronotum longer than broad; diskal impression distinctive in form, that of an inverted drop; base and apex subequal, sides slightly constricted in basal half; base and apex arcuate. Elytra generalized, longer than pronotum. Abdomen broadest at fourth segment, apical segments tapering. Abdominal chaetotaxy as in *Dinocoryna*. Length, 3–4 mm.

**SPECIES OF ECITOGLOSSA BORGMEIER**

*antennalis* n. sp. Host: *Neivamyrmex pilosus* F. Smith. PANAMA: Barro Colorado Island.


**KEY TO THE SPECIES OF ECITOGLOSSA BORGMEIER**

1. Eyes small (about one-fourth head length), distance from base of head three times eye length; base of head moderately deeply emarginate; third antennal segment three times as long as second and three-fourths as long as scape. *quadriceps*

   Eyes one-third to one-half head length (distance from base of head no more than twice eye length); base of head shallowly emarginate; third antennal segment not more than twice as long as second and about three-fifths as long as scape. .................. 2

2. Eyes large, one-half as long as head (less than eye length from base of head).

   *canaliculata*

   Eyes small, one-third as long as head (somewhat more than eye length from base of head). .................. 3

3. Antennal scape longer than segments 2, 3, and 4 combined, four times as long as segment 2, and six times as long as 4; sides of head not subparallel. *antennalis*

   Antennal scape equal to segments 2 and 3 combined, three times as long as segment 2, and three and one-half times as long as 4; sides of head subparallel. .................. *foveicollis*

**Remarks.**—Proportions of the antennal segments vary in the different species of *Ecitoglossa* as follows:

Ecitoglossa antennalis, new species. Figure 29, C.

Integuments shining, not reticulate. Head sparsely punctate in basal half, more densely so between eyes. Pronotum umbilicately punctate and with finer punctures in the intervals. Elytra very sparsely punctate (only the setigerous punctures of the long setae present). Tergites 3 and 4 with a subapical row of 6 setae (apical row in foveicollis; two rows of long setae in canalicularata), and an additional pair of sub-basal setae on each side; tergites with a pale pubescence. Tergites 5 and 6 with about 6 setae in an apical row, and several sub-basal setae; tergite 7 with three rows of about 6 setae each. Head subequal in length and width. Eyes small (one-third head length), one and a half times eye length from base of head. Vertex shallowly impressed, sides of head arcuate; base slightly emarginate. Antennae distinctive; proportions of segments as in preceding summary; segments 2–5 relatively small. Length, 3 mm.

Type from Barro Colorado Island, Panama Canal Zone; collected July 23, 1956 by Carl W. Rettenmeyer; with Neivamyrmex pilosus F. Smith. In collection of Chicago Natural History Museum. No paratypes.

Ecitophrura Reichensperger. Figure 29, D.


_Ecitophrura_ is closely related to _Dinocoryna_ and not easily differentiated from it. _Ecitophrura capito_, the type species, may be characterized as follows:

Head about one-fifth broader than long; vertex with a broad, moderately deep concavity; clypeus not deflexed, transversely convex, and almost obscuring the vertical labrum; margins behind eyes continuously arcuate with the base. Eyes about one-third as long as head. Antennae long, moderately robust; segments 4–10 cylindrical, compactly arranged, the pedicels not visible. Pronotum subequal in length and width; dorsum with a very shallow median impression and a shorter, deeper, more conspicuous impression on each side; pronotum broadest subapically, sides bisinuate, apex bisinuate, base strongly arcuate. Abdomen and legs generalized. Head finely and sparsely punctate; pronotum with a moderate number of small umbilicate punctures; elytra finely and moderately punctate. Head and thorax without reticulation; that of abdomen obsolescent. Abdomen with a moderate vestiture of long setae on sternites. Length, 2.5 mm.

_Ecitophrura reichenspergeri_ differs from _capito_ in these respects: Head about one-sixth broader than long; vertex with a relatively broad, long, and deep concavity, almost crateriform; clypeus moderately declivous; labrum horizontal, fully
visible. Eyes not much more than one-fourth as long as head. Antennae similar to those of capito, except that the terminal segment is only four-fifths as long as segments 9 and 10 combined (in capito, the terminal segment is one-fifth longer than segments 9 and 10 combined). Pronotum strongly transverse, two-fifths broader than long; dorsum with a broad, deep, median concavity—about two-fifths as broad as pronotum and almost as long, and a small, shallow, subapical impression on each side; pronotum broadest near apex, apex broadly emarginate, sides strongly convergent, base moderately arcuate. Head and pronotum, except medially, reticulated; elytra and abdomen not so.

SPECIES OF ECITOPHRURA REICHENSPERGER

ECITONIDIA Subgroup

Differing from the three preceding genera (Dinocoryna, Ecitoglossa, and Ecitophrura) in having a narrow, very deep, pronotal sulcus (fig. 29, E), Ecitonidia, Gallardoia, and Ecitocryptodes are of the same phyletic line which probably stemmed from a Dinocoryna-like ancestor. The most noteworthy feature of the three genera is the abdomen and its degree of specialization. The abdomen of Ecitonidia is generalized; that of Gallardoia is incipiently to distinctly subpetiolate, and that of Ecitocryptodes is strongly petiolate. Gallardoia bucki has the sternites of the third and fourth abdominal segments deeply constricted at the base (fig. 29, G) but the third segment is not narrower than usual; Gallardoia argentina, by contrast, has a parallel-sided third segment that is distinctly slenderized, and the remainder of the abdomen subovoidal. Ecitocryptodes, n. g. (fig. 29, F) is a remarkable myrmecoid genus with a very slender one-segmented petiole. All genera of the subgroup occur with Neiva-

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*myrmex.* *Ecitonididae* is recorded from the southern United States (west of the Mississippi River) and the other two genera are known only from southern Brazil and Argentina. It is not likely that almost the entire Neotropical Region is unoccupied by this subgroup, but only more extensive collecting can determine the ranges.

**Ecitonididae** Wasmann. Figure 29, E.


Head with numerous large, rosette-type umbilicate punctures that are partially obscured by a coarse reticulation. Intervals between the large umbilicate punctures of the pronotum smooth or with irregular reticulation. Elytra coarsely reticulated, the punctures poorly delimited. Tergites and sternites of third and fourth abdominal segments coarsely reticulate and punctulate; the remainder of abdomen almost smooth. Sternites with a *Dinocoryna*-like vestiture of long fine setae. Head one-sixth longer than broad; sides slightly arcuate, base slightly emarginate; vertex with a narrow shallow impression. Eyes about one-third as long as head, finely faceted, and moderately convex. Antennae robust; the relative length of segments as follows: 30 : 8 : 14 : 12 : 12 : 12 : 27; segments 4–10 cylindrical. Pronotum with a very deep median sulcus; apex almost straight; sides moderately arcuate and continuous with strongly arcuate base; basal angles obsolete. Sides of elytra subparallel; apex as broad as base. Scutellum not sulcate. Wings present. Abdomen generalized; third segment not distinctly narrower than the following segments and its sides not parallel; third tergite moderately impressed at base, the fourth tergite very shallowly impressed at most; third and fourth sternites not impressed nor constricted at base. Length, 2.5–3 mm.

**SPECIES OF ECITONIDIA WASMANN**


**Gallardoia** Bruch. Figure 29, G, H.

*Gallardoia* Bruch, 1924, Physis, 7, p. 257. Type species: *Gallardoia argentina* Bruch.

*Gallardoia* is distinguished by characters listed in the key to the genera of the tribe and in the introduction to this subgroup.

**SPECIES OF GALLARDOIA BRUCH**


A diagnostic key to the two species follows:

Third abdominal segment with parallel sides and thus more slender than the following segments which combined are somewhat ovoidal in form; elytral sides converging apically, the apex of the elytra narrower than the base (fig. 29, G); head one-fourth longer than broad; non-rosette umbilical punctures of head small; proportional lengths of antennal segments as follows: 21 : 8 : 10 : 8 : 8 : 10 : 10 : 8 : 8 : 16; scape more than twice as long as segment 2; segments 9 and 10 subequal; segments 4, 5, 9, and 10 subequal and slightly shorter than 6, 7, and 8; basal impressions of tergites 3 and 4 with a median carina; scutellum faintly sulcate.

Third abdominal segment not as above, its sides not parallel; elytral sides not converging apically; head about one-third longer than broad; umbilicate (rosette-type) punctures of head moderately large; proportional lengths of antennal segments as follows: 18 : 10 : 13 : 10 : 10 : 10 : 10 : 10 : 8 : 14; scape less than twice as long as segment 2; segment 10 shorter than 9; segments 4–9 subequal in length; basal impressions of tergites 3 and 4 without a median carina; scutellum sulcate.

Gallardoia bucki, new species. Figure 29, G.

Head, pronotum, elytra, metasternum, and third sternite with medium-sized umbilicate punctures (rosette-type to some degree)—punctuation of head sparse, especially medially, that of pronotum slightly more dense, and that of elytra considerably more dense. Integuments generally smooth, not reticulate except for scutellum and tergites 2 and 3. Head and thorax hairy, with numerous short and long setae; setae of tergites largely restricted to apical rows; sternites with numerous long, well scattered setae. Head about one-third longer than broad, excluding neck and labrum; clypeus long, transversely convex; vertex with a very shallow impression; sides straight behind eyes and then arcuate to shallowly emarginate base. Eyes about one-third as long as head. Antennae robust (proportions in diagnosis), scape less than twice as long as segment 2; segments 4–10 cylindrical; segments 4–9 subequal. Pronotum subequal in length and width; with a deep median sulcus about three-fifths pronotal length; apex moderately arcuate; pronotum broadest near apex, its sides converging moderately to the rounded angles; base slightly arcuate. Scutellum sulcate. Elytra generalized, their sides almost straight, converging slightly near apex; apices almost straight. Abdomen generalized in appearance; third and fourth tergites deeply impressed at base, the impressions not carinate. Third and fourth sternites moderately to deeply constricted at base. Length, 2.75–3 mm.; width, 0.6–0.75 mm.


Remarks.—Dr. Borgmeier has long recognized this species as new and sent me a specimen that he had set aside as the type (evidently from the same series as the material in the Bernhauer collection).

Ecitocryptodes, new genus. Figure 29, F.

Type species: Ecitocryptodes petiolarus, n. sp.

Ecitocryptodes is distinguished from Gallardoia by a myrmecoid abdomen with a very slender one-segmented petiole (fig. 29, F), a
longer and more slender head; elytra that taper to a relatively slender apex, emarginate elytral apex, and smaller size (2.1 mm. in length). This genus was probably derived from a Gallardoia-like ancestor as evidenced by the fact that G. argentina exhibits some of the specialized features of Ecitocryptodes in a more moderate fashion. The type of this genus, E. petiolatus, was evidently collected from the same colony of Neivamyrmex hetschkoi as Gallardoia bucki, n. sp. On first consideration, it was thought that the two kinds of individuals might be sexual forms of the same species, but more detailed analysis revealed that the two species differ in a number of important respects. In fact, the series of E. petiolatus contains both sexes, and is more closely allied to G. argentina than to G. bucki.

It might be suspected that Ecitocryptodes is closely allied to the Brazilian genus Ecitocryptus Borgmeier because the latter genus has a myrmecoid abdomen with a two-segmented petiole. In my opinion, the resemblance is superficial, and Ecitocryptus belongs to a different phyletic line that differentiated in societies of Nomamyrmex.

Head two-fifths longer than broad, excluding neck and labrum; clypeus feebly convex. Eyes a little less than one-third as long as head. Antennae as in Gallardoia. Pronotum subequal in length and width; apex arcuate; sides converging basally, the basal angles distinct; base almost straight. Scutellum broadly and very shallowly sulcate. Lateral margins of elytra converging strongly to the apex which is only three-fifths as broad as base; apex of elytra with a pronounced V-shaped emargination. Abdomen petiolate; segments two and three very slender, and the distal segments forming a swollen ovoidal "gaster"; third tergite with an impression on each side; fourth tergite with a V-shaped impression.

Ecitocryptodes petiolatus, new species. Figure 29, F.

Coloration testaceous, abdomen a little paler than foreparts. Except for third tergite, body not reticulated. Head, pronotum, and elytra with small umbilicate punctures that increase in density from head to elytra. Sternites with a Dinocoryna-like vestiture of long fine setae. Antennae with segments 4–10 subcylindrical; relative lengths of segments as follows: 16 : 6 : 8 : 8 : 7 : 8 : 8 : 8 : 8 : 9 : 12. Form very slender; length, 2.1–2.2 mm.; width, 0.5–0.65 mm.


ECITOPHILETUS Subgroup

Ecitophiletus Borgmeier. Figure 29, I.

Ecitophiletus and the following genus, Dromacamatus, represent a distinct phyletic series in the Myrmedoniini. Whether or not they should be in the Dinocoryna group is questionable. In contrast to the other genera of the group, these two genera have attenuated bodies—pronotum, elytra, metasternum and abdomen—and long appendages; large eyes; abdomen broadest at apex of third or fourth segments and somewhat ellipsoidal in form; the abdomen relatively slender at the base tapered to a slender apex; coxae exceptionally long; mesocoxae narrowly separated; mesoxcoxal acetabula weakly delimited; metasternum strongly convex.

Head, including eyes, one-third broader than long; width of head at base of eyes less than head length; antennal fossae deep; clypeus long, transversely convex; head with a moderately deep, oval vertexal impression, and a shallow occipital impression that is continuous with a moderate basal emargination; neck as broad as head. Eyes extremely large and convex (three-fifths as long and one-fourth as broad as head); moderately coarsely faceted. Antennae relatively long, four times head length; less robust than in the Dinocoryna group in general; all segments elongated; 3–11 subcylindrical. Pronotum slightly broader than long; broadest subapically; sides bisinuate, converging strongly, the base less than three-fifths as broad as maximum pronotal width; base almost straight, apex slightly bisinuate; dorsum deflexed laterad, the hypomera poorly delimited. Pronotum with a deep median sulcus (as deep as in some other genera of the Dinocoryna group, but with oblique, rather than vertical, sides). Elytra long, sutureal length greater than pronotal length; apex with a broad V-shaped emargination. Meso- and metathorax exceptionally long; meso- and metasternum relatively slender, the latter elongated and very convex; mesoxcoxal acetabula elongated, weakly margined, and narrowly separated; meso- and metasternal processes unusually slender for the tribe Myrmex. Procoxae and mesocoxae long and spindle-shaped; metacoxae long, sub-triangular in form. Abdomen exceptionally long; second tergite elongated; fourth and fifth segments especially long; third and fourth tergites deeply impressed at base. Third sternite expansive; with two deep, oval impressions, to receive hind coxae, in basal half; strongly convex apically; apical border deeply emarginate. Fourth sternite very deeply constricted at base. Legs very long and slender; without notable features. Length, 3.8–5.6 mm.; width, 0.7–0.9 mm.

SPECIES OF ECITOPHILETUS BORGMEIER


Dromacamatus Bruch


*Dromacamatus caviceps* Bruch (the only species available) differs from *Ecitophiletus* in these respects: Head subequal in length and width; clypeus produced medially as a moderately long cornate process; vertexal impression deeper and basal emargination more pronounced than in *Ecitophiletus*; postgenae more prominent; eyes moderate in size (two-fifths as long and less than one-fifth as broad as
head); pronotum one-fifth longer than broad; pronotum broadest at apex, sides sinuate, converging strongly, the base two-thirds as broad as maximum width; pronotum with a small and much less well-defined impression than in Ecitophiletus; elytral sutural length less than pronotal length; abdomen similar to that of Ecitophiletus but broadest at apex of fourth segment and narrower at base; fourth tergite scarcely impressed; third sternite without deep impressions near hind coxae and fourth sternite not constricted at base.

SPECIES OF DROMACAMATUS BRUCH


spinifer Reichensperger, 1936, Rev. Ent., 6, p. 233, pl. 1, fig. 2. Host: Neivamymex cristatum André. COSTA RICA: Hamburgfarm.

WASMANINNA-ECITOCRYPTUS Subgroup

Three genera associated with Nomamyrmex apparently represent a phyletic series within the Dinocoryna group, although their exact position in the group is not clear at this time. Due primarily to the deeply sulcate pronotum, they resemble Ecitonidia and allies, but whether or not they stemmed from the same stock is conjectural. Members of the group are robust, and notable for abdominal specializations.

The Wasmannina abdomen is the most generalized of the series. It is non-petiolate and has a subellipsoidal form, with a very strongly convex venter and a less convex dorsum. The abdomen of Ecitoplectus has deeply impressed third, fourth, and fifth tergites, and somewhat constricted third and fourth sternites. Ecitocryptus attains the most specialized condition of all—the third and fourth segments are much more slender than the following segments and constitute a definite two-segmented petiole.

Due primarily to inadequate material for study, placement of some specimens belonging to this series has been difficult. Borgmeier (1931a) tentatively assigned some specimens with non-petiolate abdomens to Ecitocryptus sulcatus and suggested the possibility that it may be a sexually dimorphic species. Evidence for this is lacking.

Wasmannina Mann. Figure 29, J.


Within the Dinocoryna group, Wasmannina is distinguished by its robust form; robust, deeply sulcate pronotum; reticulated (granulose appearing) integuments; and ellipsoidal abdomen (it is not petiolar and its tergites and sternites are not impressed).

Mann was not able to place Wasmannina in an aleocharine tribe and in catalogs (Blackwelder, 1944; Borgmeier, 1949) it is listed as "incertae sedis." Borgmeier's Ecitochlamys comes is doubtless congeneric with W. trapezicollis.

Integuments with a fine-meshed, raised reticulation. Head a little broader than long, robust; the stout neck about half as broad as head; antennae inserted under a vertexal arcade; clypeus with a long slender carina; sides of head broadly arcuate; basal border narrowly emarginate; vertex with a shallow impression; eyes one-third as long as head. Antennae very stout; segments subcylindrical, distal segment slightly compressed, the terminal one more so. Pronotum stout, slightly longer than broad; broadest subapically; sides converging evenly to the very arcuate base; apex straight or with a median process; disk with a very deep median sulcus. Abdomen ovoidal to scaphoidal; otherwise generalized. Length, 4-7 mm.

**SPECIES OF WASMANNINA MANN**


isthmiana n. sp. Host: Nomamyrmex esenbecki crassicornis F. Smith. PANAMA: Barro Colorado Island.


**Wasmannina isthmiana**, new species. Figure 29, J.

This new Panamanian species differs from trapezicollis in these respects: apical margin of pronotum almost transverse (broadly produced in trapezicollis); pronotum with an impression medial to each basal angle (impressions absent in trapezicollis); pronotal sulcus broader and uniformly V-shaped in cross-section; vertexal impression deeper; apical elytral emargination shallower, occipital emargination deeper, third antennal segment almost as long as broad (two-thirds as long as broad in trapezicollis), and antennal segments 4-8 usually more than three-fourths as long as broad (segments 4-9 only one-half to three-fifths as long as broad in trapezicollis). I did not examine the type of comes, but Dr. Borgmeier, to whom I sent specimens of isthmiana, assures me that the two species are different. Specific details, however, are lacking.

Coloration rufo-piceous. Integuments with a close-meshed, raised reticulation and appearing granulose. Head slightly broader than long; clypeus declivous, with a low median carina; vertex with a shallow pit; sides of head subparallel; basal angles nearly distinct; base arcuate but with a medial emargination; neck stout,
about half as broad as head. Antennal segments of these relative lengths: 40 : 14 : 20 : 14 : 12 : 14 : 16 : 20 : 26 : 32; basal segment clavate; segment 3 obtape-zoidal; segments 3–10 subcylindrical, except 8–10 distinctly compressed; segments 4–10 transverse (many segments are not uniform in length, being longer on one side than the other). Pronotum a little longer than broad; apex straight; broadest subapically, sides converging evenly to the arcuate base; basal angles distinct; disk with a deep median sulcus and with an impression near each basal angle. Scutellum sulcate. Elytra apex emarginate. Legs stout, tarsi very strongly compressed. Sternites with a conspicuous vestiture of long setae and finer recumbent hairs. Abdomen without noteworthy features. Length, 4.2–7 mm.; width, 0.9–1.4 mm.

_Type_ from Barro Colorado Island, Panama Canal Zone, collected May 18, 1956, by Carl W. Rettenmeyer, from an emigrating colony of _Nomamyrmex esenbecki crassicornis_ F. Smith. In Chicago Natural History Museum.

_Paratypes._—36 specimens, same data as type. Some retained by Chicago Natural History Museum and some returned to Dr. Rettenmeyer (a series will be deposited in the Snow Entomological Museum, University of Kansas).

_Ecitoplectus_ Borgmeier

_Ecitoplectus_ Borgmeier, 1931, Rev. Ent., 1, p. 364. Type species: _Ecitoplectus transiens_ Borgmeier.

Modifications of the abdomen of _Ecitoplectus_ differentiate it from _Wasmannina_. The tergites and sternites of the third, fourth and fifth abdominal segments are deeply impressed at the base, and the paratergites of these segments are produced mesad above the tergal impressions.

Integuments with a very fine-meshed reticulation. Head, excluding labrum and neck, about one-fourth broader than long; dorsum not impressed. Eyes moderate in size. Antennae stout, segments 4–10 transverse. Pronotum robust, very slightly less transverse than head; subequal in length and width; thick dorso-ventrally, the sides moderately inflexed; hypomera not delimited. Pronotal sulcus long and deep; pronotum broadest subapically, the arcuate sides converging strongly to the base which is only about two-thirds the maximum pronotal width; base with a strong arcuate medial production. Elytra large, narrowest at humeri, the lateral margins diverging caudally to the broadest (subapical) level. Legs only moderately stout, the tarsi compressed. Abdomen subellipsoidal; fifth segment longer than any of the others; third, fourth, and fifth tergites very deeply impressed; paratergites adjacent to the tergal impressions extended medially above the impressions as triangular processes. Third, fourth, and fifth sternites deeply constricted at base. Length, 5 mm.

**SPECIES OF ECITOPECTUS BORGMEIER**

_transiens_ Borgmeier, 1931, Rev. Ent., 1, p. 364, fig. 14; 1949, Rev. Ent., 20, p. 114 (locality and host). Host: _Nomamyrmex schlechtendali_ Mayr. **BRAZIL:** Goiás; Campinas.
Ecitocryptus Borgmeier


This genus and Ecitocryptodes are the only known myrmecoid genera of Myrmedoniini with distinct petiolate abdomens. Ecitocryptus is readily differentiated from all myrmedoniine ecitophiles by its two-segmented abdominal petiole.

Head transverse, one-sixth broader than long. Pronotum almost one-sixth longer than broad, broadest in front of middle, the side margins converging strongly to the base; base very strongly bisinuate; sulcus long, moderately broad and deep. Elytra broadest in basal half, the lateral margins converging in the apical half to the relatively narrow apex. Third and fourth abdominal segments forming a slender petiole, the sides of which are subparallel; the third and fourth tergites, except for a basal area, strongly convex; third sternite impressed about midway between base and apex, fourth and fifth sternites impressed at base; fifth and remaining apical segments for an ovoidal “gaster” with very convex sternites and tergites. Length, 4.2 mm.

SPECIES OF ECITOCRYPTUS BORGMEIER


(?) inopinatus Borgmeier, 1931, Rev. Ent., 1, p. 363, fig. 13. Host: Nomamyrmex schlechtendali Mayr. BRAZIL: Goiás; Campinas.

Remarks.—Two species assigned by Borgmeier to this genus probably identified as the female of sulcatus (1931, Rev. Ent., 1, p. 363, fig. 11). Neither of these species have petiolate abdomens and may belong to Ecitoplectus or an undescribed genus. It seems to me unlikely that Ecitocryptus is a dimorphic species with both petiolate and non-petiolate individuals (a very similar case occurs in the Ecitonidia series and involves the non-petiolate Gallardoia and the petiolate Ecitocryptodes).

ECITOSIUS Group

This group of Myrmedoniini comprises two new genera of exceptional interest. They are part of a fine collection of ectophiles received from Roger D. Akre after the monograph had been completed and submitted for publication. In Costa Rica Mr. Akre was able to search colonies of Neivamyrmex sumichrasti Norton for ectophiles—none having been reported with this host—and to discover a distinctive fauna.

Because of their myrmecoid facies, Ecitosius and Ecitotima are among the most unusual members of the tribe Myrmedoniini. Rec-
ognizable as members of this tribe by characteristic maxillae, long broad, metasternal process between margined acetabula, and aedeagal structure, they depart notably from the tribe's more generalized species in having cylindrical hind coxae, a distinctive integumental sculpture, and myrmecoid abdomens. *Ecitosius* is noteworthy for its petiolate, myrmecoid abdomen, and *Ecitotina* for the long abdominal process that projects cephalad beneath the thorax.


Type species: *Ecitosius gracilis*, new species.

Myrmecoid in facies, with a petiolate abdomen (fig. 36, A). Head and thorax with a coarse texture, resulting from numerous shallow setigerous impressions and elevated intervals with a coarse-meshed reticulation. Abdomen smooth, shining, faintly reticulate, and bristling with long fine setae. Head slender to robust, vertex sulcate, and the clypeus produced slightly (*robustus*) or as a long, acute rostrum (*gracilis*). Antennae robust (fig. 36, A). Gula, submentum, mentum, and mouthparts as illustrated (fig. 36, G). Maxillae with elongated galea and lacinia (fig. 36, D), as typical of the tribe. The large prosternum with a strong T-shaped carina. The strongly convex pronotum only about two-thirds as broad as long; hypomera poorly delimited; dorsum deeply impressed as illustrated (fig. 36, A, C). Scutellum with a median impression. Elytra slightly longer than pronotum, the sutural length about three-fourths that of pronotum; apical margins strongly oblique. Elytra individually convex, a narrow median area depressed; elytra broadest at humeral level, the sides converging moderately to apex. Mesosternal process broad and short; metasternal process broad and long between the middle coxae. Mesocoxal acetabula margined. Metasternum strongly convex. Hind coxae distinctive, subcylindrical in form (fig. 36, A, C). Abdomen myrmecoid, the basal half of third segment forming a petiole, the remainder of abdomen in the form of an ovoid "gaster" (fig. 36, A, B). Second tergite prominent. Basal half of third segment slender, apical half enlarged; third tergite slender basally (fig. 36, B) and expanding to twice the width in apical half. The third sternite with a deep impression on each side near the base to receive the hind coxae; the expanded apical half delimited from slender basal portion by a sulcus (fig. 36, A, C). The ovoid, myrmecoid "gaster" composed of slightly convex tergites and extremely large convex sternites. The ovoid abdomen of the female somewhat larger than that of the male. Legs long and slender. Tarsi 4, 5, 5-segmented. Aedeagus as in fig. 37, F, G.

**Ecitosius gracilis**, new species. Figures 36, A, B, G and 37, F.

Reddish-brown; abdomen somewhat paler. Integumental texture of head and thorax coarse; abdominal reticulation of third segment obsolescent, but progressively stronger and more finely meshed on the following segments. Head slender, only a little more than one-half as broad as long (fig. 36, G); apical half of vertex with a moderately deep, broad median sulcus which extends on to the clypeal declivity. Clypeus produced as a rostrum (fig. 36, A) projecting above the ante-clypeus and labrum; rostrum moderately broad but in profile acutely angulate.
Eyes moderate in size, three times their length from base of head. Antennae as in fig. 36, A. Median lobe and paramere of aedeagus as in fig. 36, F. Length, 3.5 mm.


Paratypes.—25 specimens, same data as the type (17 collected by R. D. Akre, and 8 by C. W. and M. E. Rettenmeyer). Some paratypes retained in Chicago Natural History Museum, and others returned to R. D. Akre and C. W. Rettenmeyer.

Ecitosius robustus, new species. Figures 36, C, D, E, H and 37, G, H.

Distinguished from gracilis by its larger size and more robust form, much broader head, absence of an acute clypeal rostrum, distinctive vertexal impressions, more robust mandibles and antennae, and rougher integumental texture.

Head, pronotum, and elytra rufo-piceous; abdomen and other areas reddish-brown. Integuments of head and thorax coarsely textured, the elytra especially rugose (the nature of the setigerous pits and the reticulation shown in fig. 37, H). Head about nine-tenths as broad as long; vertex with a shallow median sulcus in basal half, a small pit in front of sulcus, and a moderately deep impression between the antennal insertions. Clypeus broadly convex and produced slightly over ante-clypeus, but not prolonged as an acute rostrum. Eyes small in proportion to size of head, located about three times their length from base of head. Antennae as in gracilis, but more robust. Mandibles very stout. Pronotum impressed as in fig. 36, C; side margins strongly bisinuate (in dorsal view), the pronotum broadest in front of middle, and narrowing to only five-sixths as broad near base. Abdomen similar in form to that of gracilis. Median lobe of aedeagus as in fig. 37, G. Length, 5 mm.


Paratypes.—19, same locality as type, collected February 13–22, 1963, from two colonies of N. sumichrasti (E-294, E-304).

Ecitotima, new genus. Figure 36, F.

Type species: Ecitotima miriventris, new species.

Allied to Ecitosius, and particularly to Ecitosius gracilis. The head and thorax of Ecitotima are very similar to those of Ecitosius
gracilis (even to the presence of a clypeal rostrum), but the abdomen is remarkably distinctive. The abdomen is slightly ovoid but not petiolate and myrmecoid as in Ecitosius, and bears on its ventral surface a long cylindrical process (fig. 36, F) which extends cephalad as far as the prosternum (compare with Diploeciton of the Dorylo-mimini, fig. 24, C). The setigerous pits which contribute to the coarse integumental sculpture of this generic group occur on the abdomen in Ecitotima but not in Ecitosius.

Head long and slender, two-thirds as broad as long (almost as illustrated for Ecitosius gracilis); vertex with a broad, oval impression in anterior half, and somewhat convex in basal half; clypeus with an acute rostrum. Eyes moderate in size and prominently convex; only twice their length from base of head. Prosternum with a T-shaped carina. Pronotum slightly more than three-fourths as broad as long, impressed as in fig. 36, F. Elytra as long as pronotum, individually convex as in Ecitosius. Abdomen slightly oval in outline above, the third segment not constricted basally to form a petiole; tergites 3–6 about equal in length and moderately convex; the sternites of the third and fourth segments produced in combination to form a long filiform process extending beneath the thorax (fig. 36, F).

Ecitotima miriventris, new species. Figure 36, F.

Head, pronotum, elytra, antennae and legs (in part) rufo-piceous; abdomen light-brown. The coarse integumental sculpture of setigerous pits and raised intervals present on abdomen as well as head and thorax. Abdomen with long fine setae, sparsely arranged (less numerous than in Ecitosius). Length, 2.8–3 mm.


Paratypes.—Five specimens, same data as type.

Old World Dorylophilous Groups of Myrmedoniini

**DRUSILLA** Group

*Zyras* Stephens, s. l. Host: *Dorylus* (Anomma)

**MYRMECHUSA** Group (Ethiopian Region)

*Gapia* Blackwelder (=*Acanthonia* Wasmann) Host: *Dorylus* (Anomma)

*Myrmechusa* Wasmann Host: *Dorylus* (Anomma)

*Myrmechusina* Cameron Host: *Dorylus* (Anomma)

*Trichodonia* Wasmann Host: *Dorylus* (Anomma)

**OCYPLANUS** Group (Ethiopian Region)

*Anepipleuronia* Bernhauer Host: *Dorylus* (Anomma)

*Astilbides* Wasmann Host: *Dorylus* (Anomma)
Numerous species of Myrmedoniini have been recorded in association with army ants in Africa but only three have so far been found in the Oriental Region. In most cases the African species were with *Dorylus (Anomma)*, although a few were associated with *Aenictus*, as were all of the Oriental species. The Myrmedoniini that occur in *Anomma* societies, or in close proximity to them, may be placed in four groups—*Zyras*, sensu latu, *Myrmechusa* group, *Ocyplanus* group, and *Aenictonia* group.

More than 300 species of Ethiopian *Zyras* have been described but little is known about the ecology of most of them. Although it is likely that a majority of Old World species of *Zyras*, if not all, are facultative synechthrans of ant and termite societies, most of those collected were attracted to lights. Of some 320 species of Old World *Zyras*, s. l., in the Bernhauer collection, Chicago Natural History Museum, only two have labels indicating association with doryline ants—*Zyras delamarei* Cameron, and *Zyras satanas* Cameron, both from Ghana. The literature indicates a few more associations, but not many.

Only a brief review of the African genera of dorylophilous Myrmedoniini is feasible at this time. Of the Old World Myrmedoniini, only *Aenictonia* is known to occur in both Ethiopian and Oriental Regions. There is little to indicate a common myrmedoniine fauna in army ant societies of Old and New Worlds, although the Oriental genera, *Aenictobia* and *Aenictophila*, could conceivably be linked to the American fauna.
MYRMECHUSA Group

Four genera, *Myrmechusa* Wasmann, *Trichodonia* Wasmann, *Gapia* Blackwelder (=*Acanthoma* Wasmann), and *Myrmechusina* Cameron, occur in equatorial Africa. Observations of Patrizi (1948) indicate that these genera are probably synechthrans and are not true inquilines. They may be recognized by this combination of characters: a very broad, explanate pronotum; broad elytra and abdomen; large eyes, long slender antennae and tarsi; a conspicuous vestiture of black bristles on pronotum and abdomen, and in at least two cases (*Myrmechusa* and *Gapia*) spinous apical angles of the seventh tergite.

No attempt is made to characterize individual genera.

*Myrmechusa* Wasmann


Wasmann thought that *Myrmechusa* was a symphile of the driver ants (*Anomma*), which implied a close integration with the colonies. Patrizi (1948), on the basis of his observations in Ethiopia, and those of Meneghetti in Kenya, concluded that this genus lives only on the margin of the colony and captures and devours abandoned adults and immature stages. He characterized *Myrmechusa* as a genus of synechthrans that do not march with the colony. In artificial nests *Myrmechusa* did not establish intimate relations with the hosts as did *Smectonia* (another genus of Myrmedoniini) under similar circumstances. *Myrmechusa* tended to hide and emerged only to seize small workers, which they were able to decapitate. In the presence of large workers, *Myrmechusa* moved its abdomen rapidly and may have released a repellent secretion.

In testing other supposed dorylophiles in observation nests, Patrizi noted that *Zyras inermis* Cameron, *Oxytelopsis dorylinus* Cameron, and *Aenictonia minarzi* Bernhauer kept to themselves and appeared agitated.

**SPECIES OF MYRMECHUSA WASMANN**

*brunni* Eichelbaum, 1908, in Sjöstedt, Kilimandj.-Meru Exp., (8), 7, p. 92 (*Myrmedonia*). No host. TANGANYIKA.

SEEVERS: STAPHYLINID BEETLES

*feae* Bernhauer, 1927 (1928), Mem. Soc. Ent. Ital., 6, p. 207. No host. PORTUGUESE GUINEA.


**Gapia** Blackwelder


**SPECIES OF GAPIA BLACKWELDER**


**Trichodonia** Wasmann


**SPECIES OF TRICHODONIA WASMANN**


**Myrmechusina** Cameron


**SPECIES OF MYRMECHUSINA CAMERON**


**OCYPLANUS** Group

*Ocyplanus*, *Smectonia*, and a few related genera constitute a group associated with *Dorylus* (*Anomma*). It is not feasible at this time to define the generic limits within the group, but two subgenera pro-
posed by Bernhauer for *Ocypianus*—*Gryptaulacus* and *Pseudocyplanus* are raised to generic rank. It is inconsistent to retain them as subgenera and at the same time recognize *Anepipleuronia* Bernhauer as a distinct genus.

After observing individuals of *Smectonia*, collected from marching columns of *Anomma* at Addis Ababa, in observation colonies for fifteen days, Patrizi (1948) concluded that this genus is symphilous. *Smectonia*, undisturbed by its hosts, took up strategic positions in passages so that ants passed under them. Astride the hosts, they rubbed their mesosternum against the ants, and may have passed a secretion to them during the process. The beetles vibrated violently during such contacts. At times, a beetle stood immobile with one of the middle legs raised while an ant placed its mouthparts close to the articulating leg membranes. *Smectonia* exacts a toll from its hosts by feeding on larvae and ants in other stages of development. Patrizi even noted that when a beetle contested with a worker for an ant larva, it was relinquished by the worker without struggle.

**Ocypianus** Fauvel

*Ocypianus* Fauvel, 1899, Rev. d’Ent., 18, p. 43. Type species: *Ocypianus formicarius* Fauvel.


*Ocypianus* is a genus of slender, moderate-sized beetles, 5 mm. or more in length. The head is attenuated in front due to prominent mouthparts but is actually transverse because of the large, protuberant eyes. The extremely long and slender antennae are longer than the head, pronotum, and elytra combined. The elongated pronotum, broadest in apical half and with strongly bisinuate sides, bears a distinctive basal impression with a Y-shaped groove. The elytra are broader than either the pronotum or abdomen, but they and the abdomen are without notable features.

**SPECIES OF OCYPLANUS FAUVEL**


*formicarius* Fauvel, 1899, Rev. d’Ent., 18, p. 43; Wasmann, 1916, Ent. Mitt., 5, p. 137. Host: *Anomma* sp. SENEGAL.

*kohli* Wasmann, 1916, Ent. Mitt., 5, p. 137, pl. 3, fig. 5. Hosts: *Anomma wilterthi* Emery and *A. nigricans burmeisteri rubellus* Santschi. CONGO.


Pseudocyplanus Bernhauer


This genus is distinguished from *Ocyplanus* by much shorter and stouter antennae, shorter pronotum, which is subequal in length and width, the presence of only a shallow median pronotal impression; and the moderately bisinuate pronotal sides.

**SPECIES OF PSEUDOCYPLANUS BERNHAUER**


Gryptaulacus Bernhauer


Smaller than *Ocyplanus*, this genus is distinguished by a shorter and more transverse head, a pronotum that is slightly transverse and bears a very deep U-shaped sulcus in basal half, and antennae that are short and compact—no longer than head and pronotum—and have segments 3–9 transverse.

**SPECIES OF GRYPTAULACUS BERNHAUER**


Pagonogastria Bernhauer


*Pagonogastria* has a very robust build, moderately long and stout antennae, pronotum with a broad impression in front of the base, and an extremely broad abdomen. The abdomen is especially distinctive as it is almost twice as broad as pronotum and bristles with numerous very long curved setae.

**SPECIES OF PAGONOGASTRIA BERNHAUER**


Anepipleuronia Bernhauer


This genus is apparently very close to *Ocyplanus*. Its head is impressed, the pronotal impressions distinctive (a single shallow me-
dian impression flanked on each side in the basal half by a small impression), the elytra longer, and the antennae shorter.

SPECIES OF ANEPIPLEURONIA BERNHAUER


reichenspergeri Cameron, 1938, Ent. Month. Mag., 74, p. 271. Host: Dorylus (Anomma) nigricans molesta Gerst. NYASALAND.


Astinbides Wasmann


SPECIES OF ASTILBIDES WASMANN

rugipennis Wasmann, 1916, Ent. Mitt., 5, p. 141, pl. 3, fig. 6. Host: Anomma wiltonthi Emery. CONGO.


Dromanomma Wasmann


SPECIES OF DROMANOMMA WASMANN


Smectonia Patrizi


SPECIES OF SMECTONIA PATRIZI


AENICTONIA Group

Aenictonia Wasmann. Figure 30, A, B.

**Aenictonia** is an Ethiopian and Oriental genus of more than twenty species. Although the generic name implies that *Aenictus* is the host genus, this is apparently the case for only the species of *Aenictus* s. s. Records indicate that *Anomma* is the host genus for most of the African species. The range of the genus is materially increased by the first Oriental record—a new species collected by Dr. T. C. Schneirla in Thailand during a recent study of *Aenictus* in the Orient.

The species of *Aenictonia* are easily recognized by their distinctive cephalic and thoracic eminences and carinae. The pattern of ornamentation is unlike that of any Old World dorylophiles but is remarkably similar, at least superficially, to that of some groups of American ecitophiles (*Ecitoxenia* of the Ecitocharini, and *Ecitoxenia* of the Myrmedoniini). Inasmuch as the genera of Old World Myrmedoniini are poorly characterized and delimited, it is not possible now to relate *Aenictonia* to that complex.

Three subgenera of *Aenictonia* were proposed by Wasmann. Whether or not there is merit in retaining these categories can be decided only after the species of the genus have been thoroughly studied. The present basis for separating these subgenera rests on differences in the dorsal eminences and carinae and may be summarized in part as follows:

1. Elytra with a strong subsutural carina, a conspicuous oblique discal carina, and a relatively weak, convex submarginal ridge............ *Anommatonia*  
   Elytra lacking a discal carina (very faint in some *Aenictonia* s. s.)........2

2. Submarginal carina of elytra acute and strong, beginning at humerus and curving mesad to the apex where it joins an apical carina; sutural carina very weak............................... *Anommalochara*

Submarginal carina of elytra broad and weak and not curving as above.  
*Aenictonia* s. s.

**Aenictonia** Wasmann, subgenus

Three Ethiopian and one new Oriental species constitute this subgenus; three are known to occur with *Aenictus*, and the host of the fourth is unrecorded. The ornamentation (fig. 30, A) of the head and pronotum of *A. cornigera* Wasmann (Orange Free State) sets a general pattern for the genus, although there are numerous variations from it. *Aenictonia banghaasi* Bernhauer (Sudan) is very similar to *cornigera* Wasmann, and differs chiefly in the form of the vertexal eminences medial to the eyes. *Aenictonia thailandica* n. sp. from the Oriental Region differs from the African species in the form of the vertexal eminences (fig. 30, B), and in the absence of prom-
Fig. 30. *Aenictonia cornigera* Wasmann: A, head and pronotum. *Aenictonia thailandica*, n. sp.: B, head and pronotum. *Aenictobia longicornis* Seevers: C, dorsal view. *Aenictophila thailandica*, n. sp.: D, dorsal view; E, third and fourth sternites, ventral view; F, the deep sulcus on the fourth sternite with fine setae on its anterior and posterior margins.

inent postgenal protuberances. The pronotum of *thailandica* differs in having a bisinuate apex and prominent apical angles.

**SPECIES OF AENICTONIA WASMANN**

Aenictus (Aenictus) thailandica, new species. Figure 30, B.

Distinguished from cornigera Wasmann and banghaasi Bernhauer (hemigastrophysa Eichelbaum not studied) by distinctive contours of head and pronotum (fig. 30, B) and by the form of the pronotum. The absence of postgenal protuberances and the form of the pronotal apex are especially noteworthy.

Coloration testaceous. Integuments with few to many very coarse, smooth, setigerous punctures, each bearing at its anterior margin a short, fine seta—the punctures are relatively sparse and irregular on head, more numerous and often ill-defined on pronotum (which appears rugulose), densely arranged on elytra (the intervals are raised and the elytra appear rugulose), and large and well-defined on tergites 2-6 (finer on apical half of each). Punctures of tergites 7-8 obsolete, surface smooth. Sternites smooth, impunctate, and not pubescent (except on lateral areas of sternites 3-6).


Pronotum subequal in length and width, form distinctive (fig. 30, B). Elytral surface slightly impressed near lateral margin so that the margin appears elevated, but the elytra lacks carinae. Length, 5 mm.

Type from Pak Chong (80-90 miles north of Bangkok), Thailand; collected May 31, 1961, by T. C. Schneirla, with Aenictus binghami, var. gatesi Wheeler (det. by E. O. Wilson); in collection of Chicago Natural History Museum. No paratypes.

Anommatonia Wasmann, subgenus

Anommatonia Wasmann, 1915, Ent. Mitt., 4, p. 27. Type species: Anommatonia anommatophila Wasmann.

SPECIES OF AENICTONIA (ANOMMATONIA) WASMANN


costata Eppelsheim, 1885, Deut. Ent. Zeitschr., 29, p. 107; Wasmann, 1915, Ent. Mitt., 4, p. 27. GHANA.

feae Gridelli, 1926, Ann. Mus. Genova, 52, p. 177, fig. 2. PORTUGUESE GUINEA.


reichenspergeri Cameron, 1938, Ent. Month. Mag., 74, p. 271. Host: not stated. NYASALAND.

scheabni Wasmann, 1915, Ent. Mitt., 4, p. 31. Host: Anomma sjoestedti Emery. CAMEROON.


tristis Wasmann, 1915, Ent. Mitt., 4, p. 31. Host: Anomma wileverthi Emery. CONGO.

vosseleri Wasmann, 1921, Ent. Rund., 29, p. 42; 1915, Ent. Mitt., 4, p. 30, pl. 2, fig. 3. Host: Anomma molesta Gerst. TANGANYIKA.


SPECIES OF AENICTONIA (ANOMMATOCHARA) WASMANN


rubella Wasmann, 1915, Ent. Mitt., 4, p. 33. Host: Anomma sjoestedti Emery. CAMEROON.

AENICTOBIA Group

The position of Aenictobia Seevers in the Myrmedoniini is at present not clear. In habitus it is not unlike some genera of the American Ecitopora group, but whether or not this indicates relationship or is due to convergence is difficult to decide. The meso- and metasternal processes of Aenictobia are exceptionally narrow for the tribe, but the fact that the latter is the longer of the two is significant; the slenderness is probably a secondary modification. More material from the Oriental Region is needed to clarify the position of this genus.
Aenictobia Seevers. Figure 30, C.


Head slightly longer than broad; vertex with a broad, shallow impression and three eminences, one above each eye, and one in the center. Front of head vertical, the median eminence continues ventrad as a narrow clypeal keel which narrowly separates the deep antennal fossae. Occiput convex, slightly swollen laterad, its sides almost perpendicular. Antennae inserted below the low ridges connecting the vertexal eminences, their insertions relatively close together. Eyes large, somewhat bulbous. Postgenae with narrow ridge-like elevations behind eyes; shallowly concave below ridges that parallel the gular sutures. Antennae very long, capable of reaching the middle of abdomen; all segments elongated. Pronotum with the dorsum convex medially and explanate laterally; hypomera entirely visible from side; apical border straight, apical angles broadly rounded; sides almost straight; base very strongly arcuate for most of its width, but straight for a short distance near each basal angle. Pronotal disk with a shallow impression. Elytra generalized. Prosternum keeled; mesosternum short; mesocoxal acetabula narrowly separated; bluntly rounded mesosternal process constituting one-third and the more slender metasternal process two-thirds of the intercoxal isthmus. Legs generalized, tarsi 4, 5, 5-segmented. Abdomen one-sixth broader than elytra; dorsum almost flat; paratergites forming an elevated margin; sides scarcely converging apically. Length, 2.5 mm.

**SPECIES OF AENICTOBIA SEEVERS**


**AENICTOPHILA Group**

Aenictophila, new genus. Figure 30, D–F.

Type species: *Aenictophila thailandica* n. sp.

General habitus as in fig. 30, D. Head subtriangular in outline above, subequal in length (excluding labrum and neck) and width, broadest at eye level, the sides converging strongly to the narrow neck (only about one-fourth maximum head width). Eyes very large, almost one-half as long as head. Head strongly convex both dorsally and ventrally; dorsum not impressed. Mouthparts typically myrmenediine. Gula very narrow throughout most of its length. Antennae moderately robust and moderately long; scape about half as long as head, third segment three-fourths as long as scape; three basal segments articulating by ball and socket devices; segments 4–10 subcylindrical. Pronotum one-third longer than broad; broadest in front of middle, sides converging basically and apically, the apex narrower than base; dorsum with a moderately deep median suture; sides strongly deflexed, hypomera not delimited. Elytra generalized. Wings present. Prosternum large, keeled. Meso-metasternal relations typically myrmenediine. Middle coxae not set in fully margined acetabula. Metasternum very strongly convex. Procoxae long and spindle-shaped; mesocoxae shorter and somewhat spindle-shaped. Metacoxae transverse, but with the medial condylar area exceptionally elongated. Legs long, without noteworthy features.
Abdomen broadest at level of seventh segment. Third segment broader at apex than base, due largely to the apical expansion of the third sternite; third tergite with a basal sulcus and a subapical convexity; third sternite with a strong basal constriction and apical expansion; tergites 4–6 with basal sulci, that of fourth tergite exceptionally deep; fourth tergite with a prominent, basally directed eminence. Paratergites and parasternites of segments 4–6 apparently fused on each side and recurved dorsad as a thin lamella. Sternites 4–6 with basal sulci, that of fourth sternite exceptionally deep; fourth sternite with a prominent, basally directed eminence.

Remarks.—The numerous fine golden hairs of the fourth sternite are somewhat trichome-like in appearance but there is no evidence that they are glandular hairs.

**Aenictophila thailandica**, new species. Figure 30, D–F.

Rufotestaceous. Head and elytra smooth, non-reticulate; pronotum finely granulose due to a fine, close-meshed reticulation. Tergites 3–5, and basal half of sixth with irregular reticulation, varying in coarseness and form; apical half of sixth and remaining tergites smooth. Basal half of third sternite, sternites 4 and 5, and basal half of sixth reticulate. Head and pronotum with very sparse short pale setae; the pronotum with several coarser dark setae; each elytron with about 35 longer, courser pale setae. Tergites sparsely setose, the only conspicuous setae are a pair on the third, a pair on each side of the median eminence of the fourth, and one near each lateral margin of tergites 5–7. Sternites with a moderately dense vestiture of median length setae on the apical half. Sternite 4 with a distinctive vestiture of fine recurved golden hairs (fig. 30, F). Length, 5.5 mm.

*Type* from Pak Chong (80–90 miles north of Bangkok), Thailand; collected May 31, 1961, by T. C. Schneirla (T-AT-2), with *Aenictus binghami*, var. *gatesi* Wheeler (det. by E. O. Wilson); in collection of Chicago Natural History Museum. Two paratypes, same data as type, in the American Museum of Natural History and Chicago Natural History Museum.
Tribe ECITOCHARINI, new tribe

Ecitochara Wasmann  
Ecitodaemon Reichensperger  
Ecitosymbia Bruch  
Ecitozenia Wasmann  
Ecitozenides Borgmeier, new synonym

Eciton

In the large, heterogeneous tribe Myrmedoniini of current catalogues, there is a small group of genera which I propose to set apart as the Ecitocharini. The affinities of the ten recorded neotropical species of this group are probably with the Athetini, a vast assemblage of species also placed in the Myrmedoniini by most cataloguers. From the Myrmedoniini, s.s., of this work, the Ecitocharini may be distinguished as follows: mesocoxae narrowly separated, the meso- sternal process long and slender, the metasternal process short and slender; galea and lacini of moderate length.

Inasmuch as the characteristics of the Athetini have never been defined nor the group delimited, it is not feasible at this time to provide morphological criteria for distinguishing the Ecitocharini from that tribe. The Ecitocharini are set apart to emphasize their evolutionary and ecological divergence from the Athetini; their obligate relationship with Eciton societies doubtless has a genetic basis. No true ecitophilous Athetini have been recorded, although species of Atheta, sensu latu, are frequently found in the debris accumulations of Eciton colonies.

Among dorylophilous Aleocharinae, this tribe may represent a neotropical counterpart of the African tribe Deremini, a group which I also propose to remove from the Myrmedoniini, sensu latu. Both the Ecitocharini and Deremini are apparently related to the Athetini, both are very difficult to separate from the latter on morphological grounds, and both exhibit unusual integumental ornamentations. Although both of these taxa may have stemmed from Athetoid stocks, I suspect that this event occurred independently in the Old and New Worlds.

Ten species of Ecitocharini, including two described in this paper, are known, and five genera have been proposed to receive them. Ecitochara and Ecitodaemon provide no problem of delimitation, but Ecitosymbia, Ecitozenides, and Ecitozenia do. Ecitosymbia rufa Bruch and Ecitozenia mirabilis Wasmann represent extremes in a series of species which includes five more or less intermediate forms. Reich-
Enesperger considerably broadened the concept of *Ecitoxenia* by including *hamati*, but Borgmeier conceived of that genus in a more restricted sense when he proposed *Ecitoxenides* for two additional species. With two new species to place, I must choose between these concepts. If *Ecitoxenides* is retained, *hamati* and two new species must be forced into it or a series of monotypic genera proposed. I have chosen to merge *Ecitoxenides* with *Ecitoxenia* and to add the new species to it.

**Ecitosymbia** Bruch. Figure 31, A.

*Ecitosymbia* Bruch, 1923, Rev. Mus. La Plata, 27, p. 182. Type species: *Ecitosymbia rufa* Bruch.

*Ecitosymbia rufa* Bruch is probably the most generalized member of the tribe and may serve as its prototype. The head and thorax lack the integumental ornamentation that is so characteristic of *Ecitoxenia*.

Integuments reticulated, appearing granulose. Body form generalized; head and thorax without eminences, carinae, and deep sulci such as characterize other species of the tribe. Head about one-fifth longer than broad, excluding eyes; clypeus not carinate; vertex with a shallow impression; base feebly emarginate. Eyes very narrow, finely faceted. Mouthparts generalized, lacinia and galea of moderate length. Antennae robust, scape clavate; segments 3–10 transverse, subcylindrical; 2–10 incrassate (in *rufa*, segments with these relative lengths: 24 : 8 : 10 : 12 : 10 : 10 : 12 : 12 : 12 : 20). Pronotum (fig. 31, A) equal in length and width; apex binicate; dorsum with low parallel ridges enclosing a broad, shallow concavity; dorsum deflected abruptly laterad but not bordered by distinct carinae; hypomera very feebly delimited. Elytra broadly impressed, but without definite carinae. Abdomen generalized; dorsum flat; tergites 3, 4, and 5 shallowly impressed; sternites only moderately convex. Ninth tergite apparently bearing two short processes with numerous long setae. Legs moderately long, femora not especially stout, hind femora one-fifth as broad as long; hind leg proportions as follows: femur (83 x 18), tibia (78), tarsus (60); hind tarsi three-fourths as long as tibiae. Length, 4 mm.

**SPECIES OF ECITOSYMBIA BRUCH**


**Ecitoxenia** Wasmann. Figure 31, B, C, E, F, G, H.


*Pseudoecitoxenia* Costa Lima, 1932, Bol. Biol., 21, pl. 59.

As noted in the tribal introduction, this genus has been broadened by the inclusion of two species of *Ecitoxenides* as well as by the addition of two new ones. In 1902 Brues placed *brevipes* Brues, a Texas species, in *Ecitoxenia* but it was later transferred to *Ecitoxenidia* Wasmann. Although *Ecitoxenidia* bears a superficial resemblance to *Ecitoxenia* because of its integumental ornamentation, it does not, in my opinion, belong to this tribe but to the Myrmedoniini.

Head, excluding the eyes, longer than broad. Clypeus carinate (*mirabilis*) or not. Head variable in ornamentation: relatively generalized with no more than a shallow impression, or with various impressions, carinae, and eminences. Eyes moderate-sized to very large. Antennae robust; segments cylindrical to moderately compressed (apical segments); segments compactly arranged. Pronotum slightly broader than long or longer than broad; variable in form and in surface contours (figs. 31, B, C, E, F). Elytra generalized to carinate. Sternal regions typical of the tribe. Legs without noteworthy features. Abdomen generalized in form; tergites 3–5 with a broad shallow impression in most species but deeply impressed in *impressa*. Ninth tergite with strong claw-like processes (*mirabilis*); with numerous long setae in *megalops* (condition unknown in most species). Lengths, 3–5 mm.

### SPECIES OF *ECITOXENIA WASMANN*


*impressa* n. sp. Host: *Eciton mexicanum* Roger. MEXICO: Chiapas.

*megalops* n. sp. Host: *Eciton mexicanum* Roger. PANAMA CANAL ZONE: Barro Colorado Island.


*oculatus* Borgmeier, 1949, Rev. Ent., 20, p. 154; fig. 118, pl. 2, fig. 4 (*Ecitoxenides*). Host: *Eciton mexicanum* Roger. BRAZIL: Goiás; Campinas.

### KEY TO THE SPECIES OF *ECITOXENIA WASMANN*

1. Head, pronotum, and elytra with carinae and eminences as in fig. 31, F; ninth tergite with two strong claw-like processes (fig. 26, G)............. *mirabilis*

Head, pronotum, and elytra without the extreme ornamentation indicated above, although the head and pronotum may be carinate; ninth tergite apparently without claw-like processes (not determined with certainty for some species)...................................... 2

2. Head with a strong carina medial to each eye; pronotum with two strong parallel carinae (similar to those of *mirabilis*).............................. 3

Head with feeble carinae at most; pronotum not carinate, although with impressions as in fig. 31, B, C............................................. 4

3. Eyes large................................................. *oculatus*

Eyes small.................................................. *cariniceps*

4. Third, fourth, and fifth tergites very deeply and distinctively impressed (fig. 31, C); head relatively long, about two-thirds longer than broad (excluding eyes); eyes small; medial pronotal sulcus narrow and deep............. *impressa*
Third, fourth, and fifth tergite broadly, uniformly impressed but not as above; head less than two-thirds longer than broad (excluding eyes); eyes large; medial pronotal impression broader and shallower.  

5. Head (fig. 31, B) about one-third longer than broad (excluding eyes); vertexal impression relatively broad and deep, dorsum with a low carina medial to each eye; pronotal apex (fig. 31, B) strongly bisinuate, its apical angles produced; medial impression relatively deep.  

Head (fig. 31, E) about three-fifths longer than broad (excluding eyes); vertexal impression relatively shallow; head not carinate medial to eyes; pronotum (fig. 31, E) with apical angles less produced and impressions more shallow than in above.  

Ecitoxenia megalops, new species. Figure 31, B.  
Most closely allied to Ecitoxenia hamati Reichensperger; distinguished by the characters of the key.  

Head (fig. 31, B) one-third longer than broad, excluding eyes; dorsum with a broad, oval medial impression (subfoveolate at center); the impression bounded laterally by a low carina; clypeus without medial carina; sides slightly arcuate behind eyes. Eyes (28 : 10) exceptionally large, about one-third as broad as long; moderately coarsely faceted. Antennae robust; segments of these relative lengths: 26 : 8 : 10 : 14 : 12 : 14 : 13 : 13 : 14 : 18; segments 4–10 feebly incrassate; more distal segments slightly compressed; segment 4 two-fifths longer than 3 (in hamati, third segment longer than fourth). Pronotum (fig. 31, B) subequal in length and width; with the apex exceptionally strongly bisinuate, the anterior angles acute, prominent; medial impression relatively shallow; the lateral impressions shallow; lateral margins distinctive in outline; sides abruptly deflexed, the hypomera not delimited. Elytra with a broad shallow impression. Abdomen relatively generalized, tergites flat, sternites moderately convex; third tergite broadly, moderately deeply, and uniformly impressed at base; fourth and fifth tergites more shallowly impressed. Ninth tergite with numerous very fine long bristles. Hind legs with following relative proportions: femur (102 : 20); tibia (97); tarsus (56); tarsi compressed, very slender. Length, 4 mm.  

_Type_ from Barro Colorado Island, Panama Canal Zone; collected August 12, 1956, by Carl W. Rettenmeyer, with Eciton mexicanum Roger. In Chicago Natural History Museum. No paratypes.  

Ecitoxenia impressa, new species. Figure 31, C.  

Easily distinguished from all species of the genus by the extremely deep impressions of the basal tergites as well as by the combination of exceptionally long head, small eyes, feebly impressed head, and deep pronotal sulcus.  

Head (fig. 31, C) relatively long and slender, almost two-thirds longer than broad, excluding eyes; dorsum very feebly impressed; side margins feebly arcuate. Eyes small, with medium-coarse facets. Antennae with segments of the following relative lengths: 28 : 8 : 16 : 20 : 20 : 18 : 18 : 18 : 16 : 21; robust, cylindrical, slightly incrassate; apical segments only slightly compressed. Pronotum relatively long, about one-sixth longer than broad; apex bisinuate, the apical angles less pro-
ounced than in megalops; median impression slender and relatively deep; lateral impressions moderately deep; base almost straight. Elytra generalized, feebly impressed. Abdomen distinctive; third, fourth and fifth tergites with very deep impressions (fig. 31, C). Length, 3 mm.

_Type_ from Escuintla (30 km. north), Chiapas, Mexico; collected April 4, 1945, by T. C. Schneirla, with _Eciton mexicanum_ Roger. In Chicago Natural History Museum. No paratypes.

**Ecitochara** Wasmann. Figure 31, D.


_Ecitochara_ is distinguished from the preceding genera by its pronotal form, subovoidal abdomen, and relatively few surface impressions.

Integuments with a fine-meshed reticulation, appearing granulose. Head generalized; one-third longer than broad; dorsum with a small, very shallow vertexal impression; neck three-fifths as broad as head. Eyes small. Antennae stout, compact, the segments telescoped; scape relatively short, segments 2 and 3 relatively small; segments 5–8 enlarged, terminal three or four segments somewhat compressed. Pronotum (fig. 31, D) a little broader than long; dorsum relatively strongly convex, sloping laterad to the poorly delimited hypomera (sides abruptly deflexed in _Ecitosymbia_ and _Ecitozenia_); median diskal impression narrow and only moderately deep; apical margin continuously arcuate with the lateral margins; the apical angles rounded, but bearing a moderate to strong spine at their ventral margin. Elytra generalized; with only a very shallow lateral impression. Abdomen subovoidal; tergites moderately convex and sternites very strongly so; abdomen broadest at level of fourth segment, and tapering more acutely toward apex than in preceding genera; third tergite impressed slightly at base; ninth tergite apparently unmodified. Legs relatively short; femora relatively short and stout, hind femora one-fourth as broad as long; proportions of parts of hind leg as follows: femur (68 : 18), tibia (54 long), tarsus (36 long). Tarsi short, two-thirds as long as tibia, strongly compressed.

**SPECIES OF ECITOCHARA WASMANN**


**Ecitodaemon** Reichensperger


This distinctive genus probably belongs to the Ecitocharini although I am not certain about the condition of the meso-metasternal processes. Reichensperger did not describe the condition, and some
years ago when I examined the genus I did not make a note of the situation. The most notable feature of *Ecitodaemon* is its petiolate abdomen, an adaptation paralleling that of genera in several other dorylophilous tribes.

Head with a median impression. Antennae thick and compact, relatively short. Pronotum elongated, broadest in front of middle; with a broad, oval median impression. Elytra broadest in front of middle, its side margins converging apically. Third abdominal segment considerably narrower than the following segments and forming a distinct petiole; subsequent segments form an ovoidal "gaster"; sclerites of abdomen in generalized positions. Length, 3.3–3.5 mm.

**SPECIES OF ECITODAEMON REICHENSPERGER**

Tribe DEREMINI, new tribe

This new tribal category is proposed for a homogeneous group of African genera known to associate with *Dorylus* (s.s.), *Dorylus* (*Anomma*), and probably *Aenictus*. The species are small, slender, and, relative to other dorylophiles, generalized in structure. Apart from contour modifications of the upper surface—presence of impressions, carinae, and tubercles—they have few noteworthy characters. Although the genera of this group have been placed in the Myrmedoniini, sensu latu, because of their 4, 5, 5-tarsal segmentation, their affinities seem to be with the Athetini. Students of the Aleocharinae may ultimately decide that they belong to the Athetini for it is very difficult to detect diagnostic morphological characters. I am setting them apart at this time as they are easily recognized by a difficult to describe habitus and by their association with doryl-line ants. As the Athetini as a group have never been delimited nor the tribe defined, it is virtually impossible to satisfactorily compare another group with them at present. In the American tropics, the tribe Ecitocharinini seems to be almost a counterpart of the Deremini; both groups are apparently very close to the Athetini (and difficult to separate except on ecological grounds) and both occur with the large driver ants (*Anomma* and *Eciton*).

The tribal characteristics may be summarized as follows: size small (less than 4 mm. in length); form slender, somewhat athetoid; tarsi 4, 5, 5-segmented (erroneously reported as 5, 5, 5-segmented in some cases); mouthparts generalized; galea and lacinia moderate in length; upper surface with various impressions, sulci, carinae, and tubercles; pronotal hypomera strong inflexed, scarcely visible from the side; mesocoxae narrowly separated, the intercoxal isthmus composed of a long and slender mesosternal process (attaining the caudal margin of the mesocoxae) and a very short metasternal process; teguments with a close-meshed reticulation; abdomen generalized (two genera, *Dorylopora* and *Dorylobius*, with a series of large tergal tuberosities); obligate dorylophily (a majority of recorded species were attracted to lights).

The 75 recorded species have been assigned to six genera, of which the largest is *Derema*, with 65 species. *Derema* has been subdivided into seven subgenera. The tribe is badly in need of a species revision, for a delimitation of the genera is contingent on it. As I did not have time to undertake this rather formidable task, I am unable to provide satisfactory generic diagnoses or a generic key. The group is homogeneous and the species differ in such characters as proportions and
form of head and pronotum; presence of a variety of cephalic and thoracic impressions, sulci, and carinae; antennal proportions; and presence or absence of abdominal tuberosities. With only differences of this nature to rely on, generic limits are not readily established.

Species of the group are concentrated in equatorial Africa: 52 species were collected in the Congo, five in Tanganyika, two in the Cameroons, ten in west Africa (Senegal, Guinea, Ivory Coast, and Ghana). Only five species are recorded south of the Congo (Rhodesia, South Africa, Natal, and Nyasaland). Collecting has been more intensive in the Congo, but the above distribution of species is indicative of the tribe’s range.

Host records are not numerous because most species were collected at lights. It is probable that the equatorial African species occur with Anomma for the most part. The two authentic records of occurrence with Dorylus s. s. were made in South Africa (Derema foveicollis Fauvel and Dorylobius sulcicollis Raffray). One species, Derema (Demerinda) termitophila Cameron, was recorded with termites, but this association requires confirmation.

Fauvel (1899a) originally gave the name Derema to the first genus of the group, but under the erroneous impression that this name was preoccupied by Demerma Walker, 1875, renamed the genus Demera during the same year. The name Demera has been used by all subsequent taxonomists and cataloguers and all 65 species have been described under that name. Blackwelder pointed out (1952, p. 120) that the name Derema must be used because there was no justification for the change. Relatively little confusion should result from application of the correct name.

**Derema Fauvel**


Subgenus *Demerinda* Cameron, 1927, Ent. Month. Mag., 63, p. 223.

**SPECIES OF *DEREMA FAUVEL***

- aberrans Cameron, 1933, Bull. Ann. Soc. Ent. Belg., 73, p. 46 (Demerina)
- IVORY COAST; with *D. (Anomma) nigricans*.
- bickmanni Reichensperger, 1922, Ent. Mitt., 11, p. 81 (Demerina). CAMEROON; with *D. (Anomma) wilterthi*.
- CONGO; with *D. (Anomma) burmeisteri rubella*.
- cameroni Seevens, new name for *collarti* Cameron, 1939b, Ent. Month. Mag., 75, p. 6 preoccupied (*Derema*). CONGO.
- CONGO; with *D. (Anomma) burmeisteri rubella*.
- cordicollis Wasmann, 1912, Ent. Rund., 29, p. 43 (Demerina). TANGANYIKA.
- foreicollis Fauvel, 1899, Rev. d'Ent., 18, p. 42 (Derema). SOUTH AFRICA; with *Dorylus (s.s.) helvolus*.
- henningsi Cameron, 1939a, Ent. Month. Mag., 75, p. 36 (Derema). NYASALAND. *D. (Anomma) nigricans molesta*.


Remarks.—The question marks in the host records indicate that the subgenus of Dorylus was not indicated, although in almost all cases it was probably Anomma. Species without host records were probably collected at lights.

Dorylobius Raffray
Dorylobius Raffray, 1899, Rev. d'Ent., 18, p. 25.

SPECIES OF DORYLOBIUS RAFFRAY

sulcicollis Raffray, 1899, Rev. d'Ent., 18, p. 25, pl. 1. SOUTH AFRICA; with Dorylus (s.s.) helvolus.

Dorylocerus Wasmann

SPECIES OF DORYLOCERUS WASMANN


Dorylonilla Wasmann

SPECIES OF DORYLONILLA WASMANN

funcki Reichensperger, 1915, p. 123. CAMEROON.


Dorylopora Wasmann
SPECIES OF DORYLOPORA WASMANN


*minor* Eichelbaum, 1913, Arch. Naturg., 79, p. 151. TANGANYIKA; with *D. (Anomma) molestata*.


**Macfieia** Bernhauer


SPECIES OF MACFIEIA BERNHAUER

Tribe ECITOGASTRINI


Ecitogaster occupies such an isolated position among the American Aleocharinae that it should be assigned to a monobasic tribe. In many of its characteristics it bears a striking similarity to some members of the Old World tribe Pygostenini, most genera of which are dorylophiles. Whether or not this is indicative of an ancient ancestral relationship is conjectural. At my request, Dr. David Kistner, who recently monographed the Pygostenini, examined Ecitogaster and concluded that while it does not seem to belong to that group, it may have stemmed from a common ancestor. Possible relationships with the Pygostenini are discussed in the evolutionary section of this paper.

All available evidence indicates that the species of Ecitogaster occur with a single host species, Labidus praedator. How this interesting situation developed is not known.

Ecitogaster Wasmann. Figure 32, A-G.


Head one-sixth to one-fourth broader than long; robust; antennal fossae unusually deep, extending caudad beyond middle of eyes; vertexal arcade above fossae weak, the pedicel of the scape almost entirely visible; antennal fossae separated by a very acute carina; dorsum with a broad, moderately deep impression which extends to the shallow basal emargination; neck moderately long; infraorbital carinae absent. Eyes large, almost one-third as long as head. Gula broad, its base with an elevated condylar surface; submentum broad; mentum shallowly emarginate at apex. Maxilla with a small cardo and moderately long galea and lacinia (subequal in length); maxillary sinuses moderately large. Mandibles strong, edentate. Antennae long and stout; segments cylindrical and telescoped (pedicels not visible); terminal seven segments slightly to moderately compressed.

Pronotum about one-third broader than long; broadest near apex, sides converging to the arcuate base; pronotal flanks very extensive, the hypomera not delimited; dorsum deflexed apically to conform to the caudal surface of the head; general appearance that of a large collar; dorsum with a shallow to rather deep median sulcus (one area usually deeper and foveolate); surface on each side of sulcus concave to strongly convex. Contours of pronotum distinctive for each species (fig. 32, F-II). Elytral disk broadly impressed, each impression bounded by a low submarginal ridge which increases in elevation to form a conspicuous eminence near outer apical angle. Prosternum very large, prolonged for a moderate distance between the procoxae. Mesocoxae set in small margined acetabula; meso- and metasternal processes between them very broad (fig. 32, C). Metasternum

large; its outer, basal angles depressed (fig. 32, C). Procoxae long, stout, broadly spindle-shaped; mesocoxae small, oval; metacoxae transverse (generalized aleocharine type). Tarsi 4, 4, 4-segmented. Second abdominal sternite present. Abdomen broadest at third segment, tapering to a slender apex. Seventh tergite very much elongated; with a pair of shallow grooves at its base. Paratergites and parasternites slender. Ninth tergite of both sexes deeply incised (fig. 32, D), apex appearing as two heavily sclerotized "claws." Aedeagus distinctive (fig. 32, E); extremely large, occupying much of the abdomen.
SPECIES OF ECITOGASTER WASMANN


condei Wendeler, 1956, Dusenia, 7, p. 267. Host: Unknown. BRAZIL.

fossulata Borgmeier, 1949, Rev. Ent., 20, p. 130, fig. 20. Host: Labidus praedator F. Smith. BRAZIL: Goiás; Campinas.

mexicanus n. sp. Host: not known. MEXICO: Vera Cruz; Córdoba.

panamensis n. sp. Host: Labidus praedator F. Smith. PANAMA CANAL ZONE: Barro Colorado Island.


Ecitogaster panamensis, new species. Figure 32, A, B, C, I.

Distinguished from the other species by its distinctive pronotal contours (fig. 32, I).

Medium dark reddish-brown; head, pronotum and elytra darker. Head one-fifth broader than long, postgenae not prominent, sides of head only slightly arcuate. Pronotum distinctive; median sulcus less well-defined than in other species the sides of sulcus usually oblique, the deepest part in basal half; dorsum lateral to sulcus convex, coming to a distinct peak in basal half. Elytra with moderately deep impressions and prominent submarginal and apical eminences. Length, 5.4–7.2 mm.

Type from Barro Colorado Island, Panama Canal Zone; collected June 4, 1956, by Carl W. Rettenmeyer; with Labidus praedator F. Smith. In Chicago Natural History Museum. Eight paratypes, same host as type, collected June 4 and 5, July 27, and August 1, 1956; in collections of Chicago Natural History Museum and University of Kansas.

Ecitogaster mexicanus, new species. Figure 32, G.

Distinguished from the other species by its distinctive pronotal contours (fig. 32, G).

Light reddish-brown throughout. Head almost one-fourth broader than long; postgenae prominent; the median impression moderate; clypeal carina thin. Pronotum distinctive; the deep, well-circumscribed median sulcusdeepest in basal half before opening out basally to a flat surface; dorsum lateral to sulcus elevated uniformly as a distinct eminence. Elytra with relatively low eminences near apical angles and a relatively shallow impression. Length, 5.4 mm.

Type from Córdoba, Vera Cruz, Mexico, collected by A. Fenyes; date and host unknown. In California Academy of Sciences. No paratypes.
Tribe PYGOSTENINI

The genera of this Old World aleocharine tribe that were known in the nineteenth century were placed in the subfamily Tachyporinae because they superficially resemble members of that group (Kraatz, 1858, Fauvel, 1899a). In 1904, Wasmann proposed the subfamily Pygosteninae and suggested that the group is probably closest to the Aleocharinae. In 1918, Fenyes erected an aleocharine tribe, Symplemonini, for certain pygostenine genera, but Paulian (1948) established the relationship of the entire tribe Pygostenini to the Aleocharinae on the basis of the male genitalia. Kistner (1958) in a thorough revision of the Pygostenini concurred in this viewpoint.

The principal tribal characters utilized by Kistner to define the tribe are as follows: median lobe of aedeagus subdivided into articulated proximal and distal sections, ninth abdominal sclerites consisting of a median dorsal lobe and two lateral plates (each subdivided into two lobes), relatively deep-set antennal fossae, antennae generally fusiform, with the segments more or less telescoped so that their pedicels are invisible. The integumental sculpture of most genera is distinctive: fine lines, bearing yellow setae at intervals, follow the contours of various sclerites of the body.

The following review of the generic groups is abstracted from Kistner’s (1958) excellent monograph which should be consulted for detailed descriptions of genera and species, for the numerous figures, and for theoretical discussion of phyletic relationships within the tribe. The generic key is somewhat abbreviated and slightly modified.

KEY TO THE GENERA OF PYGOSTENINI

1. Mesocoxae almost contiguous; mesosternal process sharp and pointed, always carinate .......................................................... 2
   Mesocoxae widely separated; mesosternal process blunt or smoothly rounded
   (acute in Deliodes) .................................................. 12

2. Body fusiform; pronotum highly convex, overlapping the elytra and covering
most of the scutellum; legs short, procoxae expanded to cover the forelegs
in repose; antennae short, not longer than head width ................ 3
   Body not fusiform; pronotum relatively flat, not covering the scutellum; legs
relatively long; procoxae not covering the forelegs in repose; antennae long,
much longer than head width ........................................ 10

3. Tarsi 4, 5, 5-segmented ............................................. 4
   Tarsi 4, 4, 4-segmented (long fourth segment frequently broken off) ...... 6

4. Eyes absent; wings either absent or reduced to small pads; elytra fused along
the suture .......................................................... Mandera
   Eyes present; wings fully developed .................................. 5
5. Antennae 10-segmented, only the apical segment visible from above; antennal fossae very deep; size very small. **Anommatatoxenus**

Antennae 11-segmented, all segments visible from above; size large. **Pygostenus**

6. Eyes absent. **Lydorus**

Eyes present. **7**

7. Antennae 8-segmented; head with dorsal “eaves” projecting laterad and covering the eyes. **Aemietoxenus**

Antennae 11-segmented. **8**

8. Maxillary palpi 3-segmented; body size large. **Mimocete**

Maxillary palpi 4-segmented; body size small. **9**

9. Species associated with doryline ants in the Ethiopian Region; antennae shaped as in Kistner’s fig. 28F. **Doryloxenus**

Species associated with termites (Odontotermes) in the Oriental Region; antennae shaped as in Kistner’s fig. 24G. **Odontoxenus**

10. Eyes absent; wings reduced or absent; elytra reduced and fused. **Dorylotothyphlus**

Eyes present; elytra not fused. **11**

11. Pronotum with a median cleft; wings reduced to pads. **Eupygostenus**

Pronotum without a median cleft; functional wings present. **Typhloponemys**

12. Abdomen broadest at third segment. **13**

Abdomen broadest at fourth segment. **15**

13. Tarsi 4, 4, 4-segmented. **Xenidus**

Tarsi 4, 5, 5-segmented. **14**

14. Tarsi with numerous membranous setae. **Delibius**

Tarsi without membranous setae. **Neopygostenus**

15. Apical margin of third and fourth tergites not notched; tarsi 4, 5, 5-segmented. **Anommatophilus**

Apical margin of third and fourth tergites notched on each half; tarsi 4, 4, 4-segmented. **16**

16. Eyes absent; wings reduced or absent; elytra reduced in length but not fused along suture. **Typhlopoolemon**

Eyes present; wings not reduced; elytra not reduced in length. **17**

17. Mesosternal process acute but not carinate. **Deliodes**

Mesosternal process blunt. **18**

18. Anterior part of elytra grooved; size large. **Sympolemon**

Elytra not grooved; size small. **Micropolemon**

**TYPHLOPONEMYS - MIMOCETE Series**

Genera characterized by approximate mesocoxae, and slender, carinate mesosternal process. Two noteworthy trends are indicated in this series: Progressive development of fusiform body types; and regressive specializations such as eyelessness, aptery, and reduction of tarsal and antennal segmentation. The latter were evidently evolved independently on several occasions in societies of hypogaeic hosts *Dorylus*, s. s. and *Typhlopoone*. Fusiform body form character-
izes *Mandera, Pygostenus, Anommatoxenus,* and *Lydorus,* and reaches its extreme in *Doryloxenus* and *Mimocete.* Eyelessness evidently occurred independently in *Dorylotyphlus, Mandera,* and *Lydorus;* aptery in *Eupygostenus, Dorylotyphlus,* and *Mandera.* Leaf-like membranous tarsal setae occur in a line including *Doryloxenus, Odontoxenus,* and *Aenictoxenus,* and *Mimocete.*

**Typhloponemys** Rey


The species placed in this genus by Kistner, with the exception of Rey’s *hypogaea* and Kistner’s new species, were formerly assigned to *Pygostenus.* This is a large number for the genus has 62 recorded species, placed by Kistner in twenty species groups. *Typhloponemys* is regarded as the most generalized genus of the tribe, with a body form not very different from that of generalized aleocharines. Few morphological specializations, if any, that one might associate with dorylophily are manifested. A large majority of its species occur in equatorial Africa with the driver ants *Anomma.* The type species, though, was collected near a colony of *Dorylus (Typhlopone)* in Israel, and in South Africa several species are recorded with *Dorylus,* s. s. Members of the genus are attracted to lights in large numbers and a considerable number of species have been collected only in this way.

**Eupygostenus** Wasmann


One species is recorded with *Dorylus* s. s. in Eritrea. It is closely allied to *Typhloponemys* from which it is distinguished by pronotal form and reduction of wings.

**Dorylotyphlus** Bernhauer


One species is recorded with *Dorylus* s. s. in South Africa; one, host unknown, in Ethiopia. These species are distinguished from *Typhloponemys* by absence of eyes, extreme wing reduction, and fusion of elytra.

**Pygostenus** Kraatz


Two species, host unknown, are recorded from the Gold Coast and French Equatorial Africa, respectively. Distinguished from
Typhloponemys by fusiform body, relatively short antennae, and legs covered by the expanded procoxae.

**Mandera** Fauvel

*Mandera* Fauvel, 1899, Rev. d'Ent., 18, p. 15.

One species, host unknown, is recorded from Tanganyika. Related to *Pygostenus*, it is distinguished by an extremely shortened metasternum, lack of eyes and wings, and reduced elytra.

**Anommatoxenus** Wasmann


One species, with *Anomma*, is known from the Belgian Congo. It is distinguished from *Pygostenus* by its smaller size and 10-segmented antennae. This fusiform genus is reminiscent of the American tachyporine genus, *Vatesus*; the legs, in particular, with their array of strong spines (Kistner, 1958, fig. 22) are very much like those of *Vatesus*.

**Lydorus** Normand


One species recorded with *Dorylus* (*Typhlopone*) in Tunisia, one with *Aenictus* in Kenya. Most closely allied to *Anommatoxenus*, *Lydorus* may be distinguished by lack of eyes, 4, 4, 4-segmented tarsi, and membranous tarsal setae.

**Odontoxenus** Kistner


Kistner proposed this genus for twelve termitophilous Oriental species formerly in *Dorylo xenus*, a genus of Ethiopian dorylophiles. There is no reason to discuss this genus here, but it may be pointed out that close relationship between obligate termitophilous and dorylophilous genera is perhaps unique among the Staphylinidae.

**Aenictoxenus** Seevers


One species is recorded from the Philippines. Its affinities are not clear, for it has several unusual features, but Kistner places it in the vicinity of *Odontoxenus*. 
Doryloxenus Wasmann


Thirteen species are known; a majority occur with *Anomma* in equatorial Africa, but a Tunisian species was found with *Dorylus* (*Typhlopone*), and a South African species, host unrecorded, probably occurs with *Dorylus* s. s.

As now constituted, this is a genus of strongly fusiform species close to *Mimocete*. The tarsi are 4, 4, 4-segmented, the antennal insertions very deep, the antennae short and strongly compressed, and the eyes entirely on the sides of the head (no eye surface on anterior face of head).

Mimocete Fauvel


The seven species occur in equatorial Africa, all with *Anomma* when the host is known. The fusiform species are larger than those of *Doryloxenus* and the maxillary palpi are 3-segmented.

**NEOPYGOSTENUS - XENIDUS Series**

Characterized by widely separated mesocoxae; broad, non-carinate mesosternal process; and other features. Host relationships of the members of this series are unknown.

Neopygostenus Cameron


Two species, host unknown, are known from Angola and Somalia. Kistner designated this the most generalized of its phyletic series. Believing it to be derived from a *Typhloponemys*-like stock, he noted that it differs from that genus not only in the widely separated mesocoxae but in head and pronotal shape as well.

Delibius Fauvel


One species is recorded from Singapore, host unknown.

Xenidus Rey

*Xenidus* Rey, 1886, Rev. d'Ent., 5, p. 254.

One species recorded from Sumatra, host unknown.
ANOMMATOPHILUS - SYMPOLEMON Series

This series has broadly separated mesocoxae as in the preceding group and may have evolved in common with it. Kistner characterizes the species as attenuated in form with progressively longer bodies and head; all members have membranous tarsal setae.

Anommatophilus Wasmann


Three species from the Belgian Congo and Cameroons were recorded with Anomma. This is apparently the most generalized genus of this series.

Deliodes Casey


One species, host unknown, was recorded from Sumatra.

Micropolemon Wasmann


This and the following genera differ from Anommatophilus in having 4, 4, 4-segmented tarsi and membranous tarsal setae.

Typhlopolemon Patrizi


Two species, recorded with Dorylus s. s., were collected in Kenya and the Belgian Congo. The species are blind and wingless.

Sympolemon Wasmann


Sympolemon anomnatis Wasmann, the only recorded species, was designated by Wasmann as “the war companion of the driver ants.” It is a large-sized species, differing from Micropolemon in the shape of head, pronotum, and metasternum.
Tribe PHYLLODINARDINI


Wasmann proposed this African tribe for a single genus of two species, one probably invalid, associated with Anomma. Phyllodinarda is a distinctive genus having a limuloid form and a strongly compressed body. The anteroposterior axis of the head is shortened and part of the vertex and clypeus deflexed onto the ventral side. Only a small portion of the eye is visible from above and the antennae and mouthparts are visible only from the underside. The pronotum and elytra are explanate. The dorsum has an interesting vestiture of flat, subelavate setae. This type of dorylophile, with its limuloid form and protected appendages, was characterized by Wasmann as the defensive type (trutztypus).

The relationships of Phyllodinarda within the Aleocharinae are not clear; among various possibilities, it may occupy a rather isolated position of uncertain affinities, or it may be closely related to the Myrmedoniini. It may have been derived from a myrmedoniine genus, such as Myrmecohsa, which has a broadly explanate pronotum. Phyllodinarda does have exceptionally long galeae and lacinia and does have a longer metasternal than mesosternal process (although these processes are slender).

Phyllodinarda Wasmann. Figure 33, H, I.


Body form limuloid; compressed dorso-ventrally. Head with a short anteroposterior axis; strongly compressed; part of vertex and clypeus deflexed onto the ventral surface, only a small portion of each eye visible above; antennae, clypeus, labrum, and mouthparts visible only in ventral view (fig. 33, H); neck very narrow. Eyes moderately large, flat, with very fine facets. Antennae inserted under an arcade; strongly geniculate, the scape almost equal to segments 2–6 combined; segments 2–11 conjointly spindle-shaped. Maxilla large, galea and lacinia very long and slender. Pronotum very broad and explanate; apex emarginate, sides arcuate, base strongly bisinuate. Prosternum narrow (relative to pronotum), elongated between coxae to some degree; peritremes large, not fused to prosternum. Pronotal hypomera slightly inflexed to aid in incompletely closing the procoxal cavities. Elytra as broad as pronotum, explanate, their lateral margins upturned. Elytral epipleurae very broad, transverse. Mesocoxae small, set in margined acetoabula, approximate, the meso- and metasternal processes slender, the latter much the longer of the two. Legs short to moderate in length; femoral apices bilaminate, receiving up to half the tibia. Tarsi 4, 5, 5-segmented. Hind coxae strongly transverse, anteroposterior axis short. Abdomen broad at base, tapering to a
moderately broad apex; dorsum feebly convex, venter only slightly convex. Abdomen without noteworthy features, except possibly for a long groove on each side of the seventh tergite. Head, pronotum, elytra, tergites and sternites with numerous distinctive, subelavate setae. Length, 6–7 mm.; width, 3–3.5 mm.

**SPECIES OF PHYLLODINARDA WASMANN**


**Remarks.**—I have been unable to detect significant differences between Wasmann’s two species; the type series and other specimens were examined.
Tribe TRILOBITIDEINI

Subfamily Trilobitideidae, Fauvel, 1899, in Raffray and Fauvel, Rev. d'Ent., 18, p. 3.

Fauvel believed that the remarkable limuloid genus Trilobitides Raffray was distinctive enough to be set apart in a monotypic subfamily. Wasmann concurred in this view but recognized that this genus might be an aberrant aleocharine. With the discovery of Phyllodinarda, Wasmann (1916) believed that he had a link between the Aleocharinae and Trilobitides, although he still held to the concept of subfamily status for the latter. In the Coleopterorum catalogus (Bernhauer and Scheerpeltz, 1926), the subfamily category is retained.

A slide preparation of Trilobitides reveals the fact that it is, indeed, an aberrant aleocharine. The aedeagus (fig. 33, E) is unmistakably aleocharine in structure, having the distinctive parameres of the subfamily. Because Trilobitides has many specialized features and occupies an isolated position in the Aleocharinae, it seems advisable to place it in a monotypic tribe. Trilobitides may be more closely related to Phyllodinarda than I think it is, but I do not believe that present evidence supports the view that these genera stemmed from a common ancestor.

Trilobitides Raffray. Figure 33, A–G.


Form (fig. 33, D) limuloid, strongly compressed dorsoventrally. Head very broad, apical margin arcuate, basal margin bisinuate; antennae and mouthparts invisible from above. Eyeless. Antennae in deep fossae that extend almost to middle of head (fig. 33, F). Gula broad and long; with impressions in positions of gular sutures; posterior tentorial pits conspicuous; submentum short and broad; mentum very large. Maxillary palpi 4-segmented, moderate in size; labial palpi 3-segmented, small. Antennae 10-segmented; distal segments much enlarged. Neck slender. Pronotum short, broad, explanate. Elytra conjointly very similar to pronotum. Prosternum apparently fused to pronotum, sternonotal sutures absent. Procoxae globose; mesocoxae globose, widely separated by a large metasternal process. Mesosternum oblique; metasternum behind mesocoxae very short. Metacoxae transverse. Metepimera large. Legs broad and short; tarsi very small; 4, 4, 4-segmented. Abdomen broad at base, tapering to a slender apex. Aedeagus as in fig. 33, E. Length, 2–2.9 mm.
SEEVERS: STAPHYLINID BEETLES

SPECIES OF TRILOBITIDEUS RAFFRAY


_wasmanni_ n. sp. Host: _Dorylus (Anomma) sp._ CAMEROON.


**Trilobitideus wasmanni**, new species. Figure 33, D–G.

Distinguished from the other species by the pattern of tubercles on the head, pronotum, and elytra (compare figs. 33, A, B, C, D); the patterns are species specific throughout the genus. This species seems to be most closely related to _T. singularis_ Wasmann.

Coloration light-brown. Head almost two and one-half times broader than long; pronotum four times as broad as long. Length, 2 mm.

*Type* (a slide preparation) from Gr. Batanga, Cameroon, collected June 23, 1911, by G. Schwab; with _Anomma sjoestedti rufescens_. In Chicago Natural History Museum.
Tribe ALEOCHARINI (sensu latu)

Wasmann (1900) proposed *Ecitodulus* for a single Brazilian species collected from a colony of *Neivamyrmex*. Whether or not *Ecitodulus* is a true ecitophilous genus has never been determined. In view of its 5, 5, 5-segmented tarsi, *Ecitodulus* has been placed in the tribe Aleocharini. Blackwelder’s (1944) catalogue places it more precisely in the subtribe Dinardae with *Euthorax* and *Fauvelia*. Although I have not studied the problem thoroughly, the above arrangement is satisfactory for the present. *Euthorax* and the other relatives of *Ecitodulus* are myrmecophilous but do not occur with army ants.

**Ecitodulus** Wasmann


**SPECIES OF ECITODULUS WASMANN**

Subfamily PAEDERINAE:

Tribe PAEDERINI

Three groups of obligate paederine genera occur with the Ecitonini in the Neotropical Region: Mimophites, Ecitonides, and Ecitonemdon groups. Characteristics that are often associated with dorylophily, and considered to be adaptive, rarely appear in the ecitophilous paederines; there are no myrmecoid forms with petiolate abdomens, and the only limuloid form is Ecitosaurus.

More frequently than not, Mimophites has been placed in the same section of the Paederini with the Ecitonides group. Fauvel in naming Mimophites and Bolbophites apparently judged them to be close to Opithes Blackwelder (=Ophites Erichson). Bernhauer and Schubert (1916) placed Fauvel’s genera as well as Ecitonides near Opithes. In his revision of the Paederini, Blackwelder (1939) did not consider the ecitophilous genera, but in a catalogue of the Latin American beetles (1944) placed Mimophites near Ophites in the Cryptobii, and assigned Bolbophites, Ecitonides, Synecitonides, and Ecitotropis to the Echiasteres near Myrmecosaurus.

It seems evident that Mimophites and the Ecitonides generic group belong to different sections of the tribe. The resemblance of certain genera to Opithes is superficial and does not indicate relationship to the Homaeotarsus section of the Paederini. Mimophites appears to belong to Casey’s (1905) subtribe Stilici, a group included in Blackwelder’s (1944) Lathrobi. The Ecitonides group may belong to the Echiasteres but their relationship to Myrmecosaurus, a genus of myrmecophiles occurring with higher ants (e.g., Solenopsis), is questionable.

MIMOPHITES Group

It is my opinion that Mimophites is not closely allied to Opithes as all previous writers have suggested. As late as 1956, Borgmeier in a species revision of Mimophites compared that genus with Opithes. Characters that indicate a closer relationship to the Stilici are: antennae posteriorly flexible, scape moderately long, prosternum extending between procoxae but not expanded behind to approach or meet the pronotal hypomera, fourth maxillary palpmere not compressed or truncate, posterior tibiae with a ctenidium on only one surface at the distal end, neck slender, gular sutures united for most of their length, or absent.
Mimophites Fauvel. Figure 34, J.


Dorsum without tubercles or carinae (several species have a short, medial pronotal carina). Head broadest at eye level, subtriangular, tapering to a neck one-third or less maximum head width (occipital region expanded above neck in some species, e.g., *borgmeieri*). Eyes large, with a caudal notch. Antennae long and slender, all segments elongated; posteriorly flexible. Neck with a subglobose occipital condyle. Gular sutures united except immediately behind submentum. Pronotum strongly convex; broadest near middle, with or without a sharp keel in apical half. Prosternum very large, prolonged between procoxae. Peritremes small. Elytra generalized. Abdomen generalized in appearance, perhaps somewhat ellipsoidal in some species although the dorsum is not strongly convex. Legs elongated, slender. Sternites 5–8 modified in the males of some species. Ninth segment sclerites without vestiture of long, curved bristles.

**SPECIES OF MIMOPHITES FAUVEL**


**ECITONIDES Group**

This group is provisionally placed in the Echiasteres following Blackwelder (1944) although I have not made a study of that group to verify the relationship.

The two phyletic series of this group contrast strongly in appearance and one might be inclined to doubt their common origin were it not for the distinctive vestiture of long curved black bristles on
the ninth abdominal segment (fig. 34, G) of both sexes. Extreme elongation of the body and appendages characterizes the Bolbophites-Ecitonides series and integumental tubercles frequently adorn the body; in the Ecitotropis series, the body and appendages are short and compact and integumental carinae are frequently present. In the latter series, Ecitosaurus is sublimuloid in form.

**BOLBOPHITES - ECITONIDES Series**

Members of this series are characterized by extremely elongated bodies and appendages and by numerous tubercles (except in Labidophites).

**Bolbophites** Fauvel. Figure 34, B, G, H, I. *Bolbophites* Fauvel, 1904, Rev. d'Ent., 23, p. 278. Type species: *Bolbophites aspericeps* Fauvel.

Head, thorax, and abdomen extremely long and slender, the head and pronotum particularly distinctive (fig. 34, B). Antennae long and slender, with scape as long as the three following segments. Head lacks tubercles, but pronotum, elytra, and tergites 3–5 with prominent eminences; pronotum has five irregular rows, elytra also have five irregular rows (those of third row small; fifth row is on side margin), tergites have seven apical and one median subapical tubercles. Legs very long and slender. Sides of abdomen subparallel.

**SPECIES OF BOLBOPHITES FAUVEL**


**Ecitonides** Wasmann. Figure 34, A.


This genus is noteworthy for the extreme development of integumental tubercles (fig. 34, A). These eminences are distributed as follows: upper and lower surfaces of head, pronotum, prosternum, elytra (six rows), meso- and metasternum, and tergites 3–5 (or 6). The sixth tergite and the sternites may have ridges that extend beyond the apical margin giving the border a scalloped effect. The antennae are shorter than those of the other members of this series; the scape is elongated, however, and may equal segments 2–5 (or 6) combined; segments 2–11 are not much longer than broad. The head is slender and elongated and the sides converge feebly to a moderately broad base. The legs are relatively short and stout and
have numerous peculiar setigerous tubercles. The distal half of the tibiae may have extensive areas of golden pile (usually distal to a tibial constriction). The abdomen tapers moderately from base to apex.

SPECIES OF ECITONIDES WASMANN


*verrucosus* Bruch, 1933, Rev. Ent., 3, p. 12, figs. 1–9, pl. 1, fig. 3. Host: *Labidus coecus* Latreille. ARGENTINA: Misiones, Loreto.

**Synecitonides** Reichensperger. Figure 34, C.

*Synecitonides* Reichensperger, 1936, Rev. Ent., 6, p. 236. Type species: *Synecitonides phasma* Reichensperger.

Seemingly closer to *Bolbophites* than *Ecitonides*, this genus differs from the former in having rows of tubercles on the head, smaller sized tubercles in general, and in the form of the head and pronotum (fig. 34, C).

SPECIES OF SYNECITONIDES REICHENSPERGER


**Labidophites** Borgmeier


Allied to *Synecitonides*, this genus closely resembles it in body form and in the structure of the appendages. *Labidophites* lacks the rows of tubercles that characterizes *Synecitonides* and bears several prominent carinae. The head has a supra-orbital carina extending from the antennal insertion to a point behind the eye and a median
carina extending from base of head to the level of the base of the eyes (this carina bifurcates at base), the pronotum has a median, non-keeled, ridge. The antennae of *Labidophites* are longer and more slender than in *Synecitonides*, and are more than twice as long as the head (less than half as long as head in the latter).

**SPECIES OF LABIDOPHITES BORGMEIER**


**ECITOTROPIS - ECITOBİUM - ECITOSAURUS Series**

The three genera of this series contrast strongly with the other genera of the *Ecitonides* group. The body is shorter, broader, and more compact, and in *Ecitosaurus* sublimuloid. The appendages are moderate in length in *Ecitotropis* and short, stout, and compact in the other genera. All three genera have carinae and other eminences on the head, pronotum, and elytra and *Ecitobium* and *Ecitosaurus* have carinae on the abdomen as well. The eyes are partially to almost entirely covered by extensions of the head but are completely visible from the side and front.

**Ecitotropis** Borgmeier. Figure 34, D.


Relatively generalized in form. Head and pronotum with eminences as in fig. 21, D. Elytra with five longitudinal carinae. Abdomen without carinae. Antennae moderately long; scape clavate but not extremely broad; segments 3–10 transverse (*micromma*) to elongated (carinata). Eyes scarcely visible from above (*micromma*) to moderately so (carinata). Legs relatively generalized.

**SPECIES OF ECITOTROPIS BORGMEIER**


**Ecitobium** Wasmann. Figure 34, E.


Form shorter and more compact than in the preceding genus; head, pronotum, and elytra transverse; abdomen relatively broad and compact. Head and pronotum with eminences as in fig. 34, E. Elytra with five longitudinal carinae (lower and broader than in *Ecitotropis*). Antennae very short and stout; basal segment
exceptionally broad and stout; segments 2–10 strongly transverse and compactly arranged (segments 4–6 extremely short and plate-like). Tergites 3–6 with 8 low, smooth ridges (obsolescent on 6); apical margin appear scalloped due to emarginations between apices of the ridges. Legs very short and compact; femora and tibiae exceptionally broad and short, femora grooved to receive tibiae; tarsal segments short and broad.

SPECIES OF ECITOBium Wasmann


Ecitosaurus Fischer. Figure 34, F.


This bizarre genus attains a sublimuloid form, broad in front and tapering to a slender abdominal apex. The body is strongly compressed dorsoventrally. The head, pronotum and elytra are broad and somewhat explanate laterally. Head and pronotum as in fig. 34, F. Eyes partially concealed. Antennae similar to those of Ecitobium but less extreme, the segments are not as short nor as transverse. Many antennal segments bear a dense golden pile on the medial side. Elytral carinae low and obsolescent. Tergites with ridges as in Ecitobium but they are low and less conspicuous. Legs are very short and compact as in Ecitobium.

SPECIES OF ECITOSAURUS FISCHER

crustaceus Borgmeier, 1931, Rev. Ent., 1, p. 356, figs. 1–5, 8–9 (Labidosaurus); 1949, Rev. Ent., 20, p. 106.

ECITOMEDON Group

This small group includes two genera of obligate ecitophiles without particularly noteworthy features. Blackwelder (1944) places Ecitomedon near Medon in his catalogue of Latin American Staphylinidae.

Ecitomedon Bernhauer

SPECIES OF ECITOMEDON BERNHAUER


*harpaz* Reichensperger, 1933, Rev. Ent., 9, p. 95. Host: *Eciton vagans* Olivier COSTA RICA: San José.


**Ecitocleptis** Borgmeier


SPECIES OF ECITOCLEPTIS BORGMEIER


*microps* Borgmeier, 1958, Stud. Ent., 1, p. 228, fig. 2. Host: *Labidus coecus* Latreille. COSTA RICA.


**Subfamily STAPHYLININAE**

A very few species of the major subfamily Staphylininae, which includes many of the largest and most colorful rove beetles, are adapted to life in insect societies. Termitophilous species are unknown, and the myrmecophilous species are almost all associates of army-ant societies in the American tropics. Thus, several groups fall within the scope of this work—the obligate Ecitophytes and Ecitolycus groups and Phileciton.

**ECITOPHYTES** Group (Tribe Staphylinini)

Ecitophytes Wasmann Host: Eciton
Proxenobius n. gen. Eciton
Xenobius Borgmeier Nomamyrmex

**ECITOLYCUS** Group (Tribe Quediini)

Termitoquedius Bernhauer Eciton
Ecitolycus Wasmann n. syn.

**PHILECITON** Wasmann Labidus
(This genus is very doubtfully distinct from Erichsonius Fauvel.)

**Tribe STAPHYLININI: ECITOPHYTES Group**

The most noteworthy of the staphylinine ecitophiles is Ecitophytes, a remarkable myrmecoid genus with a petiolate abdomen. Ecitophytes bears a striking resemblance to the aleocharine genus Ecitophyta, and Wasmann was doubtless influenced by this fact in his assignment of the genus to the Aleocharinae. My early suspicion that Ecitophytes is not an aleocharine was easily verified by examination of its aedeagus.

None of the three genera of the Ecitophytes group has previously been placed in the tribe Staphylinini. None bears a superficial resemblance to the members of this tribe and only a careful analysis reveals the affinity. Of the three genera, Proxenobius is the most generalized, Xenobius modified but not myrmecoid, and Ecitophytes very highly specialized, indeed. When studied without reference to its closest allies, Ecitophytes is not easily placed in the proper subfamily. The structure of its aedeagus does not clearly indicate whether the genus is paederine or staphylinine. The relatively long fourth segment of the maxillary palpus, which is short in the Paederini, and the distinctive pattern of the intersegmental abdominal membranes (Blackwelder, 1936) indicate staphylinine relationship.
Conclusive evidence of its membership in the Staphylininae is established through its link with Xenobius which has the same distinctive areas of golden-yellow pile on special areas of the tibiae.

Tribal assignment within the Staphylininae has required careful consideration. Xenobius was placed in the Xantholini by Borgmeier (1931a) but membership in that tribe is precluded for the following reasons: the pair of distinctive xantholine sclerites in front of the prosternum is absent; the prominent frontal lobe between antennal insertions is absent; and the inner elytral margins do not overlap. Thus, the choice of tribes is narrowed to the Quediini, Xanthopygini, and Staphylinini. These tribes are usually differentiated by pronotal characters involving the hypomera and their margination. Inasmuch as Xenobius and Ecitophytes have very specialized pronota, it would be preferable to use characters of other parts of the body for final judgment as to tribal position, but apparently such diagnostic characters have not been determined. In Xenobius (fig. 35, D), the pronotal hypomera are margined above and below—the so-called double margination; in Ecitophytes, the sides of the pronotum are so deeply inflexed behind the procoxae that the hypomera are very poorly delimited, but in front of the procoxae the double margin is faintly visible for a short distance. The double-margined condition of the hypomera apparently eliminates the Quediini from consideration, and the union of the margins a short distance in front of the coxae seems to rule out the Xanthopygini. It is my opinion that the three genera belong to the Staphylinini. Prozenobius came to my attention after I had made the above decisions, and being more generalized than other genera provided support for them. Prozenobius, although not much more generalized than Xenobius, lacks the golden-yellow pile on the tibiae.

Within the Staphylinini the position of this generic group is not clear, but, although isolated, may prove to be closest to that of Staphylinus.

Xenobius Borgmeier. Figure 35, C, D.

Xenobius Borgmeier, 1931, Rev. de Ent., 1, p. 358. Type species: Xenobius rotundiceps Borgmeier.

Head and pronotum as in fig. 35, C; elytra and abdomen generalized except that the latter tapers distally. Head subequal in length and width, circular in outline; neck two-fifths as broad as head; antennal insertions exceptionally close together; clypeus vertical; labrum horizontal. Eyes small, about one-fourth as long as head. Antennae robust; pubescent from about the fourth segment. Gular
sutures united except in the neck region. Palpi slender; fourth maxillary palpomere subequal to third, more slender; third labial palpomere longer than second. Integuments with a very fine-meshed raised reticulation, and with scattered non-umbilicate punctures.

Pronotum more than two-fifths longer than broad; sides bisinuate, converging strongly in apical two-thirds; apex narrow, almost straight; base arcuate; hypomera margined above and below, the margins united a short distance in front of procoxae. Prosternum prolonged between procoxae for a moderate distance; mesothoracic peritremes small; prothorax without secondarily formed sclerites behind prosternum. Elytra longer than pronotum. Abdomen broad at base, tapered to a slender apex. Legs with areas of pale-golden pile as follows: On inner surface of anterior
and middle tibiae (distal half); on entire inner surface (not plantar surface) of basal segment of middle tarsi. Tarsi dorsoventrally compressed.

**SPECIES OF XENOBUS BORGMEIER**


**Ecitophytes** Wasmann. Figure 35, E, F.


Head extremely long (fig. 35, E); broadest at eye level, sides converging uniformly to the slender neck; clypeus very short; labrum bilobed; antennae inserted under vertexal ridges; eyes moderate in size. Antennae robust; segments 4-11 pubescent. Gular sutures fused for about two-thirds of their length, diverging to the short submentum; mentum very short, emarginate; fourth maxillary palpomere two-thirds longer than third; third labial palpomere longer than second. Integuments with a very fine-meshed reticulation; head and pronotum with a moderate number of umbilicate punctures.

Pronotum exceptionally long (fig. 35, E); strongly constricted behind procoxae; pronotal hypomera not delimited from dorsum for the most part, and with a double margination for a short distance in front of procoxae. Prosternum produced for a short distance between procoxae, and contiguous with an independent sclerite which is contiguous with the inflexed hypomera and the mesothoracic peritremes (small, spiral-bearing sclerites wedged between the unnamed sclerite and the hypomera). Mesocoxae moderately separated. Legs very much elongated; procoxae spindle-shaped, mesocoxae similar but shorter; metacoxae elongated, subcylindrical, subequal in thickness throughout. Legs with a nearly uniform vestiture of aciculate setae. Tarsi similar in both sexes, anterior tarsi not enlarged. Legs with areas of golden-yellow pile as follows: On inner surface of distal half of anterior tibiae; on medial surface of basal segment of middle tarsi (not on plantar surface). The protarsi have a clothing of long, fine, yellowish hairs not arranged in a dense pile. Abdomen (fig. 35, F) petiolate; third segment with parallel sides, the distal segments combined form a small, ovoid "gaster." Third tergite with a median keel separating two moderately deep impressions; third sternite with a dorsal impression on each side. Length, 6.5-9 mm.

**SPECIES OF ECITOPHYTES WASMANN**


**Proxenobius**, new genus. Figure 35, B.

Type species: *Proxenobius borgmeieri* n. sp.

Distinguished from *Xenobius* by the form of the head and pronotum (fig. 35, B), and by the lack of areas of golden pile on the tibiae.
Head elongated, about one-fourth longer than broad, excluding labrum; sides subparallel, the basal angles rounded; base emarginate. Eyes small, one-third as long as head, finely faceted. Gular sutures fused in middle third only. Antennae inserted under an arcade which bears a medial process; fossae (viewed from in front) separated by a distance somewhat less than the length of antennal scape. Antennal segments with the following relative lengths: 56 : 20 : 30 : 24 : 24 : 26 : 26 : 25 : 25 : 36; third segment longer than broad, 4–10 subequal in length and width. Pronotum more than one-tenth longer than broad; form (fig. 35, B distinctive, strongly convex, the disk strongly declivous laterad to a narrow marginal horizontal area. Elytra and abdomen generalized.

Proxenobius borgmeieri, new species. Figure 35, B.

Head piceous, mouthparts reddish, antennae rufopiceous, remainder of body rufous. Head and pronotum with an extremely fine-meshed reticulation, giving the appearance of a fine granulation. Head and pronotum with a moderate number of coarse setigerous punctures, the dark setae of moderate length. Elytra finely reticulate, with a moderately dense vestiture of pale recumbent hairs and sparse, erect, dark setae. Abdomen with a uniform vestiture of recumbent rufous setae and scattered erect setae. Length, 8.75–9.25 mm.

Tribe STAPHYLININI

Phileciton Wasmann

*Phileciton* Wasmann, 1894, Krit. Verz., p. 211.

*Phileciton* is very doubtfully distinct from *Erichsonius* Fauvel, 1872 (= *Actobius* Fauvel, 1876, and *Neobisnius* Ganglbauer, 1895). It runs to *Erichsonius* in Blackwelder’s (1943) key to the West Indian Staphylinidae (the only general work available on neotropical Staphylinidae), and I have compared *Phileciton badariottii* with many species of *Erichsonius* without finding any basis for generic separation. I shall not place *Phileciton* in synonymy at this time as a more thorough study of the problem is needed.

*Phileciton badariottii* has been repeatedly collected with *Labidus praedator* in Brazil and its relationship may be an obligate one. The following are recorded in Chicago Natural History Museum: 23 from Nova Teutonia, S. Catarina, April, 1952 (Fritz Plaumann); nine from Passa Quatro, Minas Gerais (J. F. Zikan); two syntypes from Serra d. Mantisquira, S. Paulo; two cotypes from Loreno, S. Paulo. Bernhauer’s *wasmanni* falls within the range of *badariottii* and is very doubtfully distinct.

**SPECIES OF PHILECITON WASMANN**

Tribe QUEDIINI: ECITOLYCUS Group

In this large tribe of free-living species, a few have become obligate ecitophiles. The precise position of these species within the tribe is not known, and the qualities that differentiate them not easy to define.

Termitoquedius Bernhauer. Figure 35, A.


Inappropriate as the name is, it must be recognized as the valid name of this genus. It was proposed by Bernhauer who guessed incorrectly the nature of its habits; neither he nor any other writer has recorded the capture of this genus with termites. Wasmann based Ecitolycus on an undescribed species, laticollis Wasmann (Blackwelder, 1952, p. 140). Wasmann’s species is herein validated through synonymy with iheringi Bernhauer, and Ecitolycus Wasmann becomes an available name and a synonym of Termitoquedius.

Head transverse, somewhat obcordiform (fig. 35, A); somewhat compressed, although the dorsum is moderately convex; base emarginate; gular sutures united in their middle one-third or more, narrowly separated at base. Head and pronotum superficially granulose due to a fine-meshed, raised reticulation. Head and pronotum with a moderately dense umbilicate punctation. Antennae inserted under a vertexal arcade that is almost transverse. Eyes small. Elytra and abdomen generalized. Length, 9–17 mm.

SPECIES OF TERMITOQUEDIUS BERNHAUER

gigas Borgmeier, 1959, Bol. Mus. Nac. (Brasil), n. s., Zool., no. 214, p. 4 (Ecitoly-
cus). Host: Eciton quadriglume Haliday. BRAZIL: Itatiaia, R. de J. 


quadriglume Haliday. BRAZIL: Minas Gerais (Passa Quatro) to Paraná 
(Rio Negro).
Fig. 36. *Ecitosius gracilis*, n. g., n. sp.: A, lateral view (middle leg omitted); B, dorsal view of abdomen, including second tergite; G, underside of head. *Ecitosius robustus*, n. g., n. sp.: C, lateral view (antennae, legs, and abdomen behind third segment omitted); D, maxilla; E, labium; H, underside of head. *Ecitosius miriventris*, n. g., n. sp.: F, lateral view (head and legs omitted).
Fig. 37. Ecitodonia major Wasmann: A, median lobe and paramere of aedeagus. Ecitodonia setigera, n. g., n. sp.: B, median lobe and paramere of aedeagus; E, antenna. Ecitana biimpressa, n. g., n. sp.: C, median lobe and paramere of aedeagus; D, antenna. Ecitosius gracilis, n. g., n. sp.: F, median lobe and paramere of aedeagus. Ecitosius robustis, n. g., n. sp.: G, median lobe of aedeagus; H, integumental sculpture of elytra.
Subfamily TACHYPORINAE: Tribe VATESINI

The tribe Vatesini contains one genus with more than twenty-five species. *Vatesus* Sharp is strongly limuloid in form as are many of the free-living Tachyporinae. *Vatesus* differs from other tachyporines chiefly in its specialized head structure and in its ecological association with army-ant societies.

Sharp proposed *Vatesus* for a single Brazilian species in 1876. Between 1887 and 1929 Wasmann added ten valid species to the genus under the generic name *Xenocephalus* Wasmann. Bruch, Mann, and Bernhauer added species to the list, and Bernhauer renamed the genus *Wasmannotherium* to replace the homonym *Xenocephalus*. Little was accomplished by the above-mentioned studies and the species of the genus were extremely difficult to identify. In 1958 I attempted to bring some order to the genus by synonymizing *Xenocephalus* and *Wasmannotherium* with *Vatesus*, utilizing a different set of characters for diagnostic purposes, redefining some of the named species, adding some new species, and providing a key to the species. In a more recent paper Bogmeier (1961) corrected several misinterpretations of Wasmann and Bruch species in my revision, described seven new species, and revised my key to reflect these changes.

Wasmann placed this genus of ecitophiles in the tribe Xenocephalinii of the subfamily Cephaloplectinae. It was demonstrated by Seevers and Dybas (1943) that *Cephaloplectus* Sharp is not a staphylinid genus and belongs more properly in the Limulodidae of the ptilioid beetle complex and that *Vatesus* is a tachyporine staphylinid. The tribe Vatesini (the name Xenocephalinii cannot be used as it is based on a homonym) differs from the Tachyporini in these respects: Head capsule so modified that most of the vertex, the clypeus, and the labrum lie in a horizontal plane and are visible only in ventral view; head so covered by the large convex pronotum that only a small part of the vertex and the large, reniform eyes are visible from the front; mouthparts directed caudad when head is at rest; the species are obligate ecitophiles.

**Vatesus** Sharp


SIEVERS: STAPHYLINID BEETLES


Limuloid in form, the pronotum and elytra very large and convex. Head strongly compressed and covered in large part by pronotum; only a part of vertex and eyes visible from in front; most of the vertex, the antennae and anten-nal fossae, the Clypeus, the labrum, and mouthparts visible only from the underside. Clypeus and labrum transverse and very large, the Clypeus either transversely convex or deeply concave; area of antennal fossae deeply impressed; frontal suture present. Eyes large, reniform. Antennae 11-segmented, geniculate; segments 4–10 transverse, 3–11 more or less compressed. Gula broad and moderately long; submentum indistinctly separated from postgenae; mentum large, its apex arcuate and its sides sinuate; ligula broadly bilobed. Labial palpi filiform, the third segment with few to many sensory papillae. Pronotum strongly convex, the hypomera extensive. Prosternum short, with or without short spines. Mesosternum not carinate, the mesosternal process slender to moderately broad. Metasternum very short behind middle coxae. Wings fully developed as a rule, greatly reduced in brevicornis. Anterior coxae extremely large, globose. Hind coxae transverse, with or without a lamina over base of femora. Legs moderately to heavily adorned with spines. Tarsi 5, 5, 5-segmented. Abdomen tapering to a slender apex, its segments frequently telescoped and subject to retraction under the large elytra. Eighth male sternite deeply emarginate; eighth female sternite arcuate medially and incised on each side.

SPECIALS OF VATESUS SHARP


panamensis Mann, 1925, Psyche, 32, p. 166 (Barro Colorado Island, Panama Canal Zone; with Eciton hamatum Fabricius).


punctipennis Bernhauer, 1917, Coleopt. Rund., 6, p. 5; Seevers, 1958, Rev. Bras. Ent., 8, p. 195, fig. 27; Borgmeier, 1961, An. Acad. Bras. Cien., 33, p. 205, figs. 21, 36. Host: Labidus praedator F. Smith. BRAZIL: Rio de Janeiro; Minas Gerais (Passa Quatro); Santa Catarina (Nova Teutonia); São Paulo (Boraceia); Goiás (Campinas).
KEY TO THE SPECIES OF VATESUS SHARP

1. Metacoaxae without a lamella that extends over base of femora
2. Metacoaxae with a large lamella that extends over base of femora
3. Pronotal hypomera closely pressed to dorsum and forming an acute angle with it
4. Pronotal hypomera curving away from the dorsum at the junction with it
5. Dark reddish-brown; sutural length of elytra about four-fifths pronotal length; pronotum and elytra with a vestiture of very short pale hairs (more numerous along sides than on disk)
6. Castaneous or light-brown; sutural length of elytra more than four-fifths pronotal length; pronotum and elytra with extremely few hairs
7. Elytral apices strongly emarginate near outer angles; metasternum with about eight bristles
8. Elytral apices weakly emarginate near outer angles; metasternum with two bristles
9. Elytral apices emarginate near outer angles
10. Elytral apices not emarginate near outer angles
11. A large species, 6–10 mm. in length (4.5 mm., excluding abdomen); sternal chaetotaxy as in Seevers, 1958, fig. 24
12. Sutural length of elytra equal to pronotal length; light to moderately dark reddish-brown; 3.5–4 mm. in length
13. Sutural length of elytra about nine-tenths pronotal length; flavo-testaceous; 3 mm. in length
14. Elytra with fine striations; sternites with the chaetotaxy of splendidus
15. Elytra with fine reticulation; sternites with the chaetotaxy of rettenmeyeri
16. Hind tarsi slender, subcylindrical
17. Hind tarsi stout, somewhat compressed
18. Pronotum smooth, without ground sculpture
19. Pronotum finely striated and sparsely punctulate
20. Eyes pale and indistinctly faceted; 2.5 mm. in length
21. Eyes dark; 3.1–4 mm. in length
22. Elytral apices almost straight; each elytron longer than broad
23. Elytral apices emarginate; elytron as long as broad
24. Seventh male sternite emarginate; sixth sternite not emarginate
25. Six male sternite emarginate


15. Elytral apices strongly emarginate. ........................................ 16
Elytral apices very slightly emarginate. ..................................... amapaensis
16. Elytra very minutely and relatively sparsely punctulate. .......... rufus
Elytra densely punctulate; the punctules accompanied by a fine transverse “fine”. .... 17
17. Coloration brown ............................................................... schuppi
Coloration rufous. .................................................................... argentinus
18. Associated with Labidus praedator ...................................... trilobita
Associated with Eciton quadriglume ........................................ limulus
19. Elytral apices emarginate; outer apical angles distinct. .... 20
Elytral apices not emarginate; outer apical angles obsolete. .... 23
20. Pronotum smooth, without ground sculpture. ...................... lucidus
Pronotum finely striated. ............................................................ 21
21. Hind tarsi broad and strongly compressed. ......................... 22
Hind tarsi relatively narrow. ..................................................... simulans
22. Sternites 3–7 (each half) with black bristles as follows: 2, 3, 3, 3, 3. punctipennis
Sternites 3–7 (each half) with black bristles as follows: 2, 4, 4, 4, 4, 2. praedatorius
23. Sternites 3–7 (each half) with black bristles as follows: 2, 4, 4, 4, 4, 3; coloration reddish-brown. .......... schneirla
Sternites 3–7 (each half) with black bristles as follows: 1, 2, 2, 2, 3; coloration reddish-yellow. .... 24
24. Elytra sutural length, 1 mm.; apical border of elytra not sinuate .... goeldii
Elytra sutural length, 0.85 mm.; apical border of elytra sinuate ... cincinnati

My 1958 key to the species of Vatesus attempted to bring some order to a genus which was in a taxonomically chaotic state. Borgmeier (1961) revised the key to correct several errors of species determination and to integrate seven new species. The revised key of this paper is designed to correct additional errors in both previous keys.

The section of the 1958 key dealing with clypeatus and its allies requires modification. The antennal character used to separate clypeatus from gigas is invalid; the third antennal segment of a large majority of specimens of clypeatus is longer than broad. At present I know of no means of differentiating clypeatus, gigas, and pana-mensis and in the key include them in the clypeatus species complex. This complex covers a wide range in the Neotropical Region from Mexico to southern Brazil and occurs with at least five species of Eciton: burchelli, hamatum, vagans, mexicanum, and rapax. Present collections provide an inadequate basis for analyzing a complicated situation. Borgmeier’s recently described goianus, a relative to clypeatus, is included in the key. V. goianus occurs with Eciton dulcius in Brazil and probably in Panama as well. Carl Rettenmeyer called my attention to the fact that specimens he collected with the same
host in Panama differ from *clypeatus*. They agree well with Borgmeier's description of *goianus*.

The section of Borgmeier's key dealing with the *schuppi* group of species seems to me to require revision; this group includes *schuppi*, *amapaensis*, *rufus*, *argentinus*, *trilobita*, and *limulus*. Studies on these species have been based on inadequate samples and errors of interpretation have been frequent. The material before me is certainly inadequate and the following conclusions tentative.

In 1958 I considered *trilobita* to be a synonym of *schuppi*, but Borgmeier (1961) correctly concluded that both species are valid. It seems unlikely, though, that his interpretation of *schuppi* is correct. His material came not from the type locality of *schuppi* (Sao Leopoldo, Rio Grande do Sul, Brazil) but from the Chaco Region of Argentina. Borgmeier stated that the male of *schuppi* has only the eighth sternite emarginate and keyed out the species on that character. Two specimens of *schuppi* in the Bernhauer collection bearing the label "Sao Leopoldo, R. G. do S., Heyer, Eciton omnivorum" are probably correctly determined and were probably seen by Wasmann. The male of the two has the seventh sternite emarginate. In this respect *schuppi* is similar to *rugus* and *amapaensis* (presumably *argentinus* as well, but I have not seen a male). *V. schuppi* and *amapaensis* differ from *rufus* and *argentinus* in coloration; the former are reddish-brown while the latter are reddish with a slight yellow cast. The difference in color is not a very safe key character as it is not easy to express. *V. schuppi* and *rufus* are much more closely allied than I originally thought they might be and they are easy to confuse. *V. trilobita* and *limulus* differ from the other species of this series in having the sixth male sternite emarginate. Except for its slightly larger size and different host relationship, I have found no reliable criteria for separating *limulus* from *trilobita*. Borgmeier separates them on the basis of antennal characters, but I am unable to confirm his observations. Measurements of dried, mounted specimens indicate that the tenth antennal segment in both species is almost twice as broad as long (Borgmeier stated that the tenth segment is one-half broader than long in *trilobita* and three-fifths broader than long in *limulus*). Borgmeier also stated that the terminal segment is as long as the two preceding segments in *limulus*, but shorter than these segments in *trilobita*. In the specimens that I examined there appeared to be little species difference and in all cases the terminal segment was shorter than the two preceding segments combined. Whether or not there are antennal differences be-
tween these two species I am not prepared to say, but the differences, if existing, do not make good key characters because of the telescoping of segments.

In his recent paper, Borgmeier placed considerable emphasis on antennal structure in *Vatesus* and provided outline drawings for twenty-three species. I am not convinced that antennal differences will provide suitable means of separating many of the closely allied species in this genus. Small differences are discouragingly difficult to express and delineate.
Subfamily OXYTELINAE

In the New World the genus Ecitoclimax Borgmeier was proposed for a Brazilian species associated with Nomamyrmex, and in the Old World the Anisopsis complex of African species was considered by Fagel to be dorylophilous. As Ecitoclimax has been collected on only one or a few occasions, its importance as an ecitophilous genus has not been determined. A majority of the 26 recorded species of the Anisopsis complex were collected at light, but Fagel (1960) reports enough cases of association with army ants to strongly suggest an obligate relationship for all.

None of the dorylophilous Oxytelinae is myrmecoid in form, and the most noteworthy morphological feature of the Anisopsis group is their ornamentation of carinae, tubercles, and spinose eminences. There is an interesting parallel in the above respect between this and other groups of doryphiles such as the Paederinae, Ecitocharini, Deremini, and Myrmedoniini.

ANISOPSIS Complex (Old World)

In an excellent revision of this group, Fagel (1960) has summarized the present knowledge of the taxonomy of six genera and 26 species. About one-third of the species have been collected with Anomma, but a large majority of specimens were collected at lights.

GENERAS OF THE ANISOPSIS COMPLEX


Ecitoclimax Borgmeier (New World)


Borgmeier (1934) originally placed Ecitoclimax in the Aleocharinae and proposed the tribe Ecitoclimacini to receive it, but in 1949
he correctly assigned it to the Oxytelinae. Although I have not studied the Oxytelinae very intensively, it seems to me that Ecito-
climax is a distinctive genus probably related to Carpelimus Leach.

Head transverse; antennae inserted under exceptionally prominent ridges; vertex with a deep, uniformly concave, sulcus that broadens at base and contains in its basal half a pair of low, smooth eminences. Neck moderately broad. Antennae long, extending almost to middle of elytra; scape short, little longer than the following two segments combined; segments 2 and 3 small, 4–10 incrassate and moderately robust. Pronotum subequal in length and width; its sides and base slightly and continuously arcuate; basal angles obsolete; dorsum with a strong, irregular impression on each side, and with a narrow median ridge. Elytra generalized. Abdomen slender, narrower than elytra; tergites 3–7 strongly impressed at base and with basal half inordinately convex; a distinct impression between tergites and elevated paratergites and parasternites present. Legs generalized, anterior tibiae without row of external spines; tarsi 3, 3, 3-segmented. Coloration light reddish-brown (exceptionally light for the subfamily). Length, 4 mm.

SPECIES OF ECITOCLIMAX BORGMEIER
Position Uncertain: SYNAENICTUS PATRIZI

Patrizi (1947) described and figured a very remarkable beetle from Kenya, probably a guest of Aenictus, which he presumed belongs to the Staphylinidae. If it does belong to this family its subfamily affinities are certainly enigmatic. It seems to me that serious consideration should be given to the possibility that it belongs to the Pselaphidae. The most noteworthy features of Synaenictus Patrizi (which has not been available for study) seem to be: absence of eyes; the form of the 8-segmented antennae; the point of insertion of the antennae; the glabrous, one-segmented tarsi; the tubular abdominal segments of which all sclerites are fused; the distinctively modified terminal abdominal sclerites; and the presence of a large, deep, oval fossa presumably on the eighth tergite.

Synaenictus Patrizi

Type species: Synaenictus forcicauda Patrizi.

SPECIES OF SYNAENICTUS PATRIZI

Host: Aenictus sp. KENYA: Elmenteita.
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