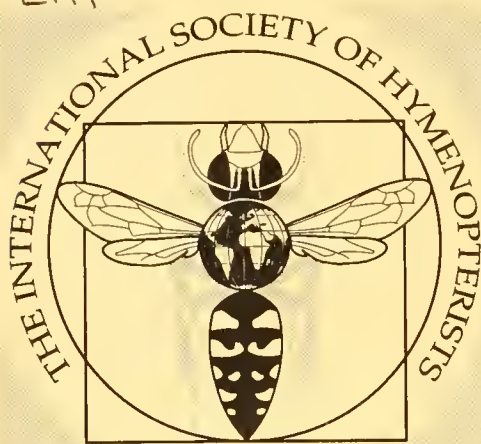




563
568X
E27



Journal of Hymenoptera Research

Volume 3

August 1994

ISSN 1070-9428

CONTENTS

ANTROPOV, A. V. A review of the *agile* species group of *Pison* (Hymenoptera: Sphecidae: Trypoxylini) 119

AZEVEDO, C. O. Descriptions of two new species and notes on the genus *Bakeriella* Kieffer from Brazil and Ecuador (Hymenoptera, Bethyridae) 145

BELSHAW, R. and B. BOLTON. A survey of the leaf litter ant fauna in Gahana, West Africa (Hymenoptera: Formicidae) ... 5

BITONDI, M. M. G., Z. L. P. SIMÕES, A. M. do NASCIMENTO and S. L. GARCIA. Variation in the haemolymph protein composition of confined *Apis mellifera* and potential restoration of vitellogenin titre by juvenile hormone analogue treatment 107

BOHART, R. M. A review of North American *Belomicrus* (Hymenoptera, Sphecidae, Crabroninae) 207

DINIZ, I. R. and K. KITAYAMA. Colony densities and preferences for nest habitats of some social wasps in Mato Grosso State, Brazil (Hymenoptera, Vespidae) 133

FIELD, S. A. and M. A. KELLER. Localization of the female sex pheromone gland in *Cotesia rubecula* Marshall (Hymenoptera: Braconidae) 151

GUPTA, V. K. A review of the world species of *Orthomiscus* Mason (Hymenoptera: Ichneumonidae: Tryphoninae) 157

HERATY, J. M., J. B. WOOLLEY and D. C. DARLING. Phylogenetic implications of the mesofurca and mesopostnotum in Hymenoptera..... 241

KERR, W. E and E. B. SOARES REZENDE. Genetic characters of African bees that have high adaptive value in the tropics . 1

KUGLER, C. Revision of the ant genus *Rogeria* with descriptions of the sting apparatus (Hymenoptera: Formicidae) 17

NIEVES-ALDREY, J. L. Revision of West-European genera of the tribe Aylacini Ashmead (Hymenoptera, Cynipidae) 175

OVRSKI, S. M. Immature stages of *Aganaspis pelleranoi* (Brèthes) (Hymenoptera: Cynipoidea: Eucilidae), a parasitoid of *Ceratitidis capitata* (Wied.) and *Anastrepha* spp. (Diptera: Tephritidae) 233

POLASZEK, A. and K. V. KROMBEIN. The genera of Bethylinae (Hymenoptera: Bethyridae) 91

QUICKE, D. L. J. *Myosomatoides* gen. nov. (Hymenoptera: Braconidae), a Neotropical larval parasitoid of stem-borer pests, *Diatraea* (Lepidoptera: Pyralidae) 227

QUINTERO A., D. and R. A. CAMBRA T. Systematics of *Pseudomethoca areta* (Cameron): sex association, description of the male and a gynandromorph, and a new synonymy (Hymenoptera: Mutillidae) 303

TANG, Y. and P. M. MARSH. A taxonomic study of the genus *Ascogaster* in China (Hymenoptera: Braconidae: Cheloninae) 279

Additions and corrections to Volume 2, Number 1, 1993 309

INTERNATIONAL SOCIETY OF HYMENOPTERISTS

Organized 1982; Incorporated 1991

OFFICERS FOR 1994

George C. Eikwort, *President*
Donald L. J. Quicke, *President-Elect*
Michael E. Schauff, *Secretary*
Gary A. P. Gibson, *Treasurer*
Paul M. Marsh, *Editor*

Subject Editors

John Huber, Arnold Menke, David Rosen, Mark Shaw, Robert Matthews

All correspondence concerning Society business should be mailed to the appropriate officer at the following addresses: President, Department of Entomology, Cornell University, Ithaca, New York 14853; President-Elect, Department of Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY, England; Secretary, c/o Department of Entomology, NHB 168, Smithsonian Institution, Washington, D.C. 20560; Treasurer, Biological Resources Division, CLBRR, Agriculture Canada, K.W. Neatby Building, Ottawa, Ontario, Canada K1A 0C6; Editor, P. O. Box 384, North Newton, Kansas 67117.

Membership. Members shall be persons who have demonstrated interest in the science of entomology. Annual dues for members are \$25.00 (U.S. currency) per year, payable to The International Society of Hymenopterists. Requests for membership should be sent to the Treasurer (address above).

Journal. The *Journal* is published once a year by the International Society of Hymenopterists, c/o Department of Entomology, NHB 168, Smithsonian Institution, Washington, D.C. 20560, U.S.A. Members in good standing receive the *Journal of Hymenoptera Research*. Nonmember subscriptions are \$50.00 (U.S. currency) per year.

The Society does not exchange its publications for those of other societies

Please see inside back cover of this issue for information regarding preparation of manuscripts.

Statement of Ownership

Title of Publication: *Journal of Hymenoptera Research*.

Frequency of Issue: Once a year (currently).

Location of Office of Publication, Business Office of Publisher and Owner: International Society of Hymenopterists, c/o Department of Entomology, NHB 168, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Editor: Paul M. Marsh, P. O. Box 384, North Newton, Kansas 67117.

Managing Editor and Known Bondholders or other Security Holders: none

This issue was mailed 15 October 1994



George Campbell Eickwort
1940-1994

We were saddened to hear of the untimely death of George Eickwort, President, International Society of Hymenopterists, on July 11, 1994. George died from injuries suffered in an automobile accident while vacationing in Jamaica. This issue of the Journal of Hymenoptera Research is dedicated to his memory and to honor his contributions to the study of Hymenoptera and to this Society.

First Announcement

Third International Hymenoptera Conference

**August 12-17, 1995
University of California
Davis, California, USA**

Talks, poster presentations and symposia on all aspects of Hymenoptera, including:

- Biological control
 - Behavior
 - Morphology
 - Genetics
 - Systematics

Also, possible tours of the Bohart Museum, California Academy of Sciences, San Francisco and the northern California wine country

To be put on mailing list for second announcement with registration and call for papers, send name, address, phone, fax and/or e-mail numbers to:

Dr. Lynn S. Kimsey
Department of Entomology
University of California
Davis, California 95616 USA
Phone: (916) 753-5373 FAX (916) 752-1537

A few grants to cover travel costs may be available to participants from countries with foreign currency or other financial problems. Mention your need when requesting the second announcement.

Genetic Characters of African Bees That Have High Adaptive Value in the Tropics

WARWICK ESTEVAM KERR AND EDUARDO BADUE SOARES REZENDE

Universidade Federal de Uberlândia, Departamento de Biociências, 38400-902, Uberlândia, MG, Brazil

Abstract.- The Ac gene present in Africanized *Apis mellifera* populations is male limited and confers bronze color to the abdomen; females are non-affected. The gene ac confers yellow abdomen equally to Italian female and male bees. African-mt-DNA is found in African and most Africanized populations, and European-mt-DNA occurs in European populations, and descendents. The original frequency in Camaquã in 1957 of ac was 0.939 and for Ac 0.061. In 1991, after about 68 generations, these frequencies changed to 0.038 to ac and 0.962 to Ac, what gives an adaptive value to ac in the tropics of 0.952 (considering 1.00 to Ac). The same may happen to the mt-DNAs, what may cause the mates European-mt-DNA queens X African-mt-DNA males to be less fit than the African-mt-DNA queens X European-mt-DNA males.

INTRODUCTION

There is a constant search in tropical research for characters that give to the bearer species a higher adaptive value when compared to European ones. This happened with corn, wheat, cabbage, apples, cattle, goats, etc. Many morphological, behavioral and physiological characters are being studied in European and African bees, and in their hybrids under different ecological conditions. Among them, two of the African characters are particularly interesting because within a few generations they became predominant in a tropical environment, but not in a temperate one. These characters are the gene Ac and the African-mt-DNA (that acts as a single gene). The population of this area is being well studied as far as their enzymes are concerned and show that the Africanized honeybee is an admixture of *Apis mellifera mellifera* (19.5%), *Apis mellifera ligustica* (3.8%) and *Apis mellifera scutellata* (76.7%) (Lobo et al. 1989; Del Lama et al. 1990).

The African-mt-DNA has been studied by Hall and Muralidharan (1989), Sheppard et al. (1991), Sheppard et al. (1991), Soares (1992) and others. It shows indications of high adaptive value in the tropics and low in southern South America (that has European-like climate), where it is dominated by European mt-DNA.

The Ac gene has been observed by Brazilian bee biologists since 1957. In 1969 the information published that it is male sex limited: it confers bronze color to the abdomen, especially to the tergites, while workers are yellow (Kerr 1969). It was present in 100% of the 145 queens collected in Africa and brought to Brazil in 1956. There was some information (Prof.V.Portugal Araujo, p.c.) that yellow males were occasionally present in Angolan populations. However, they were never seen by W. E. Kerr in his 1956 trip to Africa. It is an allele of b(=black) (Woyke and Kerr 1989), segregates 1Ac: 1ac in different genetic background, and is not linked to five components of aggressive behavior (Stort 1978).

MATERIAL AND METHODS

Between 19 July 1990 and 17 September 1991, 14 swarms of Africanized bees (*Apis mellifera* Linné) entered empty stingless bee hive boxes located in the Apiary of the Universidade Federal de Uberlândia, MG, Brazil. Hive boxes varied in size, from 15 to 45 litres in volume, located 420 km from Camaquã, the point of introduction of African bees, in 1957. All swarms contained many males. A sample of males was taken from each swarm and the numbers expressing the Ac and ac alleles were determined.

Males from an additional 17 colonies of Africanized bees were sampled from commercial honeybee hives that were occupied by Africanized swarms. Frequencies of the *ac* and *Ac* genes were calculated and compared with estimates of the frequencies of the same alleles in Camaquã in 1957.

RESULTS

Six hundred and ninety (690) *Ac* drones (0.9623) and 27 *ac* drones (0.0377) were sampled from the 31 colonies. No data for 1992 and 1993 were collected because all swarms (22 and 9, respectively) had only *Ac* drones. Drones in a swarm come from several colonies.

Some additional observations made are important to note: 1. Of the 14 swarms, only one had two queens (the same proportion found in Kerr et al. 1970), 2. in three swarms many bees with wax scales were seen, which indicates that bees of different ages were in the swarms, 3. in 1992 two and in 1993 two swarms arrived without males.

The lack of *ac* drones in 1992 and 1993 swarms is assumed to be a consequence of the population reaching fixation (100% *Ac* genes) or near fixation.

DISCUSSION

Since the gene *Ac* segregates independent of the *xo* gene, is independent of genes for defensive behavior and is an allele of **black** (*b*), the hypothesis that it was linked and continues to be linked with genes for high fitness after 68 generations of meiosis was discarded.

Several traits of Africanized bees have been and are being selected for Brazilian conditions (Page and Kerr 1991; Kerr 1992). The bees are becoming less aggressive; they are being selected for greater resistance to the *Varroa jacobsoni* mite (Moretto et al. 1991); they do not any more reject Italian foundation and they use fewer armadillo holes (Kerr 1992). The high frequencies of *Ac* and of African-mt-DNA are also a result of natural selection, since the degree of natural crosses between Africanized × Italian and Italian × Africanized are about equal when queens and drones of both races use the same mating ground

(Kerr and Bueno 1970).

In 1956, there were 400 Italian hives located in the same *Eucalyptus* forest into which 26 swarms of African bees escaped. All Italian colonies had *ac* and all African colonies had *Ac* genes. Therefore, assuming equal contributions of all escaped colonies to the breeding population, a frequency of 0.939 for the gene *ac* and 0.061 for *Ac* in 1957 was obtained for that original population. According to Winston (1992 pg. 40-42) an individual Africanized colony swarms about 16 times per year. Of course, this can only happen in the expansion phase of the population, before the population approaches the carrying capacity of the environment. According to Nascimento (1981 page 166), however, this figure, obtained in 1980, is 1.5 swarms per year. For our estimate a conservative "intermediate" figure of two successful swarms per colony per year will be used.

The original frequency F^{1957} of the gene *ac* (0.939) in 1957, multiplied, per generation, by its relative adaptive value (*w*) will give us the frequency F^{1991} for *ac* in 1991, that is 0.0377, 34 years later, or after 68 generations. Therefore: $F^{1991} = w^n \cdot F^{1957}$. In this formula *n*, the number of generations, is 68, F^{1957} is 0.939, F^{1991} is 0.0377 and our estimation for *w*, the fitness of *ac*, is 0.952 (considering 1.00 to *Ac*). This relatively low adaptive value *w* of *ac* is the reason for the almost universal presence of *Ac* in feral populations of *Apis mellifera* in tropical South America. It may be a similar reason for the high frequency of African-mt-DNA found in Africanized populations, that is colonies of European-mt-DNA queens × African-mt-DNA drones should be less fit than colonies of African-mt-DNA queens × European-mt-DNA drones.

The bronze color of the *Ac* drones may not be the cause of its fitness, since the workers are yellow and heat preservation by dark color would be better in temperate climate; the physiological reason are being studied.

ACKNOWLEDGMENTS

We thank the FAPEMIG (State of Minas Gerais Research Foundation) and CNPq (Brazilian National Research Council) for financial help and Dr. Robert E. Page, Jr. for correcting our English and for sound suggestions.

LITERATURE CITED

- Del Lama, M. A., J. A. Lobo, A. E. E. Soares, S. N. Del Lama, 1990. Genetic differentiation estimated by isozymic analysis of Africanized honeybee populations from Brazil and from Central America. *Apidologie* 21: 271-280.
- Hall, H. G. and K. Muralidharan. 1989. Evidence from the mitochondrial DNA that African honey bees spread as continuous maternal lineages. *Nature* 339: 211-213.
- Kerr, W. E. 1969. Genética e melhoramento de abelhas. In: *Melhoramento e Genética*. Organized by W.E.Kerr, in homage to Prof. F.G. Brieger. EDUSP, Melhoramentos, USP, São Paulo. Cap. XIV pg. 263-295.
- Kerr, W. E. 1992. Abejas africanas: su introducción y expansión en el continente americano. Subespecies y ecotipos africanos. *Industria Apícola* N° 13: 12-21.
- Kerr, W. E. and D. Bueno. 1970. Natural crossing between *Apis mellifera adansonii* and *Apis mellifera ligustica*. *Evolution* 24(1): 145-148.
- Kerr, W. E., L. S. Gonçalves, L. F. Blotta and H. B. Maciel. 1970. Biología comparada entre abelhas italianas (*Apis mellifera ligustica*), africana (*Apis mellifera adansonii*) e suas híbridas. *Anais do 1° Congresso Brasileiro de Apicultura* (Florianópolis, SC) pg. 151-185.
- Lobo, J. A., M. A. Del Lama, and M. A. Mestriner. 1989. Population differentiation and racial admixture in the Africanized honeybee (*Apis mellifera* L.). *Evolution* 43(4): 794-802.
- Moretto, G., L. S. Gonçalves and D. De Jong. 1991. Africanized bees are more efficient at removing *Varroa jacobsoni*. Preliminary data. *American Bee Journal*. 131: 434.
- Nascimento, A. F., Jr. 1981. Estudo da influência de fatores ambientais no comportamento enxameatório, migratório e no desenvolvimento de colméias africanizadas. M.Sc. Thesis presented to the University of São Paulo at Ribeirão Preto, Brazil.
- Page, R. E., Jr., and W. E. Kerr. 1991. Honey bee genetics and breeding. 8th article of *The "African" Honey Bee*, pp 157 - 186. Ed. Marla Spivak, David J. C. Fletcher and Michael D. Breed. Westview Studies in Insect Biology. Westview Press, Boulder, USA.
- Sheppard, W. S., A. E. E. Soares, D. De Jong and H. Shimanuki. 1991. Hybrid status of honey bee populations near the historic origin of africanization in Brazil. *Apidologia* 22: 643-652.
- Sheppard, W.S., T.E. Rinderer, J.A. Mazolli, J.A. Steiner and H. Shimanuki. 1991. Gene flow between African and European derived honey bee population in Argentina. *Nature* 349: 782-784.
- Soares, A.E.E. 1992. A utilização da Genética molecular e da morfometria na caracterização de populações de abelhas africanizadas. *Naturalia* (Edição Especial, 14 a 18 de setembro de 1992) pg. 117-125.
- Stort, A. C. 1978. Genetic study of the aggressiveness of two subspecies of *Apis mellifera* in Brazil. VII. Correlation of the various aggressiveness characters among each other and with the genes for abdominal color. *Ciência e Cultura* 30(4): 492-496.
- Winston, Mark L. 1992. *Killer Bee - The Africanized Honey Bee in the Americas*. Harvard University Press, London, England.
- Woyke, I. and W. E. Kerr. 1989. Linkage test between a sex limited color gene and sex alleles in the honey bee. *Brazilian Journal of Genetics* 12(1): 9-15.

Table 1. Data on swarms and hives at Uberlândia, Minas Gerais, Brazil, with reference to frequency of **Ac** and **ac** alleles.

Nº	Day	Arrival Hour	Hive Volume (Liters)	Frequency Of Genes	Place
01	19.07.90	15:00	27	25 Ac	Kerr's House
02	05.08.90	11:00	27	16 Ac	Kerr's House
03	12.08.90	08:45	(1)(3)	10 Ac	Kerr's House
04	19.08.90	10:45	27	16 Ac	Kerr's House
05	11.09.90	12:30	27	20 Ac	Kerr's House
06	21.07.91	13:15	27	24 Ac	Kerr's House
07	14.08.91	14:20	27	15 Ac	Kerr's House
08	04.08.91	15:15	27	08 Ac	Kerr's House
09	05.08.91	14:28	(1)	05 Ac	Kerr's House
10	08.08.91	15:00	27	10 Ac	Kerr's House
11	09.08.91	12:00	45	23 Ac	Kerr's House
12	14.08.91	14:20	27 (3)	14 Ac	Kerr's House
13	27.08.91	12:29	27	47 Ac	Kerr's House
14	24.11.91	(1)	15 (3)	34 Ac	Kerr's House
15	12.05.91	(2)	—	43 Ac	Alvorada Farm
16	11.08.91	(2)	—	23 Ac	Rio Pedras Farm
17	11.08.91	(2)	—	23 Ac	Rio Pedras Farm
18	11.08.91	(2)	—	23 Ac	Rio Pedras Farm
19	11.08.91	(2)	—	23 Ac	Alvorada Farm
20	11.08.91	(2)	—	23 Ac	Alvorada Farm
21	11.08.91	(2)	—	23 Ac	Stª. Rita Farm
22	06.08.91	(2)	—	24 Ac	Stª. Rita Farm
23	06.08.91	(2)	—	24 Ac	Stª. Rita Farm
24	04.09.91	(2)	—	24 Ac	Alvorada Farm
25	04.09.91	(2)	—	23 Ac	Alvorada Farm
26	04.09.91	(2)	—	24 Ac	Rio Pedras Farm
27	06.08.91	(2)	—	24 Ac	Rio Pedras Farm
28	17.09.91	(2)	—	24 Ac	Alvorada Farm
29	17.09.91	(2)	—	23 Ac	Alvorada Farm
30	17.09.91	(2)	—	23 Ac	Alvorada Farm
31	17.09.91	(2)	—	34 Ac	Rio Pedras Farm
				690 Ac (96.23%)	
				27 ac (3.77%)	

(1) Hour not noticed.

(2) Langstroth hive.

(3) Enormous swarm.

A Survey of the Leaf Litter Ant Fauna in Ghana, West Africa (Hymenoptera: Formicidae)

ROBERT BELSHAW AND BARRY BOLTON

Biodiversity Division, Department of Entomology, Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Abstract.—Leaf litter samples were taken from 34 sites scattered across the moist tropical forest zone in Ghana. They included areas of primary forest, secondary forest and cocoa. Over 40,000 individual ants were extracted using Winkler bags and identified. The species found are listed together with their abundance and a summary of their distribution. A total of 176 species was found (excluding stray workers of arboreal and surface-foraging species), almost two-thirds of which were Myrmicinae. The composition of the fauna is discussed and compared with that found in other tropical forests. The species composition at the different sites showed little variation either between the different forest types or with geographic distance.

INTRODUCTION

In the West African forest belt there has been little quantitative sampling of the ant fauna; studies have been carried out in the Tai Forest Reserve, Côte d'Ivoire (see Lévieux 1982 and included references) and the Réserve de Campo, Cameroun (Halle and Pacal 1992: 65-109). In Ghana there has been no quantitative sampling except in the main tree-crop, cocoa. This has been studied in detail (e.g. Majer 1976 and included references) but the extent to which it resembles the original forest fauna is not known. Nevertheless, this research has led to the taxonomy of West African ants being more advanced than that of most tropical ant faunas (e.g. Bolton 1987 and included references). In consequence we can survey elements of this fauna with the hope of accurately identifying much of it to species.

Ghana has two main terrestrial biomes, savannah and forest, and these have distinct ant faunas. In turn, the forest zone is readily divisible into a canopy and a ground fauna. In this paper we survey the leaf litter element of the forest ground fauna by sampling at different localities across Ghana. In addition to identifying the species present, we discuss the composition of the fauna and compare it with that from other tropical forests. We also examine how the species composition at the sites varies geographically and between the different forest types.

Voucher specimens of all taxa are deposited in the Natural History Museum, London.

METHODS

Sites.—The locations of the sampling sites in Ghana are shown in Figure 1, with brief descriptions and sampling dates given in Table 1. Sites designated by the same letter but with different numbers (e.g. j1 and j2) are within 3km of each other. With one exception, the sites are within the moist semi-deciduous forest zone of Hall and Swaine (1976).

We sampled in a wide range of the forest habitats found in Ghana, including 14 areas of primary forest (in the broad sense of forest with a closed high canopy), 10 areas of secondary forest (of varying age, mostly on agricultural land) and 10 cocoa farms. Sampling was carried out between December 1991 and November 1992.

Sampling.—At each site an area of approximately 1000m² was measured out. Within this area ten 1m² quadrats were placed at random. All the leaf litter inside a quadrat was collected, shaken through a 1cm sieve, and then left for three days in a Winkler bag. The extracted ants were combined to form a single total for each site, each site being sampled on only one occasion. All sampling was done between 9.30 a.m. and 3.00 p.m.

At three sites (h, q1 and q2) an additional soil

sample was taken from each quadrat. This was done by collecting the soil from a 25cm by 25cm quadrat (= 0.0625m²) to a depth of approximately 5cm. This soil was then sieved and left for three days in Winkler bags in the same manner as the overlying leaf litter.

The Winkler bag (Besuchet *et al.* 1987) operates in a similar fashion to a Berlese Funnel except that the material is left hanging in a mesh bag to dry in air rather than exposed to a heat source. Winkler bags are much cheaper and easier to use and to transport than Berlese Funnels. Litter-sifting followed by extraction in Winkler bags records many species which do not turn up in pitfall traps (Olson 1991). Our extraction period of three days was chosen on the basis of a trial extraction, with daily sorting of a sample over a two week period. We found that within the first three days 86% of the individuals and 88% of the species had emerged.

We ignored winged reproductives and wingless queens found without workers, except in species where the queen is known to forage during nest foundation.

Analyses.—In order to assess the completeness of our survey for the region sampled, i.e. the moist semi-deciduous zone plus disturbed habitats within, we plotted a species accumulation curve. We first arranged the sites in five random sequences. In each sequence we calculated the number of species found at the first site, the first two sites combined, the first three sites combined, and so on. Finally, the mean of the five sequences was calculated. The extent to which the resulting curve flattens out indicates the proportion of the actual fauna which has been recorded; a failure to flatten out indicates that additional species would have been found if the sampling had been continued. Palmer (1990, 1991) compares and tests methods for estimating the species richness of a region from samples taken within it. He concludes that the first-order jackknife is the most precise method, i.e. the one whose estimates are closest to the true value, and we therefore also apply this analysis to our data.

We converted the body lengths of each species to biomass (= dry weight) using the following equation, taken from Gowing and Recher (1984).

$$\text{Log}_n \text{ weight(mg)} = -4.0 + 2.5(\text{log}_n \text{ length(mm)})$$

Table 1. Sampling sites with dates and habitat description. Sacred groves are small pieces of forest left in agricultural areas for religious reasons. (Note that Ghanaian place name spellings are often variable.)

a	Sui River Forest Reserve, 1.x.1992, primary forest.
b	Mabang, 18.xii.1991, secondary forest.
c	Tinte Bepo Forest Reserve, 31.iii.1992, primary forest.
d	Mankrang Forest Reserve, 11.iii.1992, primary forest.
e	Poano, 9.ix.1992, cocoa.
f	near Ofinso, 2.xi.1992, cocoa.
g	Jachie, 20.iv.1992, sacred grove (28 acres), primary forest
h	Effiduase, 17.xi.1992, cocoa.
i	Bobiri 1 - 6.iv.1992, Forest Reserve (primary forest); 2 - 8.iv.1992, Forest Reserve (primary forest but all mature trees killed with sodium arsenide in 1947); 3 - 13.iv.1992, secondary forest (farmland left in 1982 and burnt in 1983).
j	Juaso. 1 - 21.ix.1992, secondary forest (area of Dome River Forest Reserve burnt in 1983); 2 - 23.ix.1992, secondary forest (farmland left for c.20 years); 3 - 8.ix.1992, cocoa
k	Southern Scarp Forest Reserve (North-West of Mpraeso near Osubeng), 23.x.1992, secondary forest (burnt in 1983).
l	Kade. 1 - 6.x.1992, primary forest (in Aiyeola Forest Reserve); 2 - 12.x.1992, secondary forest (farmland left in 1957); 3 - 12.x.1992, cocoa.
m	Esukawkaw Forest Reserve, 27.x.1992, primary forest.
n	Nkawanda (near Nkawkaw), 12.xii.1991, roadside secondary forest
o	Atewa Forest Reserve, primary forest. 1 - 2.iii.1992, near Kibi, 2 - 24.iii.1992, near Potrase; 3 - 26.ii.1992, near Sagymasi (logged in 1970's); 4 - 27.iii.1992, near Sagymasi (logged in 1970's).
p	Asiakwa, 1.v.1992, cocoa.
q	Bunso. 1 - 6.xi.1992, Crops Research Institute arboretum (15 acres), primary forest, 2 - 17.iv.1992, secondary forest (primary forest partially cleared ca 20 years previously, left undisturbed for ca 12 years); 3 - secondary forest (cocoa left in 1981); 4 - 24.ii.1992, cocoa; 5 - 6.iii.1992, cocoa
r	Old Tafo sacred grove (ca 3 acres), 31.i.1992, primary forest.
s	New Tafo (Cocoa Research Institute of Ghana). 1 - 23.xii.1991, secondary forest (farmland left for ca 40-50 years); 2 - 11.xii.1991, cocoa.
t	Nankasi, 17.ix.1992, cocoa.

Body lengths (= the outstretched length of a point-mounted worker including mandibles) were taken from the literature or from an average of five specimens. In species with a dimorphic worker caste we did not count major and minor workers separately. Instead we used an estimate of 30:1 for the ratio of minor to major workers in all cases.

To assess the effect of the distance between

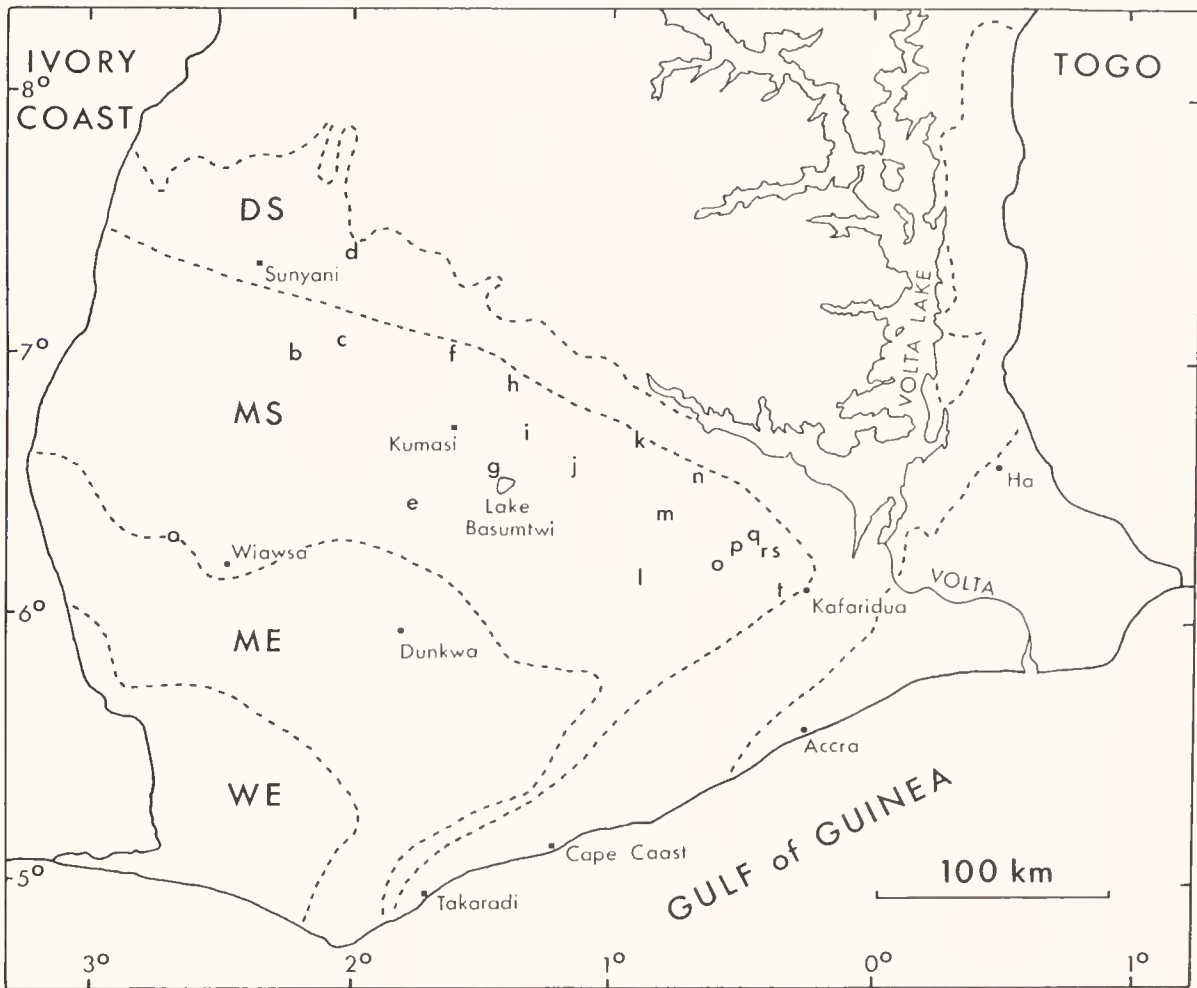


Fig. 1. Map of the forest zone of Ghana showing sampling sites (see table 1 for details). Forest and forest-type boundaries are shown by dotted lines (---). Forest-type abbreviations: DS = Dry Semi-deciduous; MS = Moist Semi-deciduous; ME = Moist Evergreen; WE = Wet Evergreen. From Hall and Swaine (1981).

sites on their species composition we first measured the similarity between all possible pairs of sites using the Morisita Index (see Wolda 1981). Their values were then plotted against the logarithm of the distance between the sites, and a regression line fitted. As the data points are not independent, this procedure is of questionable statistical validity; it does, however, allow us to see the general pattern.

RESULTS AND DISCUSSION

We extracted 43,824 ants in 197 species and 47 genera. At least 17 of these species and two of the genera were undescribed (one of these genera is

now described in Belshaw and Bolton (1994) and the other is currently being described by Prof. W.L. Brown under the name *Loboponera*). A further 57 species are in groups which lack keys or synthesising taxonomic studies, and we can therefore neither identify them nor recognise them as being undescribed. The species are listed in Table 2, along with the total number of individuals found in each species and a summary of their distribution among the sites.

Of the 197 species recorded, three were only found in the soil samples and a further 18 are known not to forage in the leaf litter and are classed here as tourists. The latter are all arboreal species except for *Camponotus*, which forage on the surface of the ground. Although these tourists

comprised 9% of the species found, they comprised only 2% of the total number of individuals.

In the leaf litter the average density of individuals (excluding tourists) was 117m^{-2} . Using Berlese funnels, other studies have found similar densities of ants in leaf litter: in tropical moist forest on Barro Colorado Island, Panama, in the wet season it was *ca* 200m^{-2} (Levings 1983); in temperate deciduous forest in Maryland, U.S.A. between May and September the mean monthly density was 194m^{-2} (Lynch and Johnson 1988).

Composition of the fauna.—The relative importance of the different subfamilies in the combined soil and leaf litter samples is shown in Fig. 2.

The fauna is dominated by Myrmicinae. Where their biology is known, the species we found are all generalist predators/scavengers except for most Dacetoniini, the workers of which forage singly for Collembola and other soft-bodied arthropods (using highly specialised mandibles), and *Decamorium decem* (Forel), which has been observed attacking termites (Bolton pers. obs.). *Paedalgus distinctus* Bolton and Belshaw has also been found in association with termites (Bolton and Belshaw 1993, see below).

The Ponerinae is the second most important subfamily in our survey. Many ponerines are large ants, so although the subfamily comprises only 8% of the total number of individuals, it comprises 27% of the total biomass. A good example is *Paltothyreus tarsatus* (Fabricius): only 25 individuals of this species were found during the survey, but its contribution to the total ant biomass was exceeded by only two other species. This subfamily contains a high proportion of genera which are specialised predators. In our survey we recorded *Amblyopone* (preys on geophilomorph centipedes), *Plectroctena macgeei* Bolton (other members of the genus prey on millipedes), *Paltothyreus tarsatus* (preys on termites), and *Discothyrea* (preys on arthropod eggs) (all sources in Hölldobler and Wilson 1990: 559).

Driver ants (Aenictinae and Dorylinae) have highly aggregated distributions - their colonies are nomadic and very large (with between 60,000 and 20,000,000 workers in other species (Hölldobler and Wilson 1990: 581)). They are represented in our survey by single workers found at three sites and by almost 1500 workers from one soil quadrat that hit part of a *Dorylus* nest. This group has

clearly not been adequately sampled in our survey, and it is probably a much more important component of African forests than our results indicate (see Hölldobler and Wilson 1990: 588).

We found one worker of *Apomyrma stygia* Brown, Gotwald and Lévioux in damp leaf litter a mile inside the Esukawkaw Forest Reserve. This is the sole described species in the Apomyrminae and was recorded previously only from one locality in Côte D'Ivoire (Brown *et al.* 1970), where four nests were found in soil under gallery forest and one under adjacent unburnt savannah. The species is clearly subterranean (the workers are blind), and the remains of a geophilomorph centipede were found in one of the Côte D'Ivoire nests, raising the possibility that the species specialises on this prey item.

Habitat and geographic variation.—In a separate paper we have investigated in detail the differences in the ant assemblages between the primary forest, secondary forest and cocoa sites in this study (Belshaw and Bolton 1993). We found that they did not differ significantly either in species composition or in species richness. Only two common species show an association with a particular forest type (see Table 2): *Serrastruma lujae* (Forel) was with the exception of a single individual found only in the Esukawkaw and Atewa Forest Reserves, and one *Oligomyrmex* species (sp. indet. 4) mostly occurred in cocoa. Given the large number of species present, one would predict that, even if all species were randomly distributed among the three forest types, a handful of such apparent associations would occur purely from chance.

The slope of the regression line in Fig. 4 is very shallow, and the (logarithmically-transformed) distance between sites only accounts for 1.9% of the variation in similarity. The distance between sites therefore had at the most only a slight effect on species composition.

Comparison with other faunas.—Several other studies of tropical forest ant faunas contain lists of leaf litter species: dry forest at Kimberley, N. Australia (Andersen and Majer 1991); moist forest on Barro Colorado Island, Panama (Levings 1983); and dry forest in Madagascar (Olson and Ward, in press). Following elimination of obvious arboreal species, these studies all show the Myrmicinae to be the largest subfamily, followed by the Ponerinae

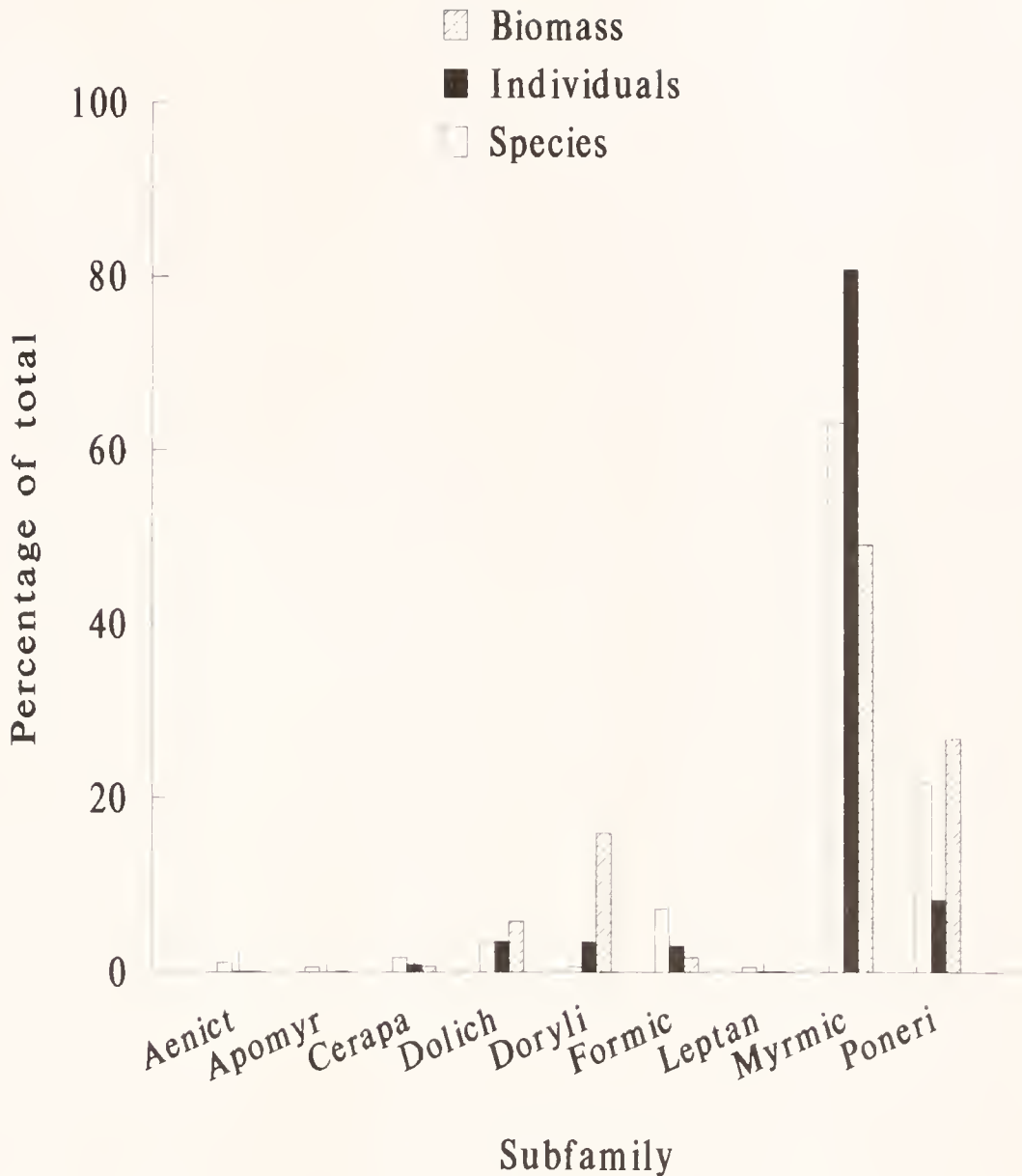


Fig. 2. Relative importance of the different ant subfamilies in the total fauna (leaf litter and soil samples combined, tourists excluded). Names are abbreviated (see table 2).

(in our study comprising 63% and 22% of the total number of species respectively). They comprised 52% and 30% at Kimberley (33 species in total), 65% and 27% on Barro Colorado Island (93 species in total), and 55% and 20% in Madagascar (44 species in total). The figures in the last study would have been higher but for the unusually large number of *Cerapachys* species. The absence of

doryline and aenictine ants from the island has possibly permitted diversification in this genus of specialised predators of other ants (Wilson 1971: 68). Unfortunately, it is not possible to compare the species richness of the four areas owing to the differences in sampling area, effort and method (Berlese funnel, Winkler bag and pitfall trapping).

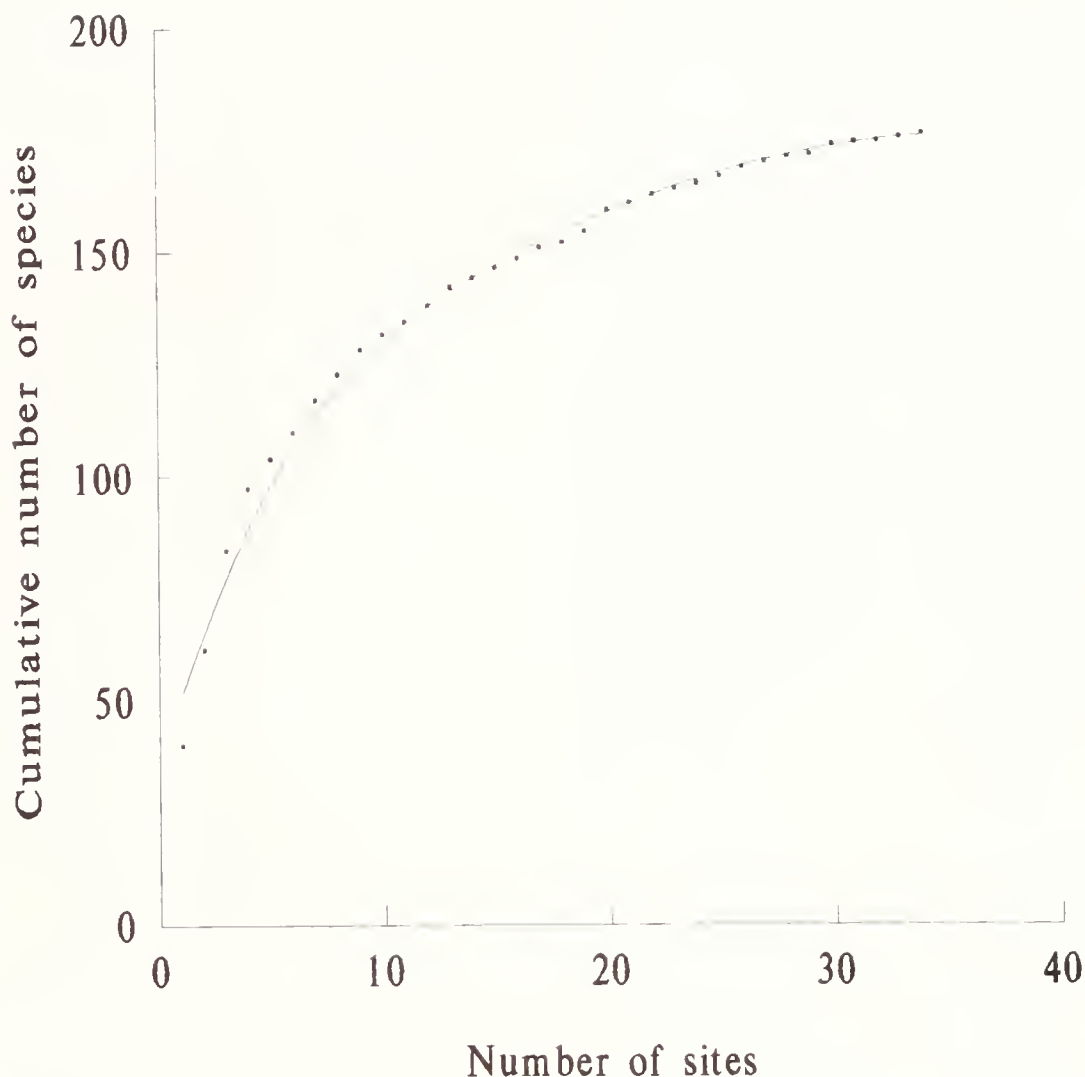


Fig. 3. Species accumulation curve for the leaf litter samples. Line fitted by DWLS smoothing option of computer program SYSTAT (Wilkinson 1990).

Efficiency of survey.—The species accumulation curve is shown in Fig. 3. If the fitted line is extrapolated beyond the data it does not continue to rise. Estimating the true regional species richness using the first-order jackknife method, we find our total of 176 species represents 81% of the actual species present. We infer from this that, within the area of Ghana sampled, we recorded a large majority of the species foraging within leaf litter.

In tropical forests the majority of ground ant species nest in the leaf litter, either in small pieces of rotting wood or between compressed leaves

(Wilson 1959; Bolton pers. obs.). In addition, some other species nest in the top 1-2cm of the soil but forage in the leaf litter. However, there are other smaller elements of the ground fauna which, because of their nesting or foraging habits, are likely to have been missed by our sampling method.

1) Completely subterranean species (= ones which nest and forage only in the soil). In Ghana only a few such species are known, e.g. *Plectroctena anops* Bolton and *P. hastifera* (Santschi) (the workers of which are either blind (*anops*) or with very small eyes (*hastifera*)). However, this microhabitat

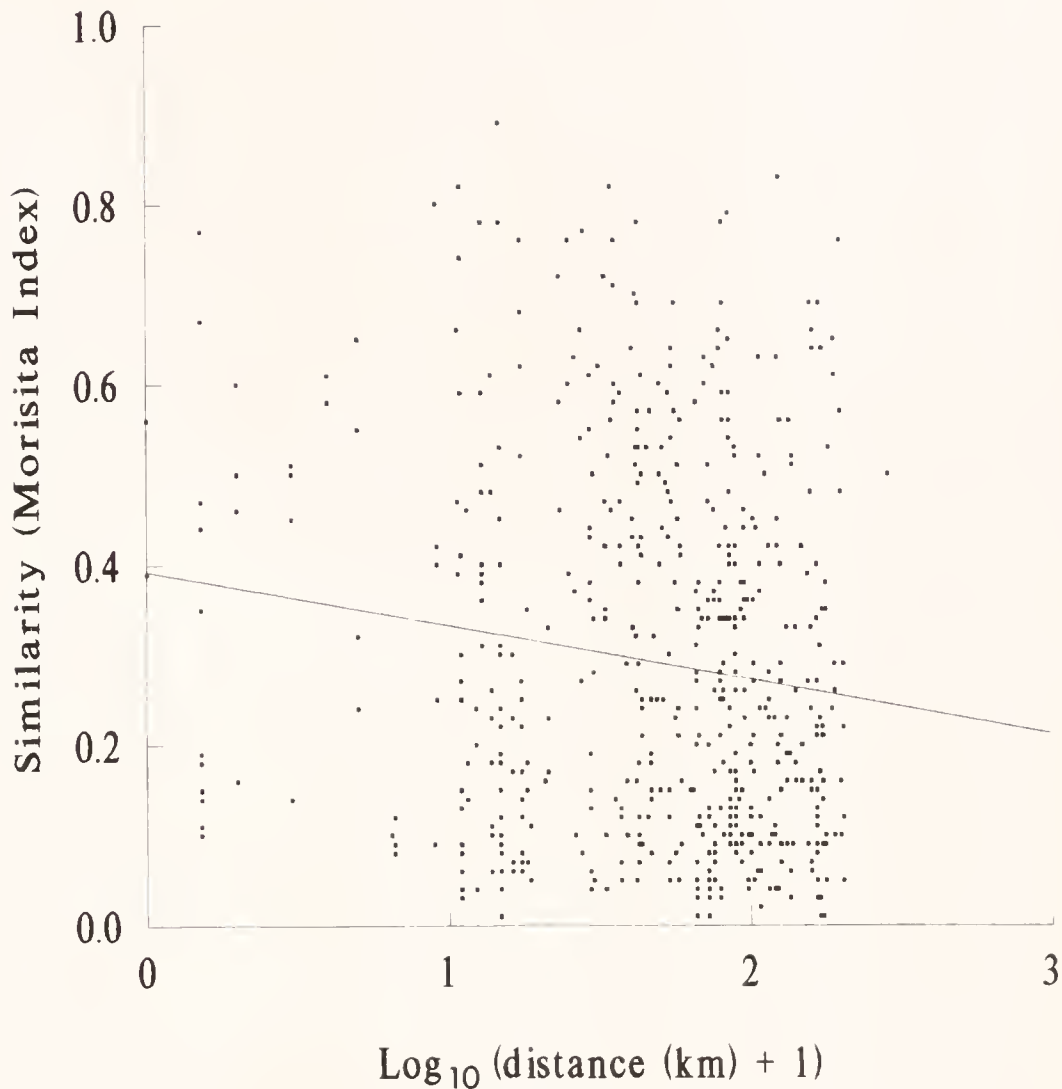


Fig. 4. Plot of similarity in species composition against distance for all possible pairwise comparisons between sites. Line fitted by linear regression ($y = 0.392 - 0.060x$), $r^2 = 0.019$.

has to date hardly been sampled at all, and its fauna is not understood.

2) Species which nest in rotting logs. Such species usually also restrict their foraging to this microhabitat (Wilson 1959). For example, we failed to find *Plectroctena minor* Emery, which is not uncommon in eastern Ghana where it is usually found in or under rotten logs (Bolton 1974). Many Tetramoriini also nest in rotting logs (see Bolton 1980, and below).

3) Obligatory termitolestic species (= species which nest and forage only within termitaria).

This is a small group: in Ghana the habit is confirmed only in species of *Carebara* and *Centromyrmex*. We found *Paedalgus distinctus* and *P. saritus* Bolton and Belshaw foraging in leaf litter which indicates that, despite observations on other members of the genus (see Bolton and Belshaw 1993), they do not belong in this group.

4) Species which only forage nocturnally are likely to be under-represented. In Ghana, among the ground fauna, this habit appears to be restricted to species of *Leptogenys* and *Camponotus*. As expected, we found only one of the 12 species

of *Leptogenys* previously recorded from Ghana (Bolton 1975), plus one undescribed species. The genus *Camponotus* is poorly known taxonomically, but there are more than 15 species from Ghana in the collection of the Natural History Museum which we did not find. Non-arboreal members of this genus, although nesting in the soil, are fast-moving surface foragers, which may also have contributed to their poor representation in our survey.

The three largest myrmicine tribes are sufficiently well known taxonomically for us to compare the list of species recorded in our survey with that of species already known from Ghana. In the Dacetoniini, 25 species were previously known (Bolton 1983), including two known to be arboreal. We found 18 of the remaining 23 species, plus 14 previously unrecorded in Ghana. In the Solenopsidini, 15 species were known (Bolton 1987), including three savannah species. We found 10 of the remaining 12 species, plus six previously unrecorded. These results show that we have found many small cryptic species which had previously been overlooked. The world-wide household pest *Monomorium pharaonis* (L.) (Pharaoh's Ant) was recorded from nine sites (including primary forest). Its range is clearly not restricted to disturbed habitats in Ghana.

In contrast, we found a smaller proportion of the Tetramoriini species known from Ghana. Previously 53 species were known (Bolton 1976, 1980), including 10 savannah and three arboreal species. We found only 21 of the remaining 40 species, plus six previously unrecorded in Ghana. Members of this tribe, however, often nest in exposed sites or in rotten logs, which may explain its relatively poor representation in our survey.

We cannot compare our results for the Pheidologetonini, Pheidolini or Crematogastrini as no synthesising taxonomic studies have been undertaken. The remaining myrmicine tribes contain a total of 40 species previously recorded from Ghana (Bolton 1981a, 1981b, 1982) including 20 arboreal (chiefly *Cataulacus*), four savannah, and two species which tunnel in living wood (*Melissotarsus*). We found 8 of the remaining 14 species: one of the three *Cardiocondyla*, one of the three *Leptothorax*, two of the four *Calyptomyrmex*, both *Pristomyrmex*, the sole *Meranoplus* and the

sole *Baracidris*. In most cases nothing is known of the ecology of the species not found in our survey except for earlier collection localities and dates. However, their absence from our survey shows that they either do not forage in the leaf litter or are rare.

The soil samples.—The density of individuals was eight times higher in the soil samples than in the leaf litter (mean of the three soil samples = 982 m⁻² (S.E.=62). Lynch and Johnson (1988) also found that in a temperate forest the density of ants was higher in the soil than the leaf litter. These data may, however, be misleading as in both studies the soil samples probably included species which, although nesting in the top few cm of the soil, forage primarily in the leaf litter.

Although similar in overall species composition to the leaf litter samples (also found by Lynch and Johnson 1988), the three soil samples contained a small distinctive subterranean element. We extracted 30 workers of *Leptanilla boltoni* Baroni Urbani from a single soil quadrat in a small patch of primary forest at Bunso. The sole Afrotropical representative of the genus, it is known previously only from 6 specimens extracted by Berlese funnel from leaf litter in a cocoa plantation at Mampong, Ghana (Baroni Urbani 1977). The genus contains a total of 33 described species, all of which appear to be very rare (Hölldobler and Wilson 1990: 590). The biology of only one species (*L. japonica* Baroni Urbani) is known: it is strictly subterranean and appears to have true legionary behaviour, employing both group predation (of geophilomorph centipedes) and colony migration (Masuko, 1990). Of the 17 individuals of *Acropyga* sp., 10 were found in soil samples. This species resembles others in the genus which tend coccids in subterranean nests for their sugary secretions (Hölldobler and Wilson 1990: 527). It is the only species found in our survey which is known not to be primarily predacious, although the habit probably occurs in species of several other formicine genera (*Pseudolasius*, *Paratrechina* and *Lepisiota*). One of the species of the undescribed Ponerini genus also appeared to be soil-dwelling.

The results of our few soil samples point tantalisingly to a rich and poorly known subterranean fauna that would repay further collecting.

Table 2. Species recorded during the survey (see table 1 for details of sites, and figure 1 for their location). "Widespread" denotes the species was recorded from more than five differently-lettered sites (the number is given in parentheses). An asterisk (*) denotes species classed as tourists (see text).

Species	Total number () = from soil samples	Sites	Species	Total number () = from soil samples	Sites
AENICTINAE			OECOPHYLLINI		
Aenictus sp. (indet.) (1)	1	s1	*Oecophylla longinoda	15	d,i3,j3,p
A. sp. (indet.) (2)	1	o3	PLAGIOLEPIDINI		
APOMYRMINAE			Acropyga sp. (indet.)	17(10)	a,f,h,q1
Apomyrma stygia	1	m	Lepisiota sp. (indet.) (1)	4	f,s1
CERAPACHYINAE			L. sp. (indet.) (2)	2	o3
Cerapachys foreli	55	widespread (11)	L. sp. (indet.) (3)	1	o4
C. nitidulus	299(134)	widespread (12)	L. sp. (indet.) (4)	10	f,q5
C. n.sp.	3	m,o2,s1	L. sp. (indet.) (5)	1	q5
DOLICHODERINAE			L. sp. (indet.) (6)	1	q5
Tapinoma sp. (indet.)	2	r	Plagiolepis sp. (indet.)	19	d
Technomyrmex sp. (indet.) (1)	821(2)	widespread (14)	LEPTANILLINAE		
T. sp. (indet.) (2)	163(8)	widespread (11)	Leptanilla boltoni	30(30)	q1
T. sp. (indet.) (3)	3	s1	MYRMICINAE		
T. sp. (indet.) (4)	3	d,p	CATAULACINI		
T. sp. (indet.) (5)	530	widespread (10)	*Cataulacus guineensis	1	d
DORYLINAE			CREMATOGASTRINI		
Dorylus sp. (indet.)	1477(1468)	l2,q1	*Crematogaster depressa	499	widespread (6)
FORMICINAE			*C. bequaerti	9	o2,p,q2
CAMPONOTINI			*C. clariventris	24	p,q4
*Camponotus acvapimensis	2	q4-5	C. striatula	2210	widespread (13)
*C. flavomarginatus	15	q4-5,s2	*C. sp.(indet.) (1)	1	d
*C. maculatus	2	q5,t	C. sp.(indet.) (2)	1	s2
*C. vividus	2	q5	C. sp.(indet.) (3)	1	o3
*Polyrhachis decemdentata	2	q4,r	C. sp.(indet.) (4)	9	o3
*P. militaris	24	p,q2	*C. sp.(indet.) (5)	103	i3
*P. rufipalpis	2	a,o4	DACETONINI		
*P. weissi	1	r	Epitritus laticeps	27	k,l1-3,m,q4
LASIINI			E. roomi	53(16)	widespread (12)
Paratrechina sp. (indet.) (1)	794	widespread (12)	E. tiglath	9	d,f,k,l1-2
P. sp. (indet.) (2)	48	d,i3,j1,m,q4-5	Glamyromyrmex crypturus	57(5)	f,i1,o3,q2-3,s1
P. sp. (indet.) (3)	148(48)	h,i2-3,q2,t	G. sistrurus	110	widespread (6)
P. sp. (indet.) (4)	1	p	G. tetragnathus	31	widespread (6)
Pseudolasius sp. (indet.)	270(4)	f,i1,o3,q1-3	G. tukultus	20	e,q1
			Microdaceton tibialis	53	widespread (7)
			Quadristruma emmae	1	n
			Serrastruma concolor	238	widespread (8)
			S. ludovici	20	g,l2,o2,t
			S. lujae	802	j3,m,o1-4
			S. serrula	823(4)	widespread (16)
			Smithistruma cavinasis	3	l1
			S. enkara	7	a,q2

Species	Total number () = from soil samples	Sites	Species	Total number () = from soil samples	Sites
<i>S. fulda</i>	2	a	<i>P. sp. (indet.) (3)</i>	180(74)	d,g,i2,p,q2
<i>S. hensekta</i>	58	widespread (9)	<i>P. sp. (indet.) (4)</i>	67	d,q5,s2
<i>S. malaplax</i>	69	s1-2	<i>P. sp. (indet.) (5)</i>	213(1)	widespread (9)
<i>S. marginata</i>	1	d	<i>P. sp. (indet.) (6)</i>	10	a,o4,p,t
<i>S. mimkara</i>	55	f,l2,o3,q3	<i>P. sp. (indet.) (7)</i>	98	o4
<i>S. ninda</i>	55	f,h,n,q1+5	<i>P. sp. (indet.) (8)</i>	8	o1,h
<i>S. sharra</i>	25	d,f,l1,o2-3	<i>P. sp. (indet.) (9)</i>	496	widespread (7)
<i>S. tacta</i>	56	widespread (8)	<i>P. sp. (indet.) (10)</i>	74	e,i3,q4
<i>S. tigrilla</i>	9	d,l1,o2	<i>P. sp. (indet.) (11)</i>	30	a
<i>S. n.sp.</i>	4	h,q5			
<i>Strumigenys korahyla</i>	1	d	SOLENOPSISIDINI		
<i>S. nimbrata</i>	70(4)	widespread (7)	<i>Monomorium bicolor</i>	1	d
<i>S. petiolata</i>	1439(31)	widespread (20)	<i>M. cryptobium</i>	1475(242)	widespread (16)
<i>S. rogeri</i>	177	widespread (6)	<i>M. draxocum</i>	5	d,g
<i>S. rufobrunea</i>	1059	widespread (15)	<i>M. exiguum</i>	605	widespread (16)
<i>S. spathoda</i>	1(1)	q2	<i>M. floricola</i>	13	l3
<i>S. vazerka</i>	22(1)	a,l3,o2,q1+3,s2	<i>M. egens</i>	8	widespread (7)
FORMICOXENINI			<i>M. gabrielse</i>	42	a,b,g,o2-3,t
<i>Cardiocondyla neferka</i>	1	d	<i>M. guineense</i>	55	g,i2
<i>Leptothorax angulatus</i>	1	q5	<i>M. invidium</i>	3432(62)	widespread (19)
* <i>Terataner piceus</i>	1	n	<i>M. pharaonis</i>	17	widespread (6)
MERANOPLINI			<i>M. rosae</i>	7	f,q4-5
<i>Meranoplus inermis</i>	1	s1	<i>M. tanysum</i>	2	d
MYRMECININI			<i>M. trake</i>	10	d,i2
<i>Pristomyrmex africanus</i>	79(3)	widespread (9)	<i>M. n.sp. (1)</i>	22	d
<i>P. orbiceps</i>	505(3)	widespread (13)	<i>M. n.sp. (2) (exiguum group)</i>	13	p,q5
PHEIDOLOGETONINI			<i>M. n.sp. (3)</i>	75	i2,j1+3,p
<i>Afroxyidris crigensis</i>	2	e,f	STENAMMINI		
<i>Oligomyrmex sp. (indet.) (1)</i>	440(7)	widespread (10)	<i>Baracidris mektra</i>	8(3)	j3,l2,m,n,q1-2
<i>O. sp. (indet.) (2)</i>	1957(333)	widespread (15)	<i>Calyptomymex kaurus</i>	18	k,l1-2,o3
<i>O. sp. (indet.) (3)</i>	1532(175)	widespread (12)	<i>C. nummuliticus</i>	11	l2,o3,p,q3
<i>O. sp. (indet.) (4)</i>	123(10)	e,j3,l3,q2+5,s2,t	TETRAMORIINI		
<i>O. sp. (indet.) (5)</i>	245	widespread (6)	<i>Decamorium decem</i>	119	widespread (7)
<i>O. sp. (indet.) (6)</i>	967(81)	widespread (13)	* <i>Tetramorium aculeatum</i>	3	o1+4,i3
<i>O. sp. (indet.) (7)</i>	98(92)	q1-2+5	<i>T. amentete</i>	106	widespread (8)
<i>O. sp. (indet.) (8)</i>	602	widespread (6)	<i>T. antrema</i>	162	widespread (10)
<i>O. sp. (indet.) (9)</i>	156(34)	q1,o3	<i>T. ataxium</i>	140(4)	widespread (11)
<i>O. sp. (indet.) (10)</i>	197	g,i1+3,m	<i>T. brevispinosum</i>	118	widespread (6)
<i>O. sp. (indet.) (11)</i>	39(27)	h	<i>T. camerunense</i>	2	o1
<i>O. sp. (indet.) (12)</i>	104	l1-3,q3	<i>T. distinctum</i>	552(16)	widespread (16)
<i>Paedalgus distinctus</i>	228(22)	widespread (13)	<i>T. flavithorax</i>	350	widespread (17)
<i>P. saritus</i>	42	j3,n,o2	<i>T. furtivum</i>	689(33)	widespread (8)
PHEIDOLINI			<i>T. guineense</i>	417	widespread (10)
<i>Pheidole sp. (indet.) (1)</i>	778	widespread (10)	<i>T. ictidum</i>	1	o2
<i>P. sp. (indet.) (2)</i>	5474(99)	widespread (20)	<i>T. invictum</i>	65	widespread (6)
			<i>T. jugatum</i>	4	d,l2,t
			<i>T. lucayanum</i>	3	e,l3
			<i>T. menkaura</i>	21	d,o2-4,s1,t

Species	Total number () = from soil samples	Sites	Species	Total number () = from soil samples	Sites
<i>T. minimum</i>	368(25)	widespread (15)	<i>P. pachyderma</i>	16	widespread (7)
<i>T. murali</i>	189	widespread (10)	<i>P. soror</i>	2	l3,q2
<i>T. muscorum</i>	18	widespread (6)	<i>P. sp. (indet.)</i>	18(7)	p,q1+3,s1
<i>T. peutli</i>	28	widespread (6)	<i>P. n.sp.</i>	1	i3
<i>T. quadridentatum</i>	1	q4	<i>Paltothyreus tarsatus</i>	25	widespread (7)
<i>T. rhetidum</i>	971(6)	widespread (9)	<i>Phrynonopona bequaerti</i>	13	l1+3
<i>T. youngi</i>	7	o2-3	<i>P. gabonensis</i>	24(1)	widespread (6)
<i>T. zambesium</i>	2293(13)	widespread (17)	<i>Plectroctena macgeeii</i>	3	j1,o3
<i>T. zapyrum</i>	33	d,r,t	<i>n.gen.,n.sp. (1)</i>	3(3)	q2,h
<i>T. n.sp. (weitzckeri group)</i>	30	l1,o4,q2	<i>n.gen.,n.sp. (2)</i>	1	l3
<i>T. n.sp. (convexum group)</i>	5	i3,m			
<i>T. n.sp. (dumezi group)</i>	2	q3			

PONERINAE

AMBLYOPONINI

<i>Amblyopone mutica</i>	3	i2,t
<i>A. santschii</i>	6	f,g,j1+3,q1

ECTATOMMINI

<i>Discothyrea oculata</i>	1	q2
<i>D. mixta</i>	3	f,l1,o4
<i>D. n.sp. (1)</i>	5(1)	f,l1,o4,q1
<i>D. n.sp. (2)</i>	3	a

PLATYTHYREINI

* <i>Platythyrea conradti</i>	1	r
<i>Probolomyrmex guineensis</i>	46	f,k,l1-3,s1

PONERINI

<i>Anochetus africanus</i>	170	g,l1-3,o1+3-4,p,q1-3
<i>A. bequaerti</i>	43(2)	widespread (9)
<i>A. katonae</i>	568(70)	widespread (17)
<i>A. maynei</i>	1	s1
<i>A. siphneus</i>	6	f,h,j3,t
<i>A. n.sp.</i>	4	o3-4
<i>Asphinctopone silvestrii</i>	5(1)	f,q1-3
<i>Cryptopone n.sp.</i>	2	j1
<i>Hypoponera sp. (indet.) (1)</i>	244(29)	widespread (13)
<i>H. sp. (indet.) (2)</i>	1828(35)	widespread (19)
<i>H. sp. (indet.) (3)</i>	11	d,g,k
<i>H. sp. (indet.) (4)</i>	98(16)	widespread (6)
<i>H. sp. (indet.) (5)</i>	223(2)	widespread (9)
<i>H. sp. (indet.) (6)</i>	6(1)	i3,o1,q2
<i>Leptogenys nuserra</i>	15(1)	l3,m,o1-2,q2,t
<i>L. n.sp.</i>	1	o2
<i>Odontomachus assiniensis</i>	8	s1
<i>O. troglodytes</i>	22	widespread (7)
<i>Pachycondyla ambigua</i>	24	a,d,f,l2,o1-2+4
<i>P. brunoi</i>	24(9)	widespread (8)
<i>P. caffraria</i>	86	widespread (8)
<i>P. fugax</i>	12	h,i1,l2,o3,t

ACKNOWLEDGMENTS

This project was funded by the Leverhulme Trust (Grant F.696A). The field work was based at the Cocoa Research Institute of Ghana, New Tafo, and we are very grateful for their hospitality and assistance. We would also like to thank the Ghanaian Forestry Department; Cocoa Services Division; Crops Research Institute; the Ghana Association for the Conservation of Nature; and the Tafohene, Old Tafo.

In addition, Paul Eggleton and two reviewers made valuable comments on the manuscript.

LITERATURE CITED

- Andersen, A. N. and J. D. Majer. 1991. The structure and biogeography of rainforest ant communities in the Kimberley region of north-western Australia, pp. 333-346. In McKenzie N.L., R.B. Johnston and P.G. Kendrick, eds. *Kimberley Rainforests of Australia*. Surrey Beatty and Sons, Chipping Norton, Australia. 490 pp.
- Baroni Urbani, C. 1977. Materiali per una revisione della sottofamiglia Leptanillinae Emery (Hymenoptera: Formicidae). *Entomologica Brasiliensia* 2: 427-488.
- Belshaw, R. and B. Bolton. 1993. The effect of forest disturbance on the leaf litter ant fauna in Ghana. *Biodiversity and Conservation* 2: 656-666.
- Belshaw, R. and B. Bolton. 1994. A new myrmicine ant genus from cocoa leaf litter in Ghana (Hymenoptera: Formicidae). *Journal of Natural History* 28: 631-634.
- Besuchet, C., D. H. Burckhardt and I. Löbl. 1987. The "Winkler/Moczarski" eclector as an efficient extractor for fungus and litter Coleoptera. *The Coleopterists Bulletin* 41: 392-394.
- Bolton, B. 1974. A revision of the ponerine ant genus *Plectroctena* F. Smith (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History) (Entomology)* 30: 309-338.
- Bolton, B. 1975. A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian region: with a review of the Malagasy species. *Bulletin of the British Museum (Natural History) (Entomology)* 31: 235-305.

- Bolton, B. 1976. The ant tribe Tetramorini (Hymenoptera: Formicidae): constituent genera, review of smaller genera and revision of *Triglyphothrix* Forel. *Bulletin of the British Museum (Natural History) (Entomology)* 34: 283-379.
- Bolton, B. 1980. The ant tribe Tetramorini (Hymenoptera: Formicidae): the genus *Tetramorium* Mayr in the Ethiopian zoogeographical region. *Bulletin of the British Museum (Natural History) (Entomology)* 40: 193-384
- Bolton, B. 1981a. A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomyrmex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. *Bulletin of the British Museum (Natural History) (Entomology)* 42: 43-81.
- Bolton, B. 1981b. A revision of six minor genera of Myrmicinae (Hymenoptera: Formicidae) in the Ethiopian region. *Bulletin of the British Museum (Natural History) (Entomology)* 43: 245-307.
- Bolton, B. 1982. Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). *Bulletin of the British Museum (Natural History) (Entomology)* 45: 307-370.
- Bolton, B. 1983. The Afrotropical dacetine ants (Formicidae). *Bulletin of the British Museum (Natural History) (Entomology)* 46: 267-416.
- Bolton, B. 1987. A review of the *Solenopsis* genus-group and revision of Afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History) (Entomology)* 54: 263-452.
- Bolton, B. and R. Belshaw. 1993. Taxonomy and biology of the supposedly lestopibiotic ant genus *Paedalgus* (Hym.: Formicidae). *Systematic Entomology* 18: 181-189.
- Brown, W. L., W. H. Gotwald Jr. and J. Léveux. 1970. A new genus of ponerine ants from West Africa (Hymenoptera Formicidae) with ecological notes. *Psyche* 77: 259-275.
- Gowing, G. and H. F. Recher. 1984. Length-weight relationships for invertebrates from forests in south-eastern New South Wales. *Australian Journal of Ecology* 9: 5-8
- Hall, J. B. and M. D. Swaine. 1976. Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology* 64: 913-951.
- Hall, J. B. and M. D. Swaine. 1981. Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana. *Geobotany* 1: 1-383.
- Halle, H and O. Pacal, eds. 1992. *Biologie d'une canopée de forêt équatoriale: volume 2*. Unpublished report.
- Holldobler, B. and E.O. Wilson. 1990. *The ants*. Springer-Verlag, Berlin. 732 pp.
- Lévieux, J. 1982. A comparison of the ground dwelling ant populations between a guinea savanna and an evergreen rain forest of the Ivory Coast, pp. 48-53. In Breed, M.D., C.D. Michener, and H.E. Evans, eds. *The biology of social insects*. Westview Press, Boulder, Colorado. 419 pp.
- Levings, S. C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecological Monographs* 53: 435-455.
- Lynch, J. F. and A. K. Johnson. 1988. Spatial and temporal variation in the abundance and diversity of ants (Hymenoptera: Formicidae) in the soil and litter layers of a Maryland forest. *The American Midland Naturalist* 119: 31-44
- Majer, J. D. 1976. The influence of ant and ant manipulation on the cocoa farm fauna. *Journal of Applied Ecology* 13: 157-175.
- Masuko, K. 1990. Behavior and ecology of the enigmatic ant *Leptanilla japonica* Baroni Urbani. *Insectes Sociaux* 37: 31-57.
- Olson, D. M. 1991. A comparison of the efficacy of litter sifting and pitfall traps for sampling leaf litter ants (Hymenoptera, Formicidae) in a tropical wet forest, Costa Rica. *Biotropica* 23: 166-172.
- Olson, D. M. and P. S. Ward. in press. The ant fauna (Hymenoptera: Formicidae) of Kirindy Forest (tropical dry forest) in Western Madagascar. In Ganzhorn, J., ed. *The ecology and economy of a tropical dry forest*. Springer-Verlag, Berlin.
- Palmer, M. W. 1990. The estimation of species richness by extrapolation. *Ecology* 71: 1195-1198.
- Palmer, M. W. 1991. Estimating species richness: the second order jackknife reconsidered. *Ecology* 72: 1512-1513.
- Wilkinson, L. 1990. *SYSTAT: the system for statistics*. Evanston, IL: SYSTAT, Inc.
- Wilson, E. O. 1959. Some ecological characteristics of ants in New Guinea rain forests. *Ecology* 40: 437-447.
- Wilson, E. O. 1971. *The insect societies*. Belknap Press, Cambridge, Massachusetts.
- Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50: 296-302.

Revision of the Ant Genus *Rogeria* (Hymenoptera: Formicidae) with Descriptions of the Sting Apparatus

CHARLES KUGLER

Biology Department, Radford University, Radford, VA 24142 USA

Abstract.— This is the first complete revision of the century-old ant genus *Rogeria*. The revision recognizes 39 species, of which 19 are **new species**: *alzatei* n. sp. (Panama, South America, Dominican Republic), *besucheti* n. sp. (Paraguay, Colombia, Peru), *carinata* n. sp. (Caribbean), *ciliosa* n. sp. (Venezuela, Ecuador), *cornuta* n. sp. (Belize, southern Mexico), *cuneola* n. sp. (Mexico, Central America), *gibba* n. sp. (Colombia, Ecuador), *innotabilis* n. sp. (Mexico, Central America), *leptonana* n. sp. (Mexico, Central America, Dominican Republic), *lirata* n. sp. (Trinidad, South America), *megastigmatica* n. sp. (Solomon Islands), *merenbergiana* n. sp. (Colombia, Ecuador), *neilyensis* n. sp. (Costa Rica), *nevadensis* n. sp. (Colombia), *prominula* n. sp. (Brazil), *scobinata* n. sp. (Trinidad, South America), *terescandens* n. sp. (Costa Rica), *tribrocca* n. sp. (Colombia), and *unguispina* n. sp. (Venezuela). Previously recognized species are *belti* Mann 1922, *blanda* Fr. Smith 1858, *bruchii* Santschi 1922, *brunnea* Santschi 1930, *creightoni* Snelling 1973, *curvipubens* Emery 1894, *exsulans* Wilson and Taylor 1967, *foreli* Emery 1894, *germani* Emery 1894, *inermis* Mann 1922, *lacertosa* Kempf 1963, *micromma* Kempf 1961, *munuma* Kusnezov 1958, *pellecta* Kempf 1963, *procera* Emery 1896, *scandens* Mann 1922, *sicaria* Kempf 1962b, *stigmatica* Emery 1897, *subarmata* Kempf 1962a, and *tonduzi* Forel 1899. Nine **new synonyms** are proposed: *caraiiba* Santschi 1936, *cubensis* Santschi 1936, *habanica* Santschi 1936, and *scabra* Weber 1934 = *brunnea* Santschi 1930; *gatzei* Forel 1914, and *huachucana* Snelling 1973 = *foreli* Emery 1894, *munensis* Santschi 1923 = *germani* Emery 1894; *sublevinodis* Emery 1914, and *manni* Santschi 1922 = *stigmatica* Emery 1897. Seven **new combinations** are proposed: *epinotalis* Mann 1919, *rugosa* Mann 1921, *striatella* Mann 1921, *tortuosa* Mann 1921, *tortuosa levifrons* Mann 1921, *tortuosa polita* Mann 1921, and *tortuosa stoneri* Mann 1925 to *Lordomyrma*. Three species occur in Polynesia and Melanesia; the rest are New World: southwestern United States to southern Paraguay. A key to the workers is provided. All species are briefly described and illustrated to show variation. Available biological information is summarized. Six informal species groups are defined for 29 species; possible affiliations of the remaining 10 species are indicated. A new character system, the sting apparatus, is used to help define the species and species-groups. Pilosity also provides an important new set of characters for species identification in this genus.

INTRODUCTION AND DISCUSSION

This revision will redefine the genus, establish new synonymies, create informal species groups, redescribe species, provide a key to the workers, and summarize ecological information. Keys to the reproductives are not included, because queens are known or proposed for less than half of the *Rogeria* species and males for only four species.

The genus *Rogeria* was erected by Emery (1894) for a few neotropical ants then in *Myrmica* and *Tetramorium*. He then extended the distribution of the genus to New Guinea with the addition of *stigmatica* (Emery 1897). Discovery of other neotropical species led Emery (1915) to create the subgenus *Irogera* for those with a clavate petiole.

This subdivision was attractive, and for a brief period *Irogera* even enjoyed generic status (Brown 1953), but with a better understanding of the variation in petiole shape within species, the splitting of *Rogeria* along these lines became untenable (Kempf 1965). Meanwhile, Melanesian and Polynesian species were being added to the genus with no discussion of the disjunct distribution of the genus or comparisons of New World and Old World species (Mann 1919, 1921, 1925; Santschi 1922, 1941). Brown (1953) recognized that many of these were actually *Lordomyrma* species, but still, the Pacific species including *stigmatica*, *epinotalis*, and later, *exsulans* remained in *Rogeria*. Wilson and Taylor (1967) called this "...one of the most anomalous discontinuous distributions found in ants."

The disjunct distribution of *Rogeria* was questioned by Kusnezov (1958) on the basis of palpal formula differences between *stigmatica* and a South American species, and by Kugler (1978b) on the basis of the sting apparatus. In contrast to all other myrmicine genera, there were two distinctly different sting apparatuses within the genus, and that difference coincided with the disjunct distribution of the genus. The sting of *inermis* from Central America was strong, acute and with an unusual low dorsal flange; the sting of *stigmatica* from the Pacific had a weak, narrowly spatulate sting shaft and no dorsal flange (among other differences). I believed a revision of *Rogeria* using sting apparatus characters would separate the Pacific and New World species into distinct genera.

The potential of the sting apparatus for defining ant genera and inferring phylogeny has been demonstrated by a number of comparative morphological studies (Kugler 1978b, 1980, 1986, 1992). In addition, Bolton (1973, 1982, 1987) has often used externally visible parts of the sting to help define some myrmicine taxa. But this is the first time that characters from the whole apparatus have been used as an integral part of a taxonomic revision. This work, then, also tests the usefulness of the sting apparatus in the alpha-taxonomy of ants.

I examined sting apparatuses of 79 workers and queens in 27 *Rogeria* species and seven *Lordomyrma* species. In the five species in which both queens and workers were dissected, there were only the usual individual differences, such as numbers of sensilla. Contrary to expectations, the Western Samoan species *exsulans* is unmistakably related to Central American *Rogeria* species in sting apparatus, pygidium, and external anatomy. Moreover, some South American species (*ciliosa*, *gibba*, *besucheti*) had sting apparatuses and pygidia with the same distinctive features of *stigmatica*. It seems the distribution of *Rogeria* really is disjunct.

Sting and pygidial characters provided support for numerous other taxonomic decisions as well. For example, they provided strong support for creating the *stigmatica*-group of species, and could conceivably be used to distinguish that group as a separate genus. Sting apparatus anatomy also supported Brown's (1953) belief that *levifrons*, *striatella*, and *tortuosa* are *Lordomyrma* species. Autapomorphic shape of the sting shaft confirmed

that *germaini* and *lirata* are sister species. The unusual shape of the spiracular plate ultimately convinced me to propose *innotabilis* as a new species after long deliberation over the welter of variation within the *creightoni*-group.

This character system must be used with caution however. The apparatus is prone to reduction and convergence of form. The sting of *Lordomyrma epinotalis* is more like those of the *Rogeria stigmatica*-group than those of *Lordomyrma*. In this case, I based my decision to transfer *epinotalis* to *Lordomyrma* on external characters, since the common sting features could well be due to reduction convergence.

Hair has not been used previously in *Rogeria* systematics, but in this revision I came to rely more and more on characteristics of pilosity for distinguishing species. Consequently it has become necessary for species descriptions to identify precisely the several kinds of hairs and their distributions on the ants, sometimes including the numbers of pairs of erect hairs on the head, mesosoma, and nodes. This means, of course, that care must be taken to not disturb the hair while cleaning and mounting the ants.

I have attempted to take a fairly conservative approach to synonymy and description of new species, choosing in ambiguous situations to err on the side of not changing the number of species in the genus. Thus, for lack of sufficient evidence, some species may actually contain several sibling species: *alzatei*, *belti*, *creightoni*, *foreli*, *leptonana*, and *scandens*. On the other hand, I have retained some names that may fall when collections improve: *bruchi*, *micromma*. Treatment of the *creightoni*-group has perhaps been somewhat less conservative (See the Species Group section).

All told, this study recognizes 39 species (including 19 new species), establishes nine new synonymies and transfers seven species to *Lordomyrma*. It fails to resurrect the subgenus *Irogera*. It retains three Polynesian/Melanesian species (*stigmatica*, *megastigmatica*, *exsulans*) with the Neotropical bulk of the genus.

As presently constituted, members of the genus *Rogeria* are distributed from Buenos Aires to southern Texas and Arizona, and in the Pacific between 10°N and 25°S from Tahiti to the western end of the island of New Guinea. So far it is unknown in Australia or southeastern United States. Table 1 shows the distribution of species in

Table 1. Geographic distribution of *Rogeria* species. The North American region is from southwestern United States through Panama. The northern region of South America extends from the north and west coasts through the Amazonian basin. The southern region of South America includes Paraguay, adjacent Brazil, and Argentina south to Buenos Aires. Trinidad is the only known Caribbean locality of three species (*blanda*, *lirata*, *scobinata*). A question mark indicates that presumed queens, but no workers, were collected in that region. See text for further discussion.

Species	North America	Caribbean	South America		Pacific
			Northern	Southern	
<i>alzata</i>	+		+	+	
<i>belti</i>	+		+		
<i>besucheti</i>			+		
<i>blanda</i>	+	+	+		
<i>bruchu</i>				+	
<i>brunnea</i>		+			
<i>carinata</i>		+			
<i>ciliosa</i>	+				
<i>cornuta</i>			+		
<i>creightoni</i>	+				
<i>cuneola</i>	+				
<i>curvipubens</i>	+	+	+		
<i>exsulans</i>					+
<i>foreli</i>	+	+	+		
<i>germami</i>				+	
<i>gibba</i>			+		
<i>inermis</i>	+				
<i>imotabilis</i>	+		+		
<i>lacertosa</i>				+	
<i>leptonana</i>	+		+		
<i>lirata</i>		+	+		
<i>metastigmatica</i>					+
<i>merenbergiana</i>			+		
<i>micromma</i>			+		
<i>minima</i>				+	
<i>neilyensis</i>	+				
<i>nevadensis</i>			+		
<i>pellecta</i>				+	
<i>procera</i>			+		
<i>prominula</i>			+		
<i>scandens</i>	+				
<i>scobinata</i>	+	+	+	+	
<i>sicaria</i>				+	
<i>stigmatica</i>					+
<i>subarmata</i>			+	+	
<i>terescandens</i>	+				
<i>tonduzi</i>	+				
<i>tribrocca</i>			+		
<i>unguispina</i>			+		

more detail. In the North American region, most species occur below the Isthmus of Tehuantepec, but two species (*creightoni*, *cuneola*) extend northward through the eastern lowlands of Mexico. Only *foreli* and *creightoni* have been collected in the United States. The North American region contains 8-10 endemic species (depending on the uncertain distributions of *innotabilis* and *leptonana*); the Caribbean, two endemic species; South America (including Trinidad), 19 endemic species and the Pacific, three endemic species. Only 5-7 species (depending on *innotabilis* and *leptonana*) are found in both Central America and northern South America.

Little is known of the biology of these cryptic ants. Collection records usually range from sea level to 1000m, but five species extend higher and two (*unguispina* and *merenbergiana*) can be found at 2000m. *Rogeria* species are generally collected in moist forests (primary or secondary forests, coffee or cacao plantations), but at higher elevations can be found in pastures (*leptonana*, *merenbergiana*). Several species (*creightoni*, *cuneola*, *foreli*) have been found in both moist and dry climates. *Rogeria foreli* is the most unusual, with some members dwelling at over 1800m in the temperate mountains of southern Arizona.

Most *Rogeria* species have only been collected as strays or by Berlese or Winkler sampling, usually in leaf litter and rotten wood, but occasionally among epiphytes and moss (*belti*, *creightoni*, *exsulans*). Nests of several species (*belti*, *blanda*, *merenbergiana*) have been found under loose bark of rotten logs. Nests of *blanda* and *tonduzi* have been taken from the trunks of cacao trees. A nest of *leptonana* was found at 1750m under a rock in a pasture.

Because nests are so rarely found, males are known for only four species (*belti*, *blanda*, *leptonana* and *stigmatica*), and queens associated through nest series for only nine species (See Synonymic List of Species).

METHODS AND TERMINOLOGY

Dissections

Mouthparts, sting apparatus, pygidium, hypopygium, and male genitalia preparations were obtained by rehydrating ants in 70% ethanol, dissecting these structures from the ants, clearing in

55-60 C lactophenol for 5 minutes (or longer if necessary), rinsing twice in 70% ethanol, and rinsing twice in 95% ethanol. After clearing, sting apparatuses and genitalia were usually cut in half, except for the aedeagus and sting, which were separated from the other sclerites. Stings, pygidia, and hypopygia were mounted in glycerin jelly for ease of repositioning. Mouthparts, genitalia, and other sting apparatus sclerites were soaked in xylene, then mounted in Canada balsam. Occasionally, whole ants were similarly cleared and mounted in balsam. Preparations were examined with a Zeiss KF-2 phase contrast microscope.

The "Materials Examined" sections of each species description identifies which specimens were dissected. Following the locality of the dissected ant, brackets identify the structures slide-mounted ("sting" means sting apparatus, pygidium and hypopygium). Dissected specimens are workers unless otherwise identified.

Pinned vouchers are identified with the label "Kugler 1991 Dissection Voucher." All are deposited in the collection of the MCZ, except for vouchers of *lacertosa*, *pellecta*, *subarmata*, the Agudos, Brazil voucher of *alzatei*, and the Surinam vouchers of *curvipubens*, which are all in the MZSP.

Illustrations

Drawings were made using a grid eyepieces and grid-backed tracing paper. Drawings of sting apparatus preparations were made at 400X with estimated accuracy of ≤ 0.001 mm. Scanning electron micrographs were taken on an AMR-900 and a JEOL JSM-35C.

Dorsal views of heads are in the same full-face view used to measure HL. Lateral views of mesosomas are in the same view used to measure WL, SpL, and MHI.

Drawings attempt to show all hairs on the left side of the body that project well above the body outline. Care was taken to present typical pilosity, rather than matted or damaged hairs. Hair is not included in line drawings of: 1) dorsal views of heads, 2) ventral portions of head profiles, 3) most dorsal views of waists, and 3) queens and males.

All line drawings of sting apparatuses are from workers.

Male genitalia drawings show the lateral view of the aedeagus and medial view of the right paramere and volsella (with associated part of the

phallobase).

Nontype specimens are identified in figure legends by affixing their collection localities in parentheses.

Measurements and Indices

Measurements and drawings of whole ants, except for the very largest, were made using a Zeiss SR stereomicroscope at 125X magnification and a fiber optic ring lamp. Estimated accuracy: ± 0.01 mm.

All specimens were measured for Weber's Length (WL) then at least the largest and smallest from each locality were measured completely. The maximum and minimum of each measurement and index were double-checked, as were all measurements of holotypes. The number of specimens (N) that follows the list of metric characters at the beginning of a species description is the number of ants that were measured *completely*. The numbers at the ends of "Material Examined" sections are *total* specimens studied.

In listing metric characters for new species, the ranges found in all type material are followed by the holotype measurements in parentheses.

If no queens or males are described for a species, none were available for study.

CL	Cephalic index: HW/HL.
EL	Eye length: Maximum diameter of compound eye viewed straight on.
FLW	Frontal lobe width: In full face dorsal view, maximum transverse distance across frontal lobes.
GL	Gaster length: In lateral view, from anterior edge of first tergum to posteriormost point usually T2 or T3, but sometimes to end of pygidium).
GW	Gaster width: Maximum transverse distance across gaster.
HL	Head length: Maximum longitudinal distance from the anteriormost portion of the clypeus (usually the clypeal apron, but sometimes the more prominent body of the clypeus) to the midpoint of a line across the back of the head.
HW	Head width: Maximum width in same view as for HL, excluding eyes. For males, HW includes compound eyes.
ML	Mandible length: In same view as for HL, from anteriormost portion of head to apex of closed mandibles.
OI	Ocular index: EL/HW.
PetL	Petiole length: In lateral view and with petiole not strongly flexed up or down, the axial distance from the dorsal corner of the posterior peduncle to the nearest edge of the metapleural lobe.

PetW	Petiole width: Maximum transverse distance across the node.
PpetL	Postpetiole length: In lateral view, the axial distance from base of node in front to tip of posterior peduncle.
PpetW	Postpetiole width: Maximum transverse distance across the postpetiole.
PSI	Petiolar spine index: SpL/WL.
PW	Pronotal width: Maximum width across pronotum in dorsal view.
SI	Scape index: SL/HW.
SL	Scape length: Maximum length excluding basal condyle and neck.
SpL	Propodeal spine length (Fig. 1): In same view as for WL, from tip of propodeal spine to nearest edge of propodeal spiracle peritreme.
MH	Mesosoma height (Fig. 1): In perfect lateral view, the vertical distance from a line tangent to the ventralmost points of the meso- and metasterna to the highest point on the mesosoma profile (for a broadly arching pronotum, estimated as the mid-point of the arc).
MHI	Mesosoma height index (Fig. 1): Mesosoma height (MH) divided by the horizontal distance from the base of the MH line to the posteroventral corner of the propodeum.
TL	Total length: Sum of ML + HL + WL + PetL + PpetL + GL to the nearest 0.1mm.
WL	Weber's length (Fig. 1): In perfect lateral view of the mesosoma, diagonally from posteroventral corner of mesosoma to farthest point on anterior face of pronotum, excluding the neck.

Additional Terminology

Terms such as vertex, occiput, malar and genal areas are of dubious accuracy when applied to ants. Consequently, there is disagreement over how to name the regions of the head (Trager 1989; Snelling 1989; Wheeler 1989). Moreover, these terms are confusing jargon that make the use of keys and descriptions difficult for the uninitiated. Instead, I prefer to rely, as much as possible, on the generally understood directional terms, anterior, lateral, etc., assuming that the mandibles are anterior. Five regions of the head usually contain distinctive sculpture in *Rogeria* (Fig. 1). 1) The **middorsum** of the head is the median portion of the dorsal surface between the maximum retraction of the scapes and extending from the frontal area to a change in sculpture near the rear of the head. 2) The **posterior** (region of the) **head** includes the actual posterior surface of the head and the **posterodorsum**, the dorsal surface between the middorsum and the posterior outline of the head. The "posterior head" seems equivalent to

the "vertex" of some authors who consider the mandibles to be ventral and the back of the head to be the top, rather than posterior. 3) The **laterodorsa** are the portions of the head seen in dorsal view that lie beneath the sweeps of the scapes. 4) The **venter** is the ventral surface of the head not seen in lateral view. 5) The **sides** of the head lie between the venter and the laterodorsa (between the lateral outline of the head in dorsal view and the ventral outline of the head in lateral view).

In **triangular mandibles** the basal angle is distinct and nearly a right angle (e.g. Figs. 43, 49, 63); in **subtriangular mandibles** the basal angle is reduced and more obtuse (e.g. Figs. 14, 58, 61). Sometimes tiny **denticles** are intercalated between or replace teeth (e.g. Figs. 35, 55); these are not included in tooth counts. The **palpal formula** is the number of maxillary palpomeres followed by number of labial palpomeres. Palpal formula is usually determined by dissection, thus the sample size is very small and may not show the variation within the species. The **body of the clypeus** is the medial portion of the clypeus anterior to the frontal lobes and dorsal to the **clypeal apron**, which is the anterior rim just above the mandibles (Fig. 1). Clypeal apron shape is described as seen from dorsal view. In describing eye shape, **elliptical** or **ellipsoid** means similarly rounded at both ends, whereas **oval** or **ovoid** means the anterior end is more narrowly rounded. The shape of the **posterior outline of the head** is as seen in the full dorsal view used for measuring HL since shape sometimes varies with the pitch of the head. The **nuchal grooves** are longitudinal impressions in the posteroventral corners of the head, into which the lower corners of the pronotum fit when the head is retracted.

A rough index of the degree of inclination of the propodeal spines is expressed by imagining a **bisecting line** that divides the lateral aspect of the spine in half and extends forward over the mesosoma side, and noting where it intersects the edge of the mesopleuron or pronotum (Fig. 1). It is important that the mesosoma be in perfect lateral view. The **diameter of a propodeal spiracle** includes the peritreme and is as seen in full lateral view of the mesosoma. The spiracle's position is measured from the outer edge of the peritreme to the nearest edge of the propodeum, which is the free edge of the infradental lamella.

The most common shapes of postpetioles as

seen from dorsal view are **subrectangular**, which have evenly convex sides that are widest midlength (e.g. Figs. 53, 58), and **subtrapezoidal**, which have convex sides that diverge caudad (e.g. Figs. 49, 50, 51).

The terga and sterna of the gaster are referred to by abbreviations **T1**, **S1**, etc. **Terminal segments of gaster rotated ventrad** means that T2 and T3 are distinctly longer than their corresponding sterna, causing the pygidium and hypopygium (T4 and S4) to shift anteroventrad and making T2 or T3 the distalmost sclerite of the gaster. Figs. 28, 40, 43, and 63 show rotated terminal segments; Figs. 2, 5, and 8 show unrotated segments.

Pygidial gland sculpture refers to a pair of microareolate patches on the anterior edge of the pygidium. The presence of this characteristic sculpture strongly suggests the presence of pygidial glands, but its absence does not necessarily mean the glands are absent (Hölldobler, et al. 1976; Kugler 1978a; Hölldobler and Engel 1978). In most species I was able to see the gland reservoirs attached to these patches, but failure to see the reservoirs does not mean they are absent; they could easily be lost during dissection.

Sting apparatus terms are identified in Figures 3 and 42.

Sculpture descriptions follow illustrations and definitions of Harris (1979). It seems to me that the term "**areolate**" in Harris' nomenclature best describes much of the sculpture in *Rogeria*, but I suspect many would prefer the term "**reticulate**." I have called the ridges on the head and mesosoma of many species "**rugae**," because they are irregular, and wrinkled to varying degrees, but others may prefer to call them "**carinae**." Also following Harris, in compound descriptors, such as rugose-areolate, the predominant type of sculpture is first.

The following are used to describe approximate hair inclination as seen in side view (Fig. 1): **erect** (> 70°), **suberect** (70°-50°), **subdecumbent** (50°-25°), **decumbent** (25°-5°), **appressed** (< 5°) (inference from Wilson 1955). To arrive at the **numbers of erect hairs** on the mesosoma dorsum, I used both dark and light backgrounds and a variety of positions to count all erect hairs on one half of the dorsum from the anterior edge of the pronotal disc to the bases of the propodeal spines. Since the hairs are distributed symmetrically, that count gives the number of pairs of erect hairs. Frequently,

both sides were counted in order to check for the presence of broken hairs. **Erect hair on head dorsum** means on frontal lobes, middorsum, and posterior head, but not under the sweep of the scapes. **Erect hair on scapes** means on the dorsal or anterior surfaces. Usually no attempt is made to describe hair on ventral and lateral aspects of body, nor on other than extensor surfaces of femora and tibiae.

DEPOSITORIES

ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia.
BMNH	British Museum (Natural History), London, U.K.
CKC	Charles Kugler Collection, Radford University, Radford, VA, U.S.A.
CUIC	Cornell University Insect Collection, Ithaca, NY, U.S.A.
DMOC	David M. Olson Collection, University of California, Davis, CA, U.S.A.
FML	Fundación Miguel Lillo, Instituto de Zoología, Miguel Lillo 251, Tucumán, Argentina.
JTLC	John T. Longino Collection
LACM	Los Angeles County Museum, Los Angeles, CA, U.S.A.
MCSN	Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy.
MCZ	Museum of Comparative Zoology, Cambridge, MA, U.S.A.
MHN	Museum d'Histoire Naturelle, Geneva, Switzerland.
MIZA	Museo Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
NMB	Naturhistorisches Museum, Basel, Switzerland.
PSWC	Philip S. Ward Collection, University of California, Davis, CA, U.S.A.
USNM	United States National Museum, Washington, D.C., U.S.A.

Genus **ROGERIA** Emery

- Myrmica* (in part); Fr. Smith 1858:131. Type: *Formica rubra* Linnaeus, 1758, designation of Wheeler, 1911.
Tetramorium (in part); Mayr 1886:359. Type: *Formica caespitum* Linnaeus, 1758.
Rogeria Emery 1894:188. Type: *Rogeria curvipubens* Emery, 1894, by designation of Wheeler, 1911.
Rogeria subgenus *Irogera* Emery 1915:191. Type: *Rogeria procerata* Emery, by original designation.

Macromischa (in part); Mann 1922:30. Type: *Macromischa purpurata* Roger 1863, by designation of Wheeler, 1911.
Irogera; Brown 1953:4.
Irogera; Kempf 1962a:435. [Redescribed].
Rogeria; Kempf 1963:195. [Key to South American species].
Irogera; Kempf 1964:66. [Key to species].
Rogeria; Kempf 1965:185.
Rogeria; Kempf 1972:227. [Catalog of New World species].

Worker Diagnosis.—Monomorphic myrmecines. Antenna 12-segmented; scape not reaching posterior margin of head; distinct 3-segmented club longer than rest of funiculus; apical antennomere longer than combined lengths of other two club segments. No antennal scrobes or fossae. Clypeus projects narrowly between frontal lobes at least to posterior edge of antennal insertions. Body of clypeus with one or more pair of longitudinal carinae. Lateral clypeus not raised into a ridge in front of antennal insertions. Nuchal grooves present on posteroventral corners of head. Anteroventral corners of pronotum angular to dentate and fitting into nuchal grooves. Propodeal spiracle 3 diameters or less from the edge of the propodeum below the propodeal spines. Metapleural lobes not sharply pointed.

Worker Description.—Mandibles usually triangular. Except in some *ciliosa* and *foreli*, mandibles with 5-7 teeth (3 apical teeth decreasing in size basad, followed by 2-3 smaller basal teeth). Additional denticles may occur among basal teeth or any basal tooth may be replaced by a pair of denticles. Palpal formula usually 3,2 or 2,2, but 3,3 in some *stigmatica*-group, and 2,1 in the very tiny *minima*. Scape neither elbowed nor ridged at the base, nor with an apron around the peduncle. Clypeus in profile usually with a very narrow anterior apron. Body of clypeus rises near vertically in most species, but occasionally projecting beyond the clypeal apron. Frontal lobes narrow, but covering antennal insertions; at most feebly notched behind. Frontal triangle small, depressed slightly. Eyes with 1-100 facets; located on sides, in the anterior half of the head (excluding mandibles). Sides of head widest just behind the eyes, forming rounded corners with the posterior head, which is weakly concave to weakly convex in full face view.

Mesosoma generally compact, broad shouldered. Anterior face of pronotum rises nearly vertically from the neck and usually forms a distinct, rounded angle with the dorsal surface. Mesosoma

dorsum without sutures; no mesonotal groove; metanotal groove absent to distinct. Anterior edge of propodeum often marked by a transverse carina. Propodeal spines absent to long. Metapleural lobes low carinae to rounded triangular. Legs not incrassate. No tibial spurs on middle or hind legs. Tarsal claws simple.

Petiolar peduncle with or without a ventral keel; inferior process dentate except in *stigmatica* group. Node unarmed; poorly to well differentiated from peduncle. Postpetiole with short peduncles and a low node that is broader than long. Terminal segments of gaster rotated ventrad in all but the *stigmatica* group.

All pygidia dissected have a pair of small pygidial gland reservoirs and/or paired microareolate patches present on anterior edge, except in the *stigmatica* group. Common features of the sting apparatus are: 1) medial connection of spiracular plate incompletely sclerotized, 2) gonostylus single-segmented, 3) dorsoterminal chaeta present, 4) at least one companion seta (except *gibba*), 5) each lancet with a single moderate to large valve, 6) sting bulb large, with arched sting base.

Mandibles usually predominantly smooth, with piligerous punctures and vestigial carinulae at insertions, but carinulae stronger and more extensive in some members of the *stigmatica*-group. In all but *ciliosa*, the body of the clypeus is smooth with a pair of carinulae extending from the frontal lobes and stopping short of the clypeal apron; these are sometimes accompanied laterally by 1-2 shorter, weaker carinulae. Lateral extremities of clypeus and adjacent cheeks with longitudinal carinulae. Frontal triangle smooth, except in *ciliosa*. If macrosculpture present, frontal lobes and middorsum with diverging longitudinal rugae; rest of body areolate, rugose, or occasionally carinate. Microsculpture when present usually microareolate, appearing granular or punctured at lower magnifications. Posterior face of propodeum smooth, except in *gibba*. Legs smooth and shiny. First segment of gaster smooth and shiny; less so in *prominula*, and *minima*. Pygidium and sometimes other terminal terga with microscopic areolate sculpture on exposed posterior surfaces; pygidium may also possess minute piligerous tubercles.

Short appressed or decumbent pilosity common, most dependably on legs (except *blanda* and

procera) and antennae. Terminal segments of gaster with erect hair. No erect hair on laterodorsa of head (undersweep of scapes). Body of clypeus just above apron with pairs of erect hairs; members of *stigmatica* group each with an additional median hair.

Color from brownish yellow to black, with mandibles, antennae, and legs lighter. Most species also with a lighter triangle on clypeus, cheeks, and frontal area.

Malpighian tubules in the one species examined (*belti*) 5 in the worker (N=2); 5 to 6 in the male (N=3) (Brown 1988).

Wings.—Notation (Fig. 30) follows Brown and Nutting (1949) and Hölldobler and Wilson (1990:9). First and second radial crossveins of primitive formicid wings are lost, creating a single large submarginal cell. The distal portion of the radial sector vein (Rs₄₊₅) vein is straight or curves forward, but never reaches the edge of the wing. The r-m crossvein present (Fig. 30) or absent (Fig. 37). Median and cubital veins of variable length, but not reaching wing margins. Medio-cubital crossvein always present in females, but may be lost in males.

Larvae.—Similarities among the larvae of *belti*, *scandens*, *procera* and *blanda* found by Wheeler and Wheeler (1973, 1976, 1986, 1988) are summarized here. Form pheidoloid, i.e. "abdomen short, stout and straight; head ventral near anterior end, mounted on short stout neck, which is the prothorax; ends rounded, one end more so than the other" (Wheeler and Wheeler 1976:8). Thorax and abdomen with at least bifid and anchor-tipped hairs; bifid hair on head (sometimes others). Cranium subtrapezoidal; clypeus bulging; antennae with 3 sensilla; labrum bilobed and narrowed dorsally. Mandibles ectatomoid (stout, gradually tapered and curved, with an apical tooth and additional teeth and denticles in some species). Maxilla shape paraboloid or lobose, with cylindrical galea and palps of varying length. Labium narrow; palps only slight elevations. Maxillae and labial surfaces coarsely spinose.

COMPARISONS WITH SIMILAR GENERA

Some members of *Leptothorax* (placed with *Rogeria* in the Leptothoracini) have antennae like *Rogeria* and some have a narrow posterior lobe of the clypeus, but these have rounded anteroventral

corners of the pronotum and no nuchal grooves. Of 65 species of *Leptothorax* examined at the MCZ, only one had an angular inferior corner of the pronotum, but in that species the scapes extend beyond the head, the posterior lobe of the clypeus is wider, and nuchal grooves are absent.

Some species of *Lordomyrma* (Myrmecini), a genus sometimes confused with *Rogeria* in pacific islands, have similar antennal and clypeal features, but have a rounded anteroventral corner of the pronotum and lack nuchal grooves. The stings of *Rogeria* species are dramatically different from those of five *Lordomyrma* species I have examined (*caledonica* Ern André, *levifrons* Mann, *punctiventris* Wheeler, *striatella* Mann, *tortuosa* Mann) in shape of quadrate plate, oblong plate, gonostylus, triangular plate and sting. Another species, *L. epinotalis* is very different from the other *Lordomyrma* I examined and has a sting apparatus somewhat like that of *Rogeria besucheti* or *R. ciliosa*, but lacks the pronotal corner or nuchal grooves of *Rogeria*. Wings of three *Lordomyrma* species I have been able to examine (*epinotalis*, *striatella*, *lae* Wheeler) are distinct from the known *Rogeria* wings in having the Rsf4+5 vein curve anteriorly to the wing margin. In *L. caledonica* this vein is like *Rogeria* in failing to reach the margin, but the m-cu vein is absent. The larvae of an unidentified *Lordomyrma* species differs from the known larvae of *Rogeria* as follows: form pogonomyrmecoid, cranium subelliptical, hairs fewer, none anchor-tipped (Wheeler and Wheeler 1977).

Stenamamma (Pheidolini) workers are similar in form of clypeus, including narrow posterior portion between frontal lobes, and some have 3-segmented antennal clubs, but in that case the apical segment is shorter than the combined length of the other two segments. Also, *Stenamamma* has no nuchal grooves, the anteroventral corner of the pronotum is rounded, and the metanotal groove is generally more distinct than in *Rogeria* species. Larvae of *Stenamamma* differ from those of *Rogeria* as follows: form aphaenogastroid; cranium subhexagonal; mandibles pogonomyrmecoid (similar to ectatommoid); body hairs bifid or denticulate, not anchor-tipped (Wheeler and Wheeler 1953, 1976).

Synonymic List of Species

Castes that have been collected are recorded in brackets in the right column. W = worker, Q = queen, M = male. Upper case Q and M are used if at least some reproductives are associated through a nest series. Lower case q and m are used if no reproductives are linked to workers by a nest series. An asterisk (*) is added if reproductives were not even found in the same localities as workers.

<i>alzatei</i> n. sp.	[W, q]
<i>belti</i> Mann, 1922	[W, Q, M]
<i>besucheti</i> n. sp.	[W]
<i>blanda</i> Fr. Smith, 1858	[W, Q, M]
= <i>foveata</i> Kempf, 1964 (synonymy by Kempf 1965)	
<i>bruchii</i> Santschi, 1922	[W]
<i>brunnea</i> Santschi, 1930	[W, q]
= <i>caraiba</i> Santschi, 1936 n. syn.	
= <i>cubensis</i> Santschi, 1936 n. syn.	
= <i>habanica</i> Santschi, 1936 n. syn.	
= <i>scabra</i> Weber, 1934 n. syn.	
<i>carinata</i> n. sp.	[W]
<i>ciliosa</i> n. sp.	[W, Q]
<i>cornuta</i> n. sp.	[W]
<i>creightoni</i> Snelling, 1973	[W, q*]
<i>cuneola</i> n. sp.	[W, q]
<i>curvupubens</i> Emery, 1894	[W, Q]
<i>exsulans</i> Wilson and Taylor, 1967	[W]
<i>foreli</i> Emery, 1894	[W, Q]
= <i>gaigei</i> Forel, 1914 n. syn.	
= <i>huachucana</i> Snelling, 1973 n. syn.	
<i>germani</i> Emery, 1894	[W, q*]
= <i>minensis</i> Santschi, 1923 n. syn.	
<i>gibba</i> n. sp.	[W, q]
<i>inermis</i> Mann, 1922	[W, Q]
<i>innotabilis</i> n. sp.	[W, q*]
<i>lacertosa</i> Kempf, 1963	[W]
<i>leptonana</i> n. sp.	[W, q*, M]
<i>lirata</i> n. sp.	[W, q*]
<i>megastigmatica</i> n. sp.	[W]
<i>merenbergiana</i> n. sp.	[W, Q]
<i>miconima</i> Kempf, 1961	[W]
<i>minima</i> Kusnezov, 1958	[Q]
<i>neilyensis</i> n. sp.	[W]
<i>nevadensis</i> n. sp.	[W]
<i>pellecta</i> Kempf, 1963	[W]
<i>procera</i> Emery, 1896	[W]
= <i>brasiliensis</i> Borgmeier, 1953 (Synonymy by Kempf 1962a)	
<i>prominula</i> n. sp.	[W]
<i>scandens</i> Mann, 1922	[W, Q]
<i>scobinata</i> n. sp.	[W, q]
<i>sicaria</i> Kempf, 1962b	[W]
<i>stigmatica</i> Emery, 1897	[W, Q, M]
= <i>sublevinodis</i> Emery, 1914 n. syn.	
= <i>manni</i> Santschi, 1922 n. syn.	

<i>subarmata</i> Kempf, 1962a	[W]
<i>terescandens</i> n. sp.	[W]
<i>tonduzi</i> Forel, 1899	[W]
<i>tribrocca</i> n. sp.	[W]
<i>unguispina</i> n. sp.	[W]

Names Transferred to Other Genera.

<i>azumai</i> Santschi 1941 (to <i>Lordomyrma</i> , Brown 1952)
<i>epinotalis</i> Mann 1919 to <i>Lordomyrma</i> , n. comb.
<i>rugosa</i> Mann 1921 to <i>Lordomyrma</i> , n. comb.
<i>tortuosa</i> Mann 1921 to <i>Lordomyrma</i> , n. comb.
<i>tortuosa levifrons</i> Mann 1921 to <i>Lordomyrma</i> , n. comb.
<i>tortuosa polita</i> Mann 1921 to <i>Lordomyrma</i> , n. comb.
<i>tortuosa stoneri</i> Mann 1925 to <i>Lordomyrma</i> , n. comb.
<i>striatella</i> Mann 1921 to <i>Lordomyrma</i> , n. comb.

SPECIES GROUPS

Some species of *Rogeria* can be assembled into more or less distinct species groups. Others can not be placed easily in any group, or seem to link several groups. These *incertae sedis* species are described with the group to which they may be most related.

The *stigmatica*-group may be distinct enough to be treated as a separate genus, but for now seems tied to the rest of *Rogeria* through *blanda*.

In the *creightoni* species group, extensive variation and often limited and scattered collections made it difficult to ascertain which specimens were simple variants and which were distinct species. At one time or another, I considered recognizing between four and 20 species in this group. Ultimately, I tried to steer a middle course between these extremes; neither masking the variation by describing large conglomerate species, nor encumbering the genus with a lot of dubious new species names. As a result, I have been somewhat more venturesome about naming new species in this group, yet there remain a number of rather heterogeneous species (*alzatei*, *brunnea*, *creightoni*, *leptonana*). I have described and illustrated some of the variants in these heterogeneous species in order to alert other taxonomists to remaining species problems and the need for extensive collecting, especially in the Caribbean Islands and circumcaribbean countries.

In the diagnoses below, if a species is listed as undissected, the palpal formula, pygidium, and sting apparatus characters are unknown.

stigmatica-group: *besucheti*, *ciliosa*, *gibba*, *megastigmatica*, *prominula*, *stigmatica*.

Diagnosis.—(*prominula* and *megastigmatica* not dissected). WL 0.67-1.30mm. Palpal formula 3,3 or 3,2. Eye with 4-41 facets. Metanotal groove distinct and extends down sides of mesosoma. Petiolar peduncle without a keel and inferior process a small step or absent. Nodes and gaster wide. Gaster with terminal segments not rotated ventrad, or only slightly rotated (*besucheti*). No pygidial gland sculpture or any evidence of reservoirs. Sting apparatus: weakly sclerotized, spiracle occupying more than 1/4 of spiracular plate; no anal plate; valve chamber not arising abruptly from base of sting shaft; sting shaft and lancets weak, spatulate (except perhaps for *prominula*); sting shaft apex without any flange; furcula a simple arch (no dorsal arm). Predominantly dense areolate macrosculpture on head (except middorsum), mesosoma (except some *stigmatica*), and nodes. Mandibles with piligerous punctures and stronger, more extensive carinate sculpture than in other *Rogeria* species. No microsculpture on most of body. Body of clypeus with a median erect hair low near anterior margin.

Similar *incertae sedis* species: *blanda*. This species has sculpture and pilosity like *ciliosa* and *gibba*, but has a 2,2 palpal formula, weak metanotal groove, dentate inferior petiolar process, and gaster, pygidium and sting apparatus typical of other groups.

scandens-group: *scandens*, *subarmata*, *terescandens*

Diagnosis.—(*terescandens* not dissected). WL 0.78-1.17mm. Palpal formula 3,2 Eyes large (30-80 facets). Propodeal spiracle faces strongly caudad. Metapleural lobes prominent, triangular. Petiolar node low, anterior face indistinct from peduncle (except some *subarmata*). Inferior petiolar process dentate. Postpetiolar sternum large. Pygidial gland sculpture and reservoirs present, at least in *subarmata*. Sting apparatus like that of *inermis* (Fig. 42). Head, mesosoma, and nodes predominantly rugose; sides of head below eye smooth. Dorsa of head, mesosoma nodes, and gaster T1 with sparse, stiff, untapered, erect hairs and sparse, inconspicuous appressed pilosity (occasional decumbent hairs in some *subarmata*). Scapes and legs with appressed hair only.

Similar *incertae sedis* species: *procera*, *tonduzi*. These both lack the stiff hairs and inflated postpetiole that make the group so distinctive, but otherwise are so similar that perhaps they should be included.

germaini-group: *germaini*, *lirata*, *lacertosa*.

Diagnosis.—WL 0.65-1.05mm, usually > 0.80mm. Mandibles triangular. Palpal formula 3,2. Body of clypeus not projecting over apron. Eye small (6-20 facets; OI 0.09-0.14). Propodeal spines rather long (PSI 0.18-0.23); directed caudad. Petiole with prominent keel and dentate inferior process. Petiolar node rises abruptly from anterior peduncle and with more or less distinct anterior, dorsal and posterior surfaces. Posterior two-thirds of postpetiolar node with parallel or slightly convergent sides. Postpetiolar sternum in side view rather long, its anterior corner perpendicular. Pygidial gland sculpture and reservoirs present. Sting apparatus similar to that of *inermis*, but sting shaft and lancets weak; lancet lacks barbule. Laterodorsal sides, and posterior head rugose-areolate (sometimes effaced on sides). Mesosoma predominantly rugose or vermiculate-rugose. Microsculpture weak; intervals on head and mesosoma shiny and nearly smooth. Mesosoma dorsum and gaster T1 with abundant fine, tapered, erect-suberect hairs, but very little, if any, decumbent or appressed pilosity.

Similar *incertae sedis* species: *pellecta*, *sicaria* (*sicaria* not dissected) These have different petiole shapes and more decumbent hair on the mesosoma. *Rogeria sicaria* also differs in clypeus, propodeal spines, and erect pilosity.

creightoni-group: *alzatei*, *brunnea*, *carinata*, *creightoni*, *innotabilis*, *leptonana*, *merenbergiana*, *nevadensis*, *scobinata*, *tribrocca*, *unguispina*

Diagnosis.—(*brunnea*, *nevadensis*, and *tribrocca* not dissected). WL 0.51-0.93mm. Mandibles triangular, except as noted. Palpal formula 3,2 or 2,2. Eyes small (6-19 facets). Petiole with a distinct node and dentate inferior process. Pygidial gland sculpture and reservoirs present. Sting apparatus like that of *inermis* unless otherwise noted. Mesosoma predominantly rugose or carinate. Head dorsum, mesosoma, nodes, and gaster covered with two distinct kinds of hairs: 1) abundant

short, decumbent pilosity and 2) equally or less abundant longer, erect-suberect hair (except for lack of erect hair on head of some *scobinata*). Usually more than 10 pairs on mesosoma dorsum (9 in some *leptonana*, 8 in *carinata*) and 2 or more posterodorsally projecting hairs on each node. All hairs tapered.

Similar *incertae sedis* species: *inermis*, *belti*, *cornuta*, *neilyensis*, *exsulans* (*cornuta* and *neilyensis* not dissected). These do not have two distinct types of hair on the mesosoma dorsum.

curvipubens-group: *cuneola*, *curvipubens*

Diagnosis.—WL 0.50-0.63mm. Mandibles triangular. Palpal formula 2,2. Clypeal apron usually convex (medially flattened in Haitian *curvipubens*). Eye small (4-11 facets). PSI 0.13-0.18. Petiole with distinct node, weak keel, and dentate inferior process. Postpetiole from above usually as in Fig. 74. Pygidial gland sculpture and reservoirs present. Sting apparatus as in *inermis* (Fig. 42), except for sting shaft and lancets of *curvipubens*. Median head and cheeks with weak longitudinal rugose-areolate macrosculpture. Mesosoma with predominantly rugose macrosculpture and areolate microsculpture, both often weak. Body covered with appressed-decumbent pilosity. Erect hairs sparse: none on scapes or extensor surfaces of legs, 0-16 on head (if present, short and limited to posterior head), usually 2-7 pairs on mesosoma dorsum (rarely 8), 0-1 pair posterodorsally projecting and 0-1 laterally projecting hairs on each node. Anterior portions of gaster T1 often lack erect hair. All hairs tapered.

Similar *incertae sedis* species: *micromma*, *minima* (neither dissected). *Rogeria micromma* has a subrectangular postpetiole in dorsal view and abundant erect hair on head. *Rogeria minima* has stiff, cuneate hairs and a 2,1 palpal formula.

foreli-group: *bruchi*, *foreli*

Diagnosis.—WL 0.50-0.80mm, usually < 0.75mm. Mandibles triangular. Palpal formula 2,2. Eye 5-20 facets. Propodeal spines wide at base. Petiole with distinct node and dentate inferior process. Pygidial gland sculpture and reservoirs present. Sting apparatus almost identical to that of *inermis* (Fig. 42). Sculpture predominantly microareolate on head, mesosoma, and waist;

macrosculpture feeble and limited to head. Most of body with short, appressed-decumbent pilosity only. Erect-suberect hairs present on mandibles, clypeus, ventral head, coxae, trochanters, sterna of gaster, and terminal terga of gaster.

KEY TO WORKERS OF *ROGERIA*

- 1 Pilosity appressed on mesosoma dorsum and gaster T1. A very small number of short decumbent hairs may also be present 2
- 1' Erect, suberect, or subdecumbent hairs present on mesosoma or gaster T1, often in addition to appressed or decumbent pilosity 4
- 2(1) Body of clypeus strongly projecting over apron. Basal angle of mandibles very reduced. (amazonian Brazil) (Fig. 14) *prominula*
- 2' Body of clypeus at most projecting only slightly over apron. Mandibles triangular 3
- 3(2') Clypeal apron emarginate. Mandible with 5 teeth. (Paraguay, Argentina) (Fig. 82) *bruchi*
- 3' Clypeal apron convex, often with faint median angle. Mandible with 6-7 teeth. (Caribbean, southwestern United States through northern South America) (Figs. 79-81, 104-105) *foreli*
- 4(1') Very dense, flexuous, erect hairs on dorsa of head, mesosoma and gaster; no decumbent or appressed pilosity. Promesonotum uniformly and densely areolate 5
- 4' Erect hair not so dense or flexuous. Decumbent hair present. Promesonotum may have some rugae or carinae 7
- 5(4). Metanotum forms an abrupt declivity between promesonotum and propodeum. (lowland Colombia, Ecuador) (Figs. 5-6) *gibba*
- 5' Shallow metanotal groove hardly interrupts mesosoma profile 6
- 6(5') Petiolar node relatively short and tall. Gaster larger (GW/WL 0.94-0.97). (lowland Ecuador, Venezuela) (Figs. 2-4) *ciliosa*
- 6' Petiolar node relatively long and low. Gaster smaller (GW/WL 0.63-0.70). (Central and South America) (Figs. 83-84) *blanda*
- 7(4'). Ventral process of petiolar peduncle reduced to a small step in petiolar profile, or absent 8
- 7' Ventral process of petiolar peduncle dentate 10
- 8(7) Propodeal spines longer (PSI 0.17-0.20). Ventral process of petiolar peduncle present as a small step. (Paraguay, Peru, Colombia) (Figs. 15-16) *besucheti*
- 8' Propodeal spines shorter (PSI 0.07-0.13). Petiolar peduncle lacking a ventral process 9
- 9(8') WL 0.72-0.92mm. (Pacific Islands) (Figs. 7-12) *stigmatica*
- 9' WL 1.18-1.30mm. (Solomon Islands) (Fig. 13) *megastigmatica*
- 10(7') WL 1.28-1.53mm. Eye large (80-100 facets). Postpetiole with an inconspicuous sternum. (Guyana, amazonian Brazil) (Fig. 18) *procera*
- 10' WL and eyes usually much smaller. If WL and eyes nearly as large, then postpetiolar sternum conspicuous 11
- 11(10') Sparse, stiff, erect-suberect hairs and short appressed hairs on dorsa of head, mesosoma, waist, and gaster T1. WL > 0.72mm. Eye with > 25 facets 12
- 11' Erect hairs more curved and tapered; shorter pilosity, if present, usually decumbent. If some erect hairs are stiff, then WL and eye are smaller 14
- 12(11) Propodeal spines very short (PSI 0.09-0.12). Pygidium with a pair of median tubercles just above the sting. (eastern Brazil) (Figs. 22-23) *subarmata*
- 12' Propodeal spines longer (PSI > 0.15). Pygidial tubercles lacking 13
- 13(12') Macrosculpture vestigial or absent on lateral pronotum and petiolar node. Waist slender (PpetW/PpetL 1.08-1.16). (Costa Rica) (Fig. 21) *terescandens*
- 13' Lateral pronotum with distinct rugae, petiolar node strongly rugose to areolate-rugose. Waist inflated (PpetW/PpetL 1.38-1.61). (Central America) (Figs. 19-20) *scandens*
- 14(11') Petiole clavate. Eye with 39-48 facets. (Central America) (Figs. 85-86) *tonduzi*
- 14' Petiole with a distinct node and/or smaller eyes 15
- 15(14') Undamaged hair on mesosoma dorsum mostly erect to suberect. Decumbent hairs, if present, much less abundant than longer, more erect pilosity 16
- 15' Mesosoma dorsum with abundant appressed or decumbent pilosity, usually in addition to longer erect to suberect hair 21

16(15)	EL/SpL > 1.00. Gaster T1 usually lacks decumbent and appressed pilosity (occasionally 1 or 2 decumbent hairs present). (Central America) (Figs. 40-42)	<i>inermis</i>
16'	EL/SpL usually < 0.90. If greater (some <i>belti</i>), then gaster T1 with abundant decumbent pilosity	17
17(16')	Clypeal apron with median tooth	18
17'	Clypeus emarginate to evenly convex	19
18(17)	Promesonotum with thick rounded vermiculate rugae. Metapleural lobes well developed, triangular. (Trinidad, Guyana, amazonian Peru and Colombia, Mato Grosso) (Figs. 28-30, 89-90)	<i>lirata</i>
18'	Promesonotum areolate-rugose to vermiculate rugose; rugae narrower, sharper. Metapleural lobes low, broadly rounded. (Paraguay, Mato Grosso and Minas Gerais) (Figs. 24-27, 87-88)	<i>germaini</i>
19(17')	Eyes small and propodeal spines long and horizontal (EL/SpL < 0.46). (Belize, southern Mexico) (Fig. 45)	<i>cornuta</i>
19'	EL/SpL > 0.46. Propodeal spines more inclined	20
20(19')	Eye smaller, elliptical (OI 0.13-0.14). Petiolar peduncle with lamellate keel. Sides of postpetiolar node distinctly areolate. (southern Brazil) (Fig. 31)	<i>lacertosa</i>
20'	Eye larger, oval (OI 0.18-0.22). Petiolar keel not lamellate. Sides of postpetiolar node smooth, or nearly so. (southern Mexico to Colombia) (Figs. 35-39, 91-92)	<i>belti</i>
21(15')	Scapes with longer erect to suberect hair in addition to shorter decumbent to appressed pilosity (in <i>exsulans</i> and some <i>brunnea</i> , erect hairs can be sparse and little longer than decumbent hair)	33
21'	No erect hair on scapes	22
22(21')	WL 0.90-0.99mm. EL/SpL 0.48-0.56. (southern Brazil) (Figs. 32-33)	<i>pellecta</i>
22'	Smaller. If WL approaches 0.90mm, then EL/SpL either < 0.30 or > 0.70	23
23(22')	Propodeal spines very long (PSI 0.29), strongly inclined. Eye small (EL/SpL 0.13). (southern Brazil) (Fig. 34)	<i>sicaria</i>
23'	Propodeal spines usually much shorter. If similar in size, then not strongly inclined. EL/SpL > 0.20 ..	24
24(23')	WL > 0.71mm. Pilosity on gaster not differentiated into two distinct kinds. (Costa Rica) (Fig. 43)	<i>neilyensis</i>
24'	WL usually < 0.71mm. If similar in size, hair on gaster differentiated into short-decumbent and longer-erect	25
25(24')	Clypeal apron with median tooth. Gaster T3 with short median spine. (Colombia) (Fig. 63)	<i>tribrocca</i>
25'	Clypeal apron without a median tooth. Gaster T3 unarmed	26
26(25')	Erect-suberect hairs absent from head dorsum (or short and limited to posterior head) and sparse on mesosoma. WL 0.51-0.63mm	27
26'	Erect hair present on middorsum and posterior head. If missing (<i>scobinata</i>), then > 10 pairs of erect hairs on mesosoma dorsum	28
27(26)	Postpetiolar sternum wedge-shaped in side view; node less vaulted. Sides of head and pronotum strongly microareolate, making macrosculpture (if present) difficult to see. (central Mexico to Costa Rica) (Figs. 77-78, 103)	<i>cuncola</i>
27'	Postpetiolar sternum not wedge-shaped; node more vaulted. Sides of head and pronotum with more or less smooth, shiny intervals. (Caribbean Islands, northern South America; possibly Central America) (Figs. 74-76, 101-102)	<i>curvipubens</i>
28(26')	Part of gaster T1 microareolate. Most erect hairs stiff, cuneate-fimbriate. (Argentina) (Figs. 72-73)	<i>minima</i>
28'	Gaster T1 smooth. Stiff hairs absent (except on some <i>micromma</i>)	29
29(28')	Rugae on pronotal dorsum and sides unbranching and nearly straight, with smooth and shiny intervals. Sides of head below eye nearly smooth, strongly shining. (northeastern Colombia over 1000m) (Figs. 65, 94)	<i>nevadensis</i>
29'	Rugae on promesonotum and sides of pronotum undulating and with lateral spurs or branches, sometimes forming areolate patches; intervals appear granular, not strongly shining. Sides of head rugose-areolate	30
30(29')	Eye with 2-5 facets. Mesosoma sides opaque with dense areolate microsculpture, but macrosculpture absent. Mesosoma dorsum with 8-10 pairs of erect hairs. (Surinam, Pará State of Brazil) (Fig. 71)	<i>micromma</i>
30'	Eye with 4-21 facets (rarely < 7). Mesosoma sides with rugose macrosculpture in addition to weak or distinct microsculpture. Mesosoma dorsum with \geq 12 pairs of erect hairs	31

- 31(30') Macrosculpture tuberculate on posterodorsum of head (Fig. 100). Erect hair usually absent from head dorsum, but sometimes short, sparse and mostly limited to posterior rim. (Trinidad, South America east of Andes to Paraguay) (Figs. 61-62, 100)..... *scobinata*
- 31' Posterodorsum of head rugose to areolate; no tubercles. Middorsum of head with long erect hair ..32
- 32(31') Clypeal apron convex. Nuchal groove clearly visible in lateral view. Propodeal spines generally wider. Petiolar keel distinct. (Mexico, Nicaragua; possibly into Colombia) (Figs. 55-57, 97-98) .. *innotabilis*
- 32' Clypeal apron truncate in Central America. Nuchal groove not clearly visible in lateral view. Propodeal spines usually slender. Petiolar peduncle with little or no keel. (Panama, South America, Dominican Republic) (Figs. 58-60, 99)..... *alzatei*
- 33(21) WL 0.93-1.02mm. Propodeal spines long (SpL > 0.20mm; PSI > 0.25), horizontal. Gaster with few or no decumbent hairs. (Belize, southern Mexico) (Fig. 45) *cornuta*
- 33' WL usually < 0.90mm. If larger (some *belti*, *brunnea*, *creightoni*), then decumbent hair abundant on gaster 34
- 34(33') Gaster T1 with two distinct kinds of pilosity: shorter, decumbent hairs and longer, erect hairs 36
- 34' Hair on gaster T1 not clearly sorting into two distinct kinds 35
- 35(34') Pilosity on gaster T1 more dense and decumbent to subdecumbent. Petiolar peduncle with very large keel. (Samoa) (Fig. 44) *exsulans*
- 35' Pilosity non gaster T1 more sparse and erect to subdecumbent. Petiolar peduncle with little or no keel. (Central America) (Figs. 40-42) *inermis*
- 36(34) Eyes larger (> 19 facets), oval. Macrosculpture on pronotal disc usually predominantly areolate and extending uninterrupted onto anterior face of pronotum (if predominantly rugose, then eye with > 25 facets). (southern Mexico to Colombia) (Figs. 35-39, 91-92) *belti*
- 36' Eyes smaller, often elliptical. Pronotal disc predominantly longitudinally rugose, vermiculate, or carinate. Anterior edge of disc transversely rugose, rugose-areolate, or carinate 37
- 37(36') Promesonotum with nearly straight, longitudinal carinae; no lateral branches; intervals very smooth and shiny. Eye small, elliptical (EL < 0.10. (Caribbean Islands) (Fig. 64) *carinata*
- 37' Promesonotum longitudinally rugose, vermiculate, or rugose-areolate. If intervals smooth and shiny, then eyes oval and EL > 0.10 38
- 38(37') Clypeus evenly convex. Postpetiolar node from above subtrapezoidal; sternum long, flat, without anterior lip. (Caribbean Islands) (Figs. 50, 93) *brunnea*
- 38' Clypeus usually emarginate or truncate. If convex, then postpetiolar node not subtrapezoidal; sternum shorter, with distinct anterior lip 39
- 39(38') Eye elongate-oval. A strong transverse carina runs across pronotal shoulders. Pronotal disc and sides with weakly undulating rugae and nearly smooth interrugal spaces. Propodeal spines often with downcurved tips. (Venezuela) (Fig. 49) *unguispina*
- 39' Eyes not elongate. Anterior pronotum may have 1 or more transverse rugae, but not carinae. Pronotal disc rugose or rugose-areolate. Propodeal spines straight 40
- 40(39') WL 0.54-0.66mm. Mesosoma low, slender (PW < 0.37mm). Propodeal spines short, sometimes absent (SpL < 0.11mm). Postpetiole generally widest in anterior half (Fig. 66) (southern Mexico, Central America, Dominican Republic) (Figs. 66-70) *leptonana*
- 40' Generally larger, with MHI > 0.90, PW > 0.37mm, and SpL > 0.10mm. Postpetiole subtrapezoidal or subrectangular (Figs. 51, 53) 41
- 41(40') Metanotum strongly interrupts contour of mesosoma profile. Sides of head rugose or effaced rugose-areolate. EL/SpL > 0.65. (Colombian and Ecuadorian Andes above 1000m) (Figs. 46-48) *merenbergiana*
- 41' Metanotum with little or no effect on overall shape of mesosoma profile. EL/SpL < 0.65. Sides of head rugose-areolate; not effaced. (southern Texas to Panama) (Figs. 51-54, 95-96) *creightoni*

SPECIES DESCRIPTIONS

Stigmatica-Group and Related Species*Rogeria ciliosa* new species

Figs. 2-4

Additions to *stigmatica*-group diagnosis. WL 1.06-1.20mm. Mandibles triangular; coarsely punctured, weakly carinulate. Anterior clypeus evenly convex. Propodeal spines long (> 0.20mm), strongly inclined and diverging. Metapleural lobes well developed; angular. Inferior petiolar process reduced to a small step. Dorsal head, mesosoma and gaster densely covered with long flexuous hairs; terminal segments of gaster with dense, stiff erect hair.

Holotype and Paratype Workers.—TL 4.1-4.8 (4.1), HL 0.90-1.02 (0.90), HW 0.78-0.89 (0.785), SL 0.69-0.77 (0.69), EL 0.14-0.16 (0.15) (32-42 facets), PW 0.60-0.66 (0.60), WL 1.06-1.20 (1.06), SpL 0.24-0.28 (0.245), PetL 0.44-0.53 (0.44), PpetL 0.23-0.29 (0.235)mm, CI 0.84-0.87 (0.87), OI 0.17-0.19 (0.19), SI 0.85-0.90 (0.88), PSI 0.21-0.23 (0.23). N=9

Mandibles with 7-9 teeth (3 apical teeth decreasing in size basad, followed by 4-6 small, subequal teeth). Palpal formula 3,2. No clypeal apron. Body of clypeus not projecting over anterior edge. Nuchal grooves weak. Pronotal shoulders rounded. Ventral petiole with a low median carina rather than a distinct keel. Node distinct, wider than long. Postpetiole dorsal view shape as in Fig. 66. Postpetiolar sternum short, with a distinct anterior lip followed by a narrow sulcus. Gaster large (GW/WL 0.94-0.97). Quadrangle plate of sting apparatus with somewhat reduced apodeme that lacks lobes on anterodorsal corner; oblong plate ventral arm very reduced (see also Fig. 3 and *stigmatica*-group diagnosis).

Body of clypeus with fragmented longitudinal rugulae surrounded by effaced areolate sculpture. Longitudinal rugae on head dorsum mostly confined to the frontal lobes, frontal area, and midline. Frontal lobes rugose-areolate in some paratypes. Rest of dorsum, cheeks, venter, and posterior head densely areolate; intervals bearing shallow piligerous punctures. Promesonotum with the same areolate sculpture. Mesopleura, metapleura, and sides of propodeum with more irregular and confused areolate sculpture. Metanotal groove scrobiculate. Dorsal face of propodeum transversely rugose with undulating,

smooth intervals or largely areolate with a few carinulae between the spines. Most of petiole and postpetiole strongly areolate as well. Sculpture on anterior petiolar node effaced; dorsum of peduncle smooth. First tergum and sternum of gaster rather coarsely punctured in front and more finely punctured caudad; smooth and shiny between punctures.

Fine, long, flexuous, erect to suberect hair covers middorsum of head, dorsum of mesosoma, dorsum and sides of waist, and first segment of gaster. On terminal segments of gaster these become denser, stiffer and more erect to form brush-like rings. Shorter, subdecumbent hairs occur on lateral and ventral surfaces of head, dorsal surfaces of scapes, sides of mesosoma, and sometimes dorsal face of propodeum. Very short, decumbent to appressed pilosity on extensor surfaces of legs and ventral petiole. Median hair on clypeus fine and often obscured by surrounding paired hairs.

Body uniformly rusty-brown; appendages lighter, more yellowish-brown.

Paratype Queen.—TL 5.3, HL 1.04, HW 0.91, SL 0.80, EL 0.27, PW 0.97, WL 1.50, SpL 0.30, PetL 0.58, PpetL 0.30mm, CI 0.88, SI 0.88, PSI 0.20. N=1

Differing from paratypes only in the normal queen characters (Fig. 4). Mandible 8-toothed. Short parapsidal furrows present on mesoscutum. Both mesoscutum and mesoscutellum with same dense areolate sculpture as in worker. Metanotum vaguely microareolate. Dorsal face of propodeum with transverse carinulae mesad; areolate laterad.

Discussion.—*Rogeria gibba* (Figs. 5-6) from western Ecuador and Colombia resembles *ciliosa* in size, sculpture and pilosity, but has different mandibles, clypeal margin, propodeal spines, and metapleural lobes. *Rogeria stigmatica* and *megastigmatica* (Figs. 7-13) from the Pacific have much shorter propodeal spines, less punctured gaster, and different pilosity.

The name *ciliosa* refers to its dense covering of flexuous hairs.

Distribution.—This species is known only from lowland rain forests in the amazonian basin of Ecuador and the Orinoco basin of Venezuela.

Material Examined.—*Holotype locality*. EC-UADOR: Napo Province, Limoncocha, 250m, 18-VI-1976, #B-348 (S. and J. Peck) [MCZ].

Paratype locality. 9 workers, 1 queen, VEN-EZUELA: Bolívar State, Campamento Río Grande, 8.07N 61.42W, 250m, 14-VIII-1986, sifted leaf mold

and rotten wood, #8572-12 (P. S. Ward) [2 workers dissected: mouthparts, 2 stings] [BMNH, LACM, MCZ, MIZA, MZSP, USNM].

***Rogeria gibba* new species**

Figs. 5-6

Additions to *stigmatica*-group diagnosis. WL 0.85-0.93mm. Mandibles subtriangular. Clypeal apron slightly convex medially, with sharp corners on either side. Eyes with 16-20 facets. Mesosoma profile humpbacked. Propodeal spines short (<0.15mm), not strongly inclined. Propodeal spiracle rather large, within one diameter of posterior edge of mesosoma. Metapleural lobes reduced to short carinae, sometimes nearly absent. No inferior petiolar process. Dorsal head, mesosoma and gaster densely covered with long flexuous hairs.

Holotype and Paratype Workers.—TL 3.5-3.8 (3.7), HL 0.78-0.85 (0.83), HW 0.73-0.81 (0.78), SL 0.54-0.60 (0.59), EL 0.09-0.10 (0.10) (15-22 facets), PW 0.51-0.57 (0.55), WL 0.85-0.96 (0.93), SpL 0.11-0.14 (0.11), PetL 0.40-0.49 (0.46), PpetL 0.21-0.23 (0.22)mm, CI 0.91-0.96 (0.94), OI 0.12-0.13 (0.13), SI 0.72-0.77 (0.76), PSI 0.12-0.15 (0.12). N=10

Mandibles with 5 teeth diminishing in size basad. Palpal formula 3,3. Body of clypeus does not project over apron. Head capsule about as wide as long. Nuchal grooves visible from below or behind. Promesonotal dorsum almost flat and dropping abruptly to metanotum (Fig. 5). Petiolar peduncle lacks inferior petiolar process. Petiolar node distinct, bulbous, wider than long. Postpetiolar node subrectangular from above; sternum short. Gaster large (GW/WL 0.90-0.97). Sting apparatus like that of *ciliosa*, except for: 1) a longer fulcral arm on the oblong plate (like *inermis* Fig. 42), 2) no companion seta on gonostylus, 3) more enlarged lancet apex, and 4) no anterolateral processes on sting base (Fig. 6).

Middorsum of head longitudinally rugose becoming rugose-areolate behind level of eyes. Laterodorsa, posterior, sides, and ventral surfaces of head areolate with minutely granulate ridges; intervals smooth except for some piligerous punctures. Promesonotum with the same sculpture as sides and back of head. Meso- and metapleura with more confused areolate sculpture, but similar ridges and intervals. Metanotal groove scrobiculate. Dorsal face of propodeum and part

of posterior face transversely rugulose. Rest of posterior face shagreened. Petiolar peduncle colliculate; anterior face of node smooth, except for piligerous punctures. Rest of petiolar node and all of postpetiolar node transversely areolate-rugose, with granulate ridges and smooth to weakly punctured intervals, as on head and promesonotum. Gaster smooth and shiny, dotted by numerous small, shallow piligerous punctures.

Dorsum of head, mesosoma, top and sides of waist, and all sides of gaster densely covered with long, flexuous, erect to suberect hairs and without interspersed shorter pilosity.

Body rusty-brown, gaster slightly darker. Antennae, legs and mandibles yellowish-brown to yellow.

Queens.—TL 4.2-4.3, HL 0.83-0.85, HW 0.80, SL 0.58-0.59, EL 0.19-0.20, PW 0.72-0.73, WL 1.14-1.15, SpL 0.15-0.17, PetL 0.49-0.53, PpetL 0.24-0.25mm, CI 0.94-0.96, SI 0.73-0.74, PSI 0.13-0.15. N=4

Queens differ from the workers in the usual and the following ways. Short parapsidal furrows present. Longitudinal areolate-rugose sculpture on median head extends to posterior of head. Median pronotum transversely rugose. Mesoscutum with longitudinally rugose sculpture that becomes more areolate on mesoscutellum.

Discussion.—See the *ciliosa* discussion for comparison. Like *stigmatica* also in many features, but differs in pilosity and shape of promesonotum. The name *gibba* is from Latin meaning humpback.

Distribution.—One worker is from the eastern side of the central cordillera in northern Colombia, the rest are from about 1000km away on the western slope of the Andes and the coastal range of northern Ecuador. In all three areas they were collected at 300-800m elevation in natural rain forest, probably by Berlese sampling.

Material Examined.—**Holotype locality**. EC-UADOR: Pichincha Province, 4 km E. Santo Domingo de los Colorados, 22-VI-1975, #B-304 (S. and J. Peck) [MCZ].

Paratype localities. COLOMBIA: 1 worker, Antioquia Department, near El Bague, Providencia, Estación Biológica, Zona Buenos Aires, 30-31-XII-1977 (C. Kugler) [MCZ]; 1 worker, Chocó Department, Río Napipi, 1968 (P. A. Silverstone) [LACM]. EC-UADOR: 5 workers, holotype locality, 22-VI-1975 and 8-VII-1976 (S. and J. Peck) [2 mouthparts, stings] [BMNH, CKC, MCZ, MZSP]; 2 workers,

Pichincha Province, 47km S. Santo Domingo, Río Palenque Station, 23-V-1976 (S. and J. Peck [MCZ]); 1 worker, Pichincha Province, Tinalandia, 16km SE. Santo Domingo de los Colorados, 4-VI-1976 (S. and J. Peck) [MCZ].

Nontype localities. ECUADOR: 3 queens, Pichincha Province, 47km S Santo Domingo, Río Palenque Station, 1975 (S. and J. Peck); 1 queen, Manabí Province, 73km NE Chone, 12-VI-1976 (S. and J. Peck) [MCZ].

Rogeria stigmatica Emery
Figs. 7-12

Rogeria stigmatica Emery 1897:589. Syntype workers, NEW GUINEA: Friedrich-Wilhelmshafen [=Madang] (Biró) [MHN] [Both syntypes examined].

Rogeria stigmatica subsp. *sublevinodis* Emery 1914:415. Syntype workers, LOYALTY ISLANDS: Maré, Raoua [MHN] [Both syntypes examined]. N. syn.

Rogeria sublevinodis; Wilson and Taylor 1967:76, Fig. 61.

Rogeria manni Santschi 1922:353. Syntype workers, SOLOMON ISLANDS: Fulakora, Ysabel Is. (Mann) [MCZ, NMB] [12 syntypes examined]. N. syn.

Lordomyrma manni; Brown 1953:4.

Additions to *stigmatica*-group diagnosis. WL 0.72-0.92mm. Mandibles usually subtriangular. EL usually ≥ 0.10 mm. Propodeal spiracle \leq half its diameter from edge of infradental lamella. Propodeal spines short (PSI 0.07-0.13), strongly inclined dorsad. Metapleural lobes much reduced. Inferior petiolar process absent. Abundant decumbent hair on head, mesosoma, waist and gaster; erect hairs rather sparse, not flexuous.

Workers.— TL 3.0-3.7, HL 0.66-0.83, HW 0.58-0.71, SL 0.46-0.61, EL 0.05-0.15 (7-34 facets), PW 0.44-0.52, WL 0.72-0.92, SpL 0.05-0.10, PetL 0.32-0.42, PpetL 0.19-0.23mm, CI 0.84-0.92, OI 0.08-0.22, SI 0.79-0.87, PSI 0.07-0.13. N=28

Mandibles subtriangular (usually) to triangular; with 5 subequal teeth or 3 apical teeth followed by 3-4 (rarely 5) smaller teeth or denticles. Palpal formula 3,3. Little or no clypeal apron; median clypeal margin truncate, weakly convex, or weakly angular. Body of clypeus not projecting over clypeal margin. Eyes oval, large (EL 0.10-0.15mm and 17-34 facets), except in some of the Papua New Guinea workers (EL 0.05-0.07mm; 7-9 indistinct facets). Nuchal groove distinct from behind, but not clear in side view. Promesonotum with evenly convex profile. Metanotal suture narrow, emphasized by a sharp ridge at anterior edge of propodeum.

Node large, wider than long, more or less symmetrical in side view (Fig. 8). Postpetiolar node in side view rounded front to back; usually widest in anterior half, much as in Fig. 66, but sometimes widest midlength. Postpetiolar sternum short. Sting apparatus like that of *ciliosa* (Fig. 3), except for: 1) spiniform medial and lateral projections from anterodorsal corner of quadrate plates, 2) smaller valve chamber, and 3) lack of anterolateral processes on sting base (Fig. 9). Gonostylus sometimes with no clear sensillar gap; sometimes lacking a companion seta. The "*Rogeria (stigmatica) group* spp. 1 and 2" in Kugler (1978b) are both *stigmatica*. The sting shown here is more accurate than the previous one, which was not in full lateral orientation when drawn.

Middorsum of head longitudinally rugose; rest of head, including venter, coarsely areolate. Dorsum of promesonotum coarsely areolate to rugose (intermediate specimens predominantly areolate, but with elongate cells or short rugae medially; rarely, rugae also occur on shoulders). Anterior and sides of mesosoma areolate, finely so on neck and ventrad on meso- and metapleura. Spaces in sculpture smooth except for piligerous punctures. Dorsal face of propodeum areolate along very anterior margin, followed by either transversely rugulose or densely punctate sculpture, or both in varying degrees of density and definition. Petiolar peduncle finely colliculate or smooth. Anterior and apex of node smooth or areolate; posterior face and sides areolate, sometimes with a few rugae. Postpetiole transversely rugose-areolate behind, becoming more effaced anteriorly, often leaving anterior face smooth and shining.

Decumbent to subdecumbent pilosity covers most of body. Sparser erect to suberect hair also on dorsa of scapes, head, mesosoma, nodes, and gaster. Erect hair moderately abundant on gaster T1 of most specimens (Fig. 8), but sparse on specimens from Papua New Guinea. Body of clypeus with strong median seta.

Color of mandibles, frontoclypeal region, antennae, and legs light brownish-yellow to brown. Rest of body light brown to blackish-brown.

Queens.— TL 3.6-4.5, HL 0.73-0.85, HW 0.66-0.75, SL 0.53-0.62, EL 0.19-0.24, PW 0.60-0.71, WL 1.00-1.17, SpL 0.10, PetL 0.41-0.48, PpetL 0.21-0.26mm, CI 0.87-0.90, SI 0.80-0.84, PSI 0.09-0.10. N=6

As in worker except for the usual caste differences. Mesosoma habitus as in Fig. 10. Queen from McAdam Park, Papua New Guinea with median bulge on pronotum. Pronotum areolate on sides; finer and transversely rugose-areolate mesad. Mesoscutum longitudinally rugose; mesoscutellum areolate-rugose. Metanotum smooth. Mesosoma sides confused areolate, except for smooth area on mesokatepisterna and costulate metapleural gland bullae. Wing venation as in *lirata* (Fig. 30), except for Rs vein as in *belti* (Fig. 37).

Males.—TL 2.6-3.1, HL 0.45-0.54, HW 0.56-0.66 SL 0.27-0.35, EL 0.20-0.26, PW 0.50-0.62, WL 0.84-1.04, PetL 0.22-0.30, PpetL 0.14-0.19mm, CI 1.22-1.27, SI 0.48-0.53. N=3

Mandibles with a large apical tooth and 4 others decreasing in size basad. Posterior lobe of clypeus projects more broadly between antennae than in worker; anterior clypeal margin weakly convex. Frontal lobes absent. No distinctly impressed frontal area. Funicular segment 6 curved and longer than 4 and 7; more extremely curved and elongate on one side of the head than the other. Posterior outline of head medially concave; sharp crests run from ocelli to posteroventral corners of head, which project slightly and fit around prothoracic sternum when head is retracted. Mesosoma and waist as shown in Fig. 11. Genitalia as shown in Fig. 12. Head integument vaguely roughened. Mesosoma and waist smooth, except along furrows and on sides of propodeum, metepimera, and petiolar peduncle. Gaster smooth and shining. Pilosity all erect to suberect, except around eyes. Propodeum nude. Color variation as in worker.

Discussion.—According to Emery (1914) and Wilson and Taylor (1967), *sublevinodis* differs from *stigmatica* in having larger size, coarser sculpture on head and mesosoma, and smooth nodes with coarser punctures on other parts of the waist. When two of Emery's *stigmatica* syntypes and two of his *sublevinodis* syntypes in the MHN were compared side by side, the TL and WL of the *stigmatica* syntypes fell within the range of the *sublevinodis* syntypes. The sculptural characteristics were not distinct either, except on the dorsal face of the propodeum, which is transversely rugulose and very weakly punctate and shiny in *stigmatica* syntypes, but densely punctate and lacking rugulae in the *sublevinodis* syntypes. However, intergrades with rugulae and various degrees of

punctuation occur in the Solomon Islands, Irian Jaya, and Pohnpei.

Santschi (1922) claimed that *manni* differed from *stigmatica* in a variety of ways. After examining *manni* types, I could confirm only one clear way they differ from the types of *stigmatica* and *sublevinodis*: the presence of rugose sculpture instead of areolate sculpture on the promesonotum. However, in non-type material, I found all intermediate states, sometimes within the same locality. Other supposedly different characters also intergrade or are due to the *manni* types being at the small end of the size distribution.

I have too few collections from Papua New Guinea to know if those specimens with unusually small eyes and few erect hairs on gaster T1 might be a distinct species.

See sister species *megastigmatica* description. See also *ciliosa* and *gibba* for discussions of related species in South America and *exsulans* for discussion of a not so related species from the Pacific.

Distribution and Behavior.—*Rogeria stigmatica* is known only from the Central and West Pacific, from as far east as Tahiti to the western tip of the Island of New Guinea and from about 22°S to 7°N.

Most collections come from berlesate or sifting of leaf mould, rotten wood, soil, moss, or bases of fern epiphytes in rain forest. The one nest series with ecological data (Sorong, Irian Jaya) is from rotten wood. Mann (1921:451) found colonies beneath stones and logs. Twelve specimens, were collected on imported coconuts in Honolulu. If nesting occurs in coconuts, colonization of Polynesia and Melanesia from South America may have occurred by rafting on the South Equatorial Current.

Mann (1921:451) observed workers producing long, worm-like stands from the anal area when the nest was disturbed.

Material Examined.—SOCIETY ISLANDS: Tahiti, Punaauia District (J. Dixon). AMERICAN SAMOA [=E. Samoa]: Tutuila [sting; whole specimen]; Tafuna; Alega (T. E. Woodward). WEST-ERN SAMOA: Falepuna [sting]; Matautu; Vaipoto; Poutasi (T. E. Woodward); Le Mafa; Gagaifomauga (G. Ettershank); Apia (H. Swale). WALLIS ISLANDS: Nukuione (G. Hunt) [mouthparts, sting, whole specimen]. ÎLES DE HORNE [=Hoorn Islands]: Futuna (G. Hunt). FIJI: Vanua Ava; Waiyanitu; Ovalau; Lasema; Somosomo; Nagasau; Saiaro; Munia; Nadarivatu; Labasa (W. M. Mann);

Sigatoka (W. L. and D. E. Brown) [2 stings; male genitalia]. VANUATU [=New Hebrides]: Espiritu Santo (E. O. Wilson). LOYALTY ISLANDS: Maré. SOLOMON ISLANDS: Ysabel, Fulakora [sting]; Ugi [=Uki] (W. M. Mann) [sting]. PAPUA NEW GUINEA: New Guinea, Huon Peninsula (E. O. Wilson); Wau, McAdam Park (S. Peck); Friedrich-Wilhelmshafen [=Madang] (Biró). INDONESIA: Irian Jaya, Sorong (W. L. Brown). CAROLINE ISLANDS: Ponape [=Pohnpei] (Y. Kondo). 170 workers, 9 queens, 3 males [CUIC, MCZ, MHN, USNM].

***Rogeria megastigmatica* new species**

Fig. 13

Holotype and Paratype Workers.— TL 4.5-4.9 (4.5), HL 1.01-1.09 (1.01), HW 0.90-1.00 (0.91), SL 0.77-0.83 (0.77), EL 0.16-0.19 (0.16) (41-52 facets), PW 0.62-0.70 (0.62), WL 1.18-1.30 (1.18), SpL 0.10-0.11 (0.11), PetL 0.51-0.52 (0.52), PpetL 0.28-0.31 (0.28)mm, CI 0.88-0.92 (0.90), OI 0.18-0.19 (0.18), SI 0.83-0.87 (0.85), PSI 0.08-0.09 (0.09). N=5

Like *stigmatica* in most respects, but markedly larger (at least 35% larger than *stigmatica* on other Solomon Islands). Metanotal groove not as narrow or sharply defined. Petiolar node strongly asymmetrical in side view (Fig. 13).

Mandibles triangular, with at least 6 teeth, some basal denticles may have been abraded. Median clypeal apron convex. Mandibular carinulae effaced. Pronotum areolate with a rugose-areolate patch in center of disc. Dorsal face of propodeum transversely rugulose. Petiolar peduncle smooth; sides of node areolate; posterior face transversely rugulose-areolate or areolate-rugose.

Material Examined.—**Holotype locality**. SOLOMON ISLANDS: Guadalcanal, Ilu Bush, 16-III-1962, #1181 (P. J. M. Greenslade) (MCZ). **Paratype localities**. SOLOMON ISLANDS: 1 worker, holotype locality [MCZ]; 3 workers, San Cristobal, Kira Kira, 24-IV-1962, #1579 (P. J. M. Greenslade) [MCZ].

***Rogeria prominula* new species**

Fig. 14

Additions to *stigmatica*-group diagnosis. WL 0.78mm. Basal angle of mandibles greatly reduced. Body of clypeus projects strongly over the trun-

cate clypeal apron. Frontal region elevated and laterodorsa slightly concave. Eyes very small. Metapleural lobes and metapleural gland bulla reduced. Body almost devoid of erect hair.

Holotype Worker.— TL 2.88, HL 0.66, HW 0.56, SL 0.51, EL 0.05 (4 facets), PW 0.435, WL 0.78, SpL 0.15, PetL 0.30, PpetL 0.19mm, CI 0.85, OI 0.09, SI 0.91, PSI 0.19.

Mandibles with 5 teeth, basal angle greatly reduced (Fig. 14). Frontal lobes wide, closely approximated. Eyes small, round, sunken; facets indistinct. Nuchal groove visible laterally as a distinct notch. Pronotal shoulders well rounded. Dorsal face of propodeum wide, weakly concave. Propodeal spiracle about 2 diameters from edge of infradental lamella. Metapleural lobes reduced to low carinae. Metapleural gland bulla small. Petiolar node large, wider than long. Petiolar peduncle short, with weak keel and small, dentate inferior process. Postpetiole subrectangular in dorsal view. Postpetiolar sternum projects shelf-like under articulation with petiole. GW/WL 0.84. Terminal segments of gaster not rotated ventrad. Shaft of undissected sting slender, with slightly enlarged apex; lancets acute and appear strong.

Mandibles strongly carinate for most of length. Frontal area impressed, smooth. Median head longitudinally rugose-areolate. Cheeks near antennal insertions microareolate. Laterodorsa, sides and posterior head densely macroareolate; cells small, usually obscuring the effaced microareolate background. Promesonotal dorsum with same areolate sculpture as on back and sides of head. Mesosoma sides strongly microareolate and macroareolate; in different places one or the other predominates. Scrobiculate sculpture in mesosoma sutures. Dorsal face of propodeum distinctly microareolate, with branching rugulae crossing between propodeal spines. Peduncle and anterior face of petiole as well as sterna of petiole and postpetiole microareolate; rest of petiole and postpetiole macroareolate, somewhat effaced mesad. Gaster T1 densely covered with piligerous punctures; punctures weaker caudad. Other terga smooth except for vaguely roughened posterior margins.

Most of body covered with very fine, appressed pilosity. Sparse erect hairs on clypeus, frontal lobes and nearby head middorsum. A few short, decumbent hairs on mesosoma dorsum; dense erect hairs on terminal segments of gaster.

No pilosity on ventral petiole.

Discussion.—This is perhaps the most aberrant *Rogeria* species, with its unusual head shape and pilosity. But it has the characteristic *Rogeria* antennae, nuchal grooves and square anteroventral corners of the pronotum. It has affinities with *ciliosa*, *gibba*, and *stigmatica*, as described in the *stigmatica*-group discussion.

The name *prominula*, meaning little prominence, describes the body of the clypeus.

Material Examined.—**Holotype locality.** BRAZIL: Amazonas, Ig. Marianil, Rio Branco Road, 24km NE Manaus, 22-VIII-1962, #M-2 (W. L. Brown) [MCZ].

Rogeria besucheti new species

Figs. 15-16

Additions to *stigmatica*-group diagnosis. WL 0.67-0.75mm. Eye small (8-10 facets). Propodeal spiracles small, more than 3/4 diameter from infradental lamella. PSI 0.17-0.20. Metapleural lobes well developed. Inferior petiolar process a small step. Head, mesosoma, nodes and gaster with abundant decumbent pilosity and more sparse erect hairs.

Holotype and Paratype Workers.— TL 2.7-3.1 (2.85), HL 0.65-0.71 (0.66), HW 0.59-0.63 (0.60), SL 0.43-0.49 (0.44), EL 0.05-0.08 (0.06) (8-10 facets), PW 0.42-0.46 (0.43), WL 0.67-0.75 (0.69), SpL 0.12-0.15 (0.13), PetL 0.30-0.34 (0.32), PpetL 0.16-0.18 (0.18)mm, Cl 0.87-0.90 (0.90), OI 0.08-0.13 (0.10), SI 0.72-0.78 (0.72), PSI 0.17-0.20 (0.18). N=7

Holotype mandible with 5 visible teeth decreasing in size basad. In paratypes, mandibles always with 3 apical teeth, but basal teeth may have additional denticles or be replaced by pairs of denticles. Palpal formula 3,2. Clypeal apron truncate; body of clypeus projecting enough to block view of apron in full dorsal view. Pronotal shoulders rounded. Shallow metanotal groove shallow present on dorsum and sides of mesosoma. Propodeum lacking a distinct transverse carina at anterior border. Peduncle of petiole with weak ventral keel; inferior process reduced to a small step. Petiolar node bulbous, wider than long. Postpetiolar node widest in anterior half (as in Fig. 74). Postpetiolar sternum short, anterior lip not greatly prominent. GW/WL 0.91-0.98. Terminal segments of gaster slightly rotated ventrad, but not enough to make T3 the distalmost point of the

gaster. Sting apparatus much like that of *ciliosa* (Fig. 3), but: 1) anterior apodeme of spiracular plate widest midlength, 2) anterodorsal corner of quadrate plate longer, narrower, 3) anterior apodeme of oblong plate longer, 4) gonostylus a little longer, with two companion setae and less distinct gap in setation and 5) sting base lower and without anterolateral processes (Fig. 16).

Longitudinally rugose macrosculpture on frontal lobes becomes rugose-areolate on middorsum. Laterodorsa, sides, and posterior head areolate with rather small areolae; intervals smooth and shining, except for piligerous punctures. Pronotal disc varies from all rugose-areolate to all areolate. Rest of promesonotum slightly less coarsely areolate. Intervals smooth, except for piligerous punctures. Dorsal face of propodeum densely microareolate, with or without overlying transverse rugulae.

Dorsum and anterior face of petiolar node smooth; rest of petiolar and postpetiolar nodes effaced areolate. Gaster predominantly smooth and shiny; T1 and S1 with piligerous punctures that in some specimens become weaker caudad. Remaining terga and sterna very weakly roughened and shiny.

Paraguayan specimens have suberect hair on scapes; others do not. Head dorsum with suberect hairs. Pilosity on mesosoma dorsum and nodes ranges from short and decumbent to long and erect; all curving quite strongly toward midline. Gaster T1 similar, but with no erect hairs. Terminal segments of gaster with rather dense erect hair and decumbent pilosity. No hair on ventral petiole.

Extremities and mandibles light brownish yellow. Rest of body brown with more yellowish than reddish accents; frontoclypeal area and terminal segments of gaster lighter.

Discussion.—*Rogeria besucheti* differs from *ciliosa*, *gibba*, *prominula*, and *blanda* in pilosity. It differs from *stigmatica* and *megastigmatica* in mesosoma shape, propodeal spine length, and generally smaller eye size.

This species is named for Claude Besuchet, who as director of the MHN in Geneva was most helpful and patient in loaning material valuable for this work.

Distribution.—Paraguayan specimens come from gallery forest with some bamboo. Peruvian specimens are from mixed broadleaf primary for-

est on a steep hillside at 1000m. In both localities collections resulted from Berlese and Winkler sampling of leaf litter and rotten wood.

Material Examined.—**Holotype locality.** PARAGUAY: Alto Paraná Province, Puerto Santa Teresa, 3-XI-1979 (F. Baud, et al.) [MHN].

Paratype localities. COLOMBIA: 3 workers, Putumayo Department, Villa Garzón, 23-VII-1977 (D. Jackson) [BMNH]. PERU: 2 workers, Pasco Department, near Pozuzo, 1000m (C. Kugler and R. R. Lambert) [mouthparts, sting] [MCZ, MZSP]. PARAGUAY: 1 worker, San Benito Province, Itapua, 29-X-1982 (F. Baud, et al.) [MHN].

Rogeria blanda Fr. Smith

Figs. 17, 83-84

Myrmica blanda Fr. Smith 1858:131. Syntype workers, BRAZIL: Amazonas, Ega [=Tefé] [BMNH] [4 syntypes examined].

Irogera foveata Kempf 1964:64, Figs. 19-20. Holotype and paratype workers, BRAZIL: Amazonas, Manaus (K. Lenko) [MZSP] [Paratype examined].

Rogeria blanda; Kempf 1965:185.

Diagnosis.— WL 0.87-1.15mm. Palpal formula 2,2. Eye rather large, oval. Propodeal spines long (PSI 0.20-0.29). Petiolar node long and low. Gaster with terminal segments rotated ventrad. Inferior petiolar process dentate. Head, mesosoma, and nodes densely areolate. Body rather densely covered with long, fine, soft, erect hair; no decumbent hair.

Workers.— TL 3.0-4.0, HL 0.73-0.92, HW 0.65-0.82, SL 0.49-0.62, EL 0.12-0.16 (27-59 facets), PW 0.48-0.63, WL 0.87-1.15, SpL 0.20-0.30, PetL 0.35-0.49, PpetL 0.18-0.25mm, CI 0.85-0.91, OI 0.18-0.21, SI 0.73-0.80, PSI 0.20-0.29. N=20

Additions to description and figures of Kempf (1964). Mandibles triangular, with 6 large teeth decreasing in size basad, then basal tooth larger than neighbor. One or two denticles sometimes added between basal teeth. Clypeal apron with a shallow median notch. Nuchal grooves not visible in lateral view. Metanotal groove weak (Fig. 83) to absent. Propodeal spiracle small, strongly directed caudad. Propodeal spines long, straight or weakly upturned at apex; distinctly longer in the two specimens from Ecuador (PSI 0.29) than in the others (PSI 0.20-0.25). Metapleural lobes triangular; apex blunt to subacute. Petiolar peduncle

curved, with weak keel and dentate inferior petiolar process. Petiolar node widest in posterior half. Postpetiolar node highest in posterior half; shape from above as in Fig. 32 or Fig. 49. Gaster not enlarged (GW / WL 0.63-0.70); terminal segments rotated ventrad. Pygidial gland sculpture present. Sting apparatus nearly identical to that of *inermis* (Fig. 42).

Longitudinal rugae on frontal lobes rapidly give way to areolate sculpture usually by mid-eye level and continuing onto posterior head. Sides of head strongly sculptured: rugose-areolate in front of eye to areolate behind. Mesosoma and nodes (Figs. 83-84) also densely areolate, except for transverse carinulae between spines and smooth posterior face of propodeum. Some elongate cells on pronotal disc. Very apex of postpetiolar node sometimes smooth. No microsculpture.

Scapes with very long erect hairs and shorter hairs ranging from suberect to decumbent. Erect hair on terminal segments of gaster not brush-like. Legs with little decumbent or appressed pilosity.

Head, mesosoma, and waist black to yellowish-brown; appendages lighter. Gaster darker than rest of body. Head sometimes with black patches around and/or between eyes.

Queens.— TL 3.6-4.1, HL 0.79-0.87, HW 0.70-0.78, SL 0.52-0.58, EL 0.19-0.20, PW 0.61-0.70, WL 1.02-1.17, SpL 0.24-0.30, PetL 0.40-0.52, PpetL 0.22-0.25mm, CI 0.87-0.90, SI 0.73-0.81, PSI 0.22-0.26. N=8

Median pronotum sometimes transversely rugose-areolate; mesonotum longitudinally rugose-areolate. Otherwise, differing from the worker only in the normal queen characters. Wing venation like that of *belti* (Fig. 37).

Males.— TL 3.2-3.4, HL 0.60-0.62, HW 0.70-0.75, SL 0.23-0.26, EL 0.32-0.35, PW 0.79-0.86, WL 1.10-1.24, PetL 0.34-0.35, PpetL 0.18-0.20mm, CI 1.16. SI 0.32-0.35. N=4

All males came from Río Akabán, Venezuela. Mandibles with 4 subequal teeth. Anterior edge of clypeus with weak median notch. Frontal area a distinctly impressed triangle. No frontal lobes. Flagellomeres 2-11 straight, subequal in length and width. Habitus much like male of *belti* (Fig. 38), but junction of dorsal and posterior faces of propodeum has blunt lateral corners, and the propodeal spiracle faces more caudad.

Back of head microareolate with piligerous

punctures in the pits; median vertex with additional longitudinal rugulae. Pronotum and mesopleura largely smooth. Mesonotum densely and finely rugulose with scattered punctures in intervals. Posterior face of propodeum, nodes, and gaster smooth. Genitalia as shown in Fig. 17. Hairs shorter, less flexuous than in worker; erect to suberect and moderately dense over much of body. Color dark brown with lighter brown appendages.

Discussion.—*Rogeria ciliosa* and *gibba* from lowland South America resemble *blanda* in having long, soft, dense pilosity and areolate sculpture, but see the *stigmatica* group diagnosis.

Distribution.—*Rogeria blanda* is found in southern Central America and in South America east of the Andes to southern Brazil. Elevations range from 50m (Costa Rica) to 1000m (Venezuela). Nests have been found in trunks of cacao trees in Costa Rica and in a small rotten log suspended about 50cm above the ground in Peru.

Material Examined.—COSTA RICA: Heredia Province, Puerto Viejo de Sarapiquí, La Selva Station (L. Garling); Santa Clara Province, Hamburg Farm (F. Nevermann); Puntarenas Province, Osa Peninsula, Corcovado (J. Longino). PANAMA: Barro Colorado Island (Brown and McCluskey; D. E. Wheeler; J. Zetek). TRINIDAD: Basin Hill Reserve (N. A. Weber) [mouthparts, sting, whole specimen]. VENEZUELA: Falcón State, near Curimagua, Haitoncito; Monagas State, Caripe; Bolívar State, Talud, south of Amarawai Tepuui and Río Akabán (J. Lattke) [2 male genitalia]. GUYANA [=British Guiana]: Oko River (N. A. Weber). BRAZIL: Amazonas State, Tefé; Manaus vicinity (W. L. Brown; K. Lenko); Pará State, Icoarici (W. L. Brown), Belém (N. Rosa), Jacareacanga (M. Alvarenga); Mato Grosso State, Municipal Diamantino (W. L. Brown); Espirito Santo State, Linhares (M. Alvarenga). ECUADOR: Napo Province, Limoncocha (R. Chadab). PERU: Madre de Dios Department, Puerto Maldonado, Lake Sandoval (C. Kugler) [mouthparts, sting]. 93 workers, 8 queens, 4 males [BMNH, CKC, CUIC, MCZ, MIZA, MZSP, USNM].

Scandens-Group and Related Species

Rogeria scandens Mann

Figs. 19-20

Macromuscha scandens Mann 1922:30, Fig. 14. Syntype workers, HONDURAS: Lombardia (Mann) [USNM] [5 of 6 syntypes examined].

Irogera scandens; Kempf 1962a:436, 438.

Rogeria scandens; Kempf 1965:185.

Additions to *scandens*-group diagnosis. WL 0.93-1.17mm. Eye very large (about 60-80 facets). Propodeal spines long (PSI 0.25-0.28). Petiole clavate, with rather large node (PetW/PetL 0.49-0.58). Postpetiole wide (PpetW/PpetL 1.38-1.61). Mesosoma and petiolar node strongly macrosculptured. Erect hairs with dentate ends.

Workers.—TL 3.5-4.2, HL 0.83-1.02, HW 0.70-0.85, SL 0.59-0.73, EL 0.17-0.20 (60-80 facets), PW 0.53-0.62, WL 0.93-1.17, SpL 0.23-0.30, PetL 0.42-0.55, PpetL 0.23-0.27mm, CI 0.82-0.86, OI 0.21-0.24, SI 0.84-0.86, PSI 0.25-0.28. N=6

Mandible in most specimens with 5 teeth decreasing in size until large basal tooth. A denticle may appear between basal and penultimate tooth. Nuchal grooves shallow, not visible in lateral view. Metanotal groove in lateral view broad and shallow to absent; groove sometimes accentuated by a low transverse ridge at anterior of propodeum. Propodeal spines more strongly inclined in Honduran (Fig. 19) than Panamanian specimens. Metapleural lobes somewhat longer and narrower in Honduran specimens. Petiolar node slightly more distinct in Honduran specimens (Fig. 19). Sting apparatus like that of *inermis* (Fig. 42), except for wider anterior apodemes and a more rounded posterodorsal corners on spiracular plates and larger anterolateral processes on the sting base (pygidium and anal plate lost in preparation).

Median clypeus with additional 1-2 pairs of fairly distinct carinulae lateral to the usual pair for the genus. Posterior head longitudinally rugose (continuing from middorsum), transversely arching rugose, or transversely rugose-areolate. Interrugal spaces on head distinctly to weakly granular; microsculpture weaker and surface shinier on posterior. Oval area on ventral half of sides of head largely smooth and very shiny. Anterior surface and neck of pronotum smooth; rest of promesonotum with widely spaced longitudinal rugae, which become vermiculate on

mesonotum. Rugae on Panamanian specimens not so vermiculate on mesonotum, and with lateral spurs. Sides of pronotum with parallel, upcurved carinae, which are more numerous and more distinct on Honduran specimens. Dorsal face of propodeum confused areolate or areolate-rugose. Intervals in mesosoma macrosulpture smooth and shiny. Petiolar node heavily areolate-rugose on sides and posterior face; sculpture weaker dorsad; no clear microsculpture. Postpetiolar node weakly rugose or rugose-areolate on sides and posterior surface, becoming weaker, sometimes absent toward midline; microsculpture vaguely microareolate to nearly smooth.

Scapes and extensor surfaces of legs without erect hair. Dorsa of head, mesosoma, nodes, and gaster T1 sparsely covered with fine appressed hair and longer, stiff, thick, erect-suberect hair with toothed apex (Fig. 20). Mandibles, clypeus and terminal segments of gaster with long erect hair that is tapered and less stiff.

Color of Honduran specimens reddish-brown. Panamanian specimens blackish-brown. Appendages often lighter.

Queen.—TL 4.2, HL 0.95, HW 0.82, SL 0.63, EL 0.22, PW 0.69, WL 1.20, SpL 0.28, PetL 0.50, PpetL 0.30mm, CI 0.86, SI 0.76, PSI 0.23. N=1

Differing from the Panamanian workers in the usual queen characteristics. Pronotum transversely rugose. Mesonotum longitudinally rugose without cross-connections or vermiculate appearance.

Discussion.—The Honduran and Panamanian specimens may be separate species. They differ slightly in shape of mesosoma and petiole, sculpture, and color, and the Honduran specimens are a little larger (WL 1.13-1.17mm) than the Panamanian specimens (WL 0.93-1.08mm). I prefer to call these geographic variants, however, until we have more specimens from more localities.

See the *terescandens* description for comparisons with its sister species.

Ecology.—Some specimens from the Canal Zone were collected from *Heliconia*.

Material Examined.—HONDURAS: Lombardia (W. M. Mann). PANAMA: Canal Zone, Barro Colorado Island (W. L. Brown and E. S. McCluskey; D. Wheeler; J. Zetek) [2 workers: mouthparts, whole specimen; sting]. 31 workers, 1 queen [CKC, LACM, MCZ, USNM].

Rogeria terescandens new species

Fig. 21

Diagnosis.—Like that of *scandens*, except: 1) Propodeal spines shorter, 2) petiolar node lower, more slender (PetW/PetL 0.40-0.41), 3) postpetiole narrower (PpetW/PpetL 1.08-1.16), and 4) macrosulpture very weak, especially on mesosoma and waist, and 5) eye slightly smaller.

Holotype and Paratype Workers.—TL 3.6, HL (0.88)-0.89, HW (0.68)-0.70, SL (0.70)-0.71, EL 0.16 (49-54 facets), PW (0.50)-0.52, WL 1.00, SpL (0.18)-0.21, PetL (0.45)-0.47, PpetL 0.25mm, CI (0.77)-0.79, OI 0.23-(0.24), SI 1.01-(1.03), PSI (0.18)-0.21. N=2.

Also differing from *scandens* in the following ways. Mandible with 6 teeth. Profile of mesosoma dorsum almost evenly convex; no metanotal groove or ridge at front of propodeum. Median carinulae on clypeus weak; no lateral carinulae. Head dorsum densely microareolate; overlain on middorsum by wisps of longitudinal rugulae, on laterodorsa by faint reticulations, and on posterior of head by fragmented, transversely arching rugulae. Microsculpture on sides and posterior head effaced. Mesosoma dorsum, including dorsal face of propodeum, densely microareolate, with superimposed patches of fine rugulose-areolate macrosulpture. Pronotal sides shiny and coriarius with some effaced longitudinal rugulae. Mesopleura and metapleura also shiny near coxae, but more opaque dorsad with microareolate and confused rugulose sculpture. Sides of petiolar node shiny, with effaced microareolate background and vestigial longitudinal rugulae. Postpetiole smooth and shiny.

Discussion.—The name of this species refers to sculpture like that of *R. scandens*, but smoother, as if rubbed (*teres* L., rubbed off).

Distribution.—Both specimens of *terescandens* were taken from trees in lowland forest on the Pacific side of Costa Rica. The holotype was collected in a two week old treefall by general collecting on trunks. The paratype was on or beneath a thick epiphyte mat on the base of a fallen branch (J. Longino unpublished field notes).

Material Examined.—**Holotype locality**. COSTA RICA: Osa Peninsula, Sirena, 8.28N 83.35W, 50m, 31-III-1982, #0950 (J. Longino) [MCZ]. Paratype locality. 1 worker, holotype locality, 28-V-1981, #1100 (J. Longino) [LACM].

Rogeria subarmata Kempf
Figs. 22-23

Irogera subarmata Kempf 1962a:438, Figs. 1-4. Holotype and paratype workers, BRAZIL: Guanabara, Rio de Janeiro, Deodoro (A. Ronna) [MZSP] [12 of 38 paratypes examined; holotype not examined].

Rogeria subarmata; Kempf 1965:185.

Rogeria subarmata; Kempf 1975:367 [new records].

Additions to *scandens*-group diagnosis. WL 0.78-1.00mm. Eye with 30-53 facets. Propodeal spines short (PSI 0.09-0.12). Pygidium with a pair of median piligerous tubercles near caudal margin. Strong macrosculpture on mesosoma and petiolar node. Erect hairs not as rigid as in *scandens*; tips acute.

Workers.— TL 2.9-3.7, HL 0.69-0.87, HW 0.60-0.75, SL 0.46-0.57, EL 0.12-0.16 (30-53 facets), PW 0.45-0.57, WL 0.78-1.00, SpL 0.08-0.10, PetL 0.37-0.47, PpetL 0.20-0.26mm, CI 0.86-0.89, OI 0.20-0.23, SI 0.73-0.77, PSI 0.09-0.12. N=6

Additions to Kempf's (1962a) description. Mandibles usually with 5 teeth that decrease in size basad. Sometimes basal tooth replaced by two very small teeth, or 1-2 denticles are found between the basal and penultimate tooth. Clypeal apron weakly notched medially to evenly convex. Frontal lobes narrow as in *scandens* (Fig. 19). Nuchal grooves shallow, forming only a weak notch in lateral view. Figs. 22-23 show the range of propodeal spine size and angle, but tips sometimes more rounded. Petiole clavate to rather distinctly set off from peduncles (Figs. 22-23). Postpetiole from above much as in Fig. 21. Posterior surface of pygidium with a caudal pair of long, columnar, piligerous tubercles that are visible at 50X with a dissection microscope. Sting apparatus nearly identical to that of *inermis* (Fig. 42); sting as in *pellecta* (Fig. 33).

Median clypeus with 1-2 pair of fairly distinct extra carinulae lateral to the usual pair. Posterior head with transversely arching rugose-areolate macrosculpture. Head covered with dense, indistinctly microareolate roughening that appears punctate or granular at lower magnifications. Mesosoma dorsum longitudinally rugose; rugae with numerous lateral spurs that occasionally connect rugae on shoulders. Macrosculpture on sides of mesosoma and dorsal face of propodeum confusedly rugose to rugose-areolate. Mesosoma microsculpture as on head. Petiolar node ver-

miculate-rugose to rugose-areolate. Postpetiolar node similar, but rugae straighter, more effaced. Microsculpture on nodes slightly weaker than on head and mesosoma.

Scapes and extensor surfaces of legs lack erect hair. Rest of body with both short, appressed-decumbent and longer, erect-suberect hairs. Erect hairs are nearly as stiff as those of *scandens* and *terescaendens* (Fig. 20), but seem to have acute tips.

Color dark brown to yellowish-brown with a reddish tint on mesosoma, waist and middle of gaster; appendages and ends of gaster lighter.

Distribution.—All available specimens are from localities along the coast of Brazil. The type series was collected from the stomach of an ant eater (*Tamandua tetradactyla*).

Material Examined.—BRAZIL: Pará State, Belém (N. Rosa) [mouthparts, sting]; Bahia State, Itabuna (J. A. Winder); Espírito Santo State, Pedro Canário near Conceição da Barra (M. Alvarenga); Guanabara State [=Rio de Janeiro State], Rio de Janeiro, Deodoro (A. Ronna). 20 workers [MCZ, MZSP].

Rogeria procera Emery
Fig. 18

Rogeria procera Emery 1896:92, Fig. 19. Holotype worker, BRAZIL: Pará, Belém [MCSN] [Holotype examined].

Rogeria (Irogera) procera; Emery 1915:191.

Macromischa brasiliensis Borgmeier 1953(1951):107, Figs. 1-4. Holotype worker, BRAZIL: Pará, Rio Cuminá, Cachoeira do Breu [MZSP] [Holotype examined]. [Synonymy by Kempf 1962a:437].

Irogera procera; Kempf 1962a:436 [partial description].

Irogera procera; Kempf 1964:66 [partial key].

Rogeria procera; Kempf 1965:185.

Diagnosis.—WL 1.28-1.53mm. Eye very large. Propodeal spines long, not inclined. Postpetiolar node small, subconical; sternum inconspicuous and without a differentiated peduncle. Middorsum and posterior head with fine, nearly straight longitudinal rugae. Mesosoma and petiolar node with thick, vermiculate rugae. Erect hairs tapered; rarely any appressed or decumbent hairs on mesosoma dorsum, gaster, or legs. Scapes and extensor surfaces of legs with erect hairs and appressed to decumbent pilosity. Palpal formula, propodeal spiracle, metapleural lobes, petiole, pygidium, and sting apparatus as in *scandens*-group diagnosis.

Workers.— TL 4.5-5.4, HL 1.07-1.19, HW 0.91-1.08, SL 0.66-0.78, EL 0.19-0.23 (about 80-100 fac-

ets), PW 0.67-0.80, WL 1.28-1.53, SpL 0.26-0.32, PetL 0.60-0.73, PpetL 0.28-0.33mm, CI 0.85-0.91, OI 0.20-0.22, SI 0.70-0.75, PSI 0.18-0.23. N=7

Mandibles triangular with 6 teeth; basal larger than neighbor. Clypeal apron with shallow median notch. Nuchal grooves shallow, not visible in lateral view. Sting apparatus like that of *inermis* (Fig. 42), but spiracular plate with more rounded anteroventral corner and gonostylus with separate proximal and distal patches of sensilla.

Laterodorsa of head longitudinally rugose-areolate; sides below eye smooth and shiny. Microsculpture vaguely microareolate on anterior laterodorsa; more effaced on rest of head, imparting a vaguely granular, shiny appearance between rugae. Promesonotum longitudinally vermiculate-rugose. Meso- and metapleura rugose. Interrugal spaces on mesosoma and petiole almost smooth. Postpetiolar node shiny with vague rugae and weak microsculpture.

Scapes and head dorsum with erect hair and much shorter appressed to decumbent pilosity. Mesosoma, legs, waist, and gaster with erect hairs, but rarely any decumbent or appressed hairs.

Mesosoma and waist black to dark brown; appendages and sometimes gaster lighter brown.

Material Examined.—GUYANA (British Guiana): Oronoque River (N. A. Weber). BRAZIL: Pará State, Rio Cuminá (A. Sampaio), Ourém (A. Schulz); Amazonas State, Manaus (K. Lenko); Manaus to Itacoatiara (W. L. Brown) [mouthparts, sting]. 23 workers [CUIC, MCZ, MZSP].

Rogeria tonduzi Forel

Figs. 85-86

Rogeria tonduzi Forel 1899:53. Holotype worker, COSTA RICA (Tonduz) [MHN] [Holotype examined].

Rogeria tonduzi; Emery 1915:191.

Rogeria tonduzi; Kempf 1962a:436.

Rogeria tonduzi; Kempf 1965:185.

Diagnosis.—WL 0.81-0.90mm. Eye large. Palpal formula 2,2. Propodeal spiracle faces laterally. Propodeal spines long. Postpetiolar sternum not enlarged. Posterior head with transversely arching rugae. Rugae on mesosoma and petiolar node thick and rounded. Decumbent hair abundant on head dorsum and legs; little on gaster; no decumbent or appressed hair on mesosoma or nodes. Scapes, head dorsum, mesosoma, nodes and gaster with abundant flexible, tapered, erect hair; none

on extensor surfaces of legs. The following as in *scandens*-group diagnosis: metapleural lobes, petiole, pygidial gland sculpture, sting apparatus, and sculpture.

Workers.—TL 3.0-3.2, HL 0.72-0.78, HW 0.61-0.68, SL 0.48-0.53, EL 0.12-0.15 (39-48 facets), PW 0.46-0.50, WL 0.81-0.90, SpL 0.18-0.21, PetL 0.37-0.40, PpetL 0.17-0.19mm, CI 0.85-0.88, OI 0.19-0.24, SI 0.78-0.81, PSI 0.20-0.25. N=7

Mandibles triangular; most specimens with 6 teeth, the first 5 decreasing in size basad then a large basal tooth. In others, the penultimate basal is replaced by 2-3 denticles. Clypeal apron convex with median angle or small tooth. Body of clypeus rises perpendicularly. Eyes oval with narrow anterior point. Nuchal groove inconspicuous.

Pronotum in lateral view lacks a distinct angle between anterior and dorsal faces. Metanotal groove very weak to absent. Propodeal spines long, weakly inclined. Postpetiole subtrapezoidal from above; sternum flat, with a distinct peduncle. Sting apparatus like that of *inermis* (Fig. 42) except for more elongate anterolateral processes on sting bulb.

Middorsum of head longitudinally rugose; laterodorsa and dorsal part of sides rugose-areolate. Mesosoma (Figs. 85-86) with thicker rugae and narrower interrugal spaces than on head. Rugae transverse on anterior pronotum, transverse to confused on metanotum and dorsal face of propodeum, predominantly longitudinal on sides and pronotal disc. Petiolar node longitudinally rugose on sides; smooth along midline. Postpetiole smooth. Microsculpture weak or absent throughout, integument very shiny.

Scapes and head with erect to suberect hair along with the typical short decumbent pilosity. Mesosoma dorsum and waist generally with erect to suberect hair of a variety of lengths; no decumbent-appressed pilosity. Gaster with long, erect hair and a few short, decumbent hairs.

Color shiny black with dark brown mandibles, scapes and legs to reddish-brown with yellowish-brown appendages.

Discussion.—*Rogeria belti* occurs in the same localities and could be confused with *tonduzi*, but *belti* has a distinct petiolar node and predominantly areolate pronotal sculpture. *Rogeria lirata* (Figs. 28-30, 89-90) from northern South America is similar to *tonduzi* in size, clypeus, and sculpture, but *lirata* has smaller eyes (6-12 facets), a distinct

petiolar node, and scapes with suberect hair only.

Distribution.—With the exception of one specimen from Guatemala, all *tonduzi* specimens come from Costa Rica at elevations of 0-100m on both sides of the cordillera. Most specimens were collected by Jack Longino as strays on ground and vegetation. He found one worker in a *Cyphomyrmex* nest and another "...on the base of a small tree, amongst some *Pheidole* workers" (unpublished field notes). Lyn Garling found a nest with a "tubular entrance with white 'fuzz'" in a cacao tree (field note on label).

Material examined.

GUATEMALA (no locality or collector). COSTA RICA: Heredia Province, Puerto Viejo de Sarapiquí, La Selva Station (L. Garling); Puntarenas Province Carara Biological Reserve (P. S. Ward), Osa Peninsula, Corcovado National Park (J. Longino) [mouthparts, sting]. 24 workers [BMNH, CKC, JTLC, LACM, MCZ, MZSP, USNM]. *Germaini*-Group and Related Species

Rogeria germaini Emery

Figs. 24-27, 87-88

Rogeria germaini Emery 1894:189. Syntype workers, BRAZIL. Mato Grosso (Germain) [MCSN] [1 of 2 syntypes examined].

Rogeria germaini minensis Santschi 1923:1262. Lectotype and paratype workers, BRAZIL: Minas Gerais, Passa Quatro (Reichensperger) [NMB] [Both lectotype and paratype examined]. N. syn.

Rogeria germaini; Kempf 1962b:20, Figs. 18, 19 [Redescribed]. *Rogeria minensis*; Kempf 1963:189, Figs. 1, 2 [Redescribed, raised to species].

Additions to *germaini*-group diagnosis. WL 0.74-0.90mm. Clypeal apron with median tooth. Metanotal groove very weak or absent. Metapleural lobes reduced, not angular. Petiolar keel not lamellate. Sting shaft apex weak, lacks dorsal flange; lancets spatulate. Macrosculpture effaced on side of head below eye; sometimes nearly smooth. Promesonotal rugae sharp and narrow like those on head; rugae low on sides of pronotum do not continue onto metanotum. Macrosculpture on both nodes and petiolar peduncle vestigial. Scapes without erect hair. Mesosoma with erect-suberect only. Head and gaster with both erect and decumbent pilosity.

Workers.—TL 2.7-3.5, HL 0.66-0.85, HW 0.59-0.74, SL 0.45-0.59, EL 0.06-0.10 (7-13 facets), PW 0.44-0.51, WL 0.74-0.90, SpL 0.15-0.21, PetL 0.30-

0.44, PpetL 0.19-0.23mm, CI 0.86-0.89, OI 0.09-0.14, SI 0.75-0.80, PSI 0.20-0.23. N=9

Additions to Kempf (1962b). Dentition variable; simplest pattern is 6 teeth of decreasing size, however, it seems that any or all of the last 3 teeth may be replaced by a pair of denticles. FLW/HW 0.32-0.36. Posterior outline of head concave to convex. Anterior propodeum marked by a transverse carina. Petiolar node distinct; Figs. 24 and 26 show extremes of shape. Postpetiolar node with a distinct posterior face; shape from above as in Figs. 24 or 32. Sting apparatus differing dramatically from that of *inermis* (Fig. 42) in some features: 1) sting shaft and lancets very weak, 2) lancets spatulate as in Fig. 29, 3) sting shaft apex with eroded sides, and no dorsal flange (Fig. 27), and 4) furcula with a shorter dorsal arm that broadly merges with the lateral arms, thus appearing broadly V-shaped in anterior view.

Posterior head transversely arching rugose to rugose-areolate. Promesonotal dorsum varies from predominantly areolate (with occasional elongate cells) (Fig. 88) to predominantly vermiculate-rugose. Pronotal sides rugose; rugae subparallel with ventral edge of pronotum to diagonal. Microsculpture vestigial, leaving irregular, but shiny spaces in macrosculpture; sides of mesosoma especially smooth.

Color brownish-yellow to brown with darker gaster; appendages at times slightly lighter.

Queen.—TL 4.1, HL 0.90, HW 0.79, SL 0.73 EL 0.17, PW 0.67, WL 1.12, SpL 0.15, PetL 0.48, PpetL 0.28mm, CI 0.88, SI 0.92, PSI 0.13. N=1

Differing from the worker in the normal queen characteristics and the following. Notch formed by nuchal groove not so distinct in lateral view. Anteroventral corner of pronotum not as clearly dentate. Parapsidal furrows not distinguishable from furrows in sculpture. Diverging rugae on middorsum of head continue onto posterior head, with few or no lateral spurs. Laterodorsa and sides of head similarly rugose. Anterior face of pronotum transversely areolate, mesonotum with longitudinal rugae diverging from an anterior point, then parallel in posterior half; some branching, but no cross-ridges; less vermiculate than in worker.

Discussion.—Kempf (1963) examined the types of *germaini* and *minensis* and noted that they were very similar, but chose to retain both names on the basis of a list of differences he saw in those speci-

mens. I have also examined the types as well as 11 specimens collected in Paraguay in 1979 and 1982. These new collections bridge the gap between the types of *germaini* and *minensis*. They are all intermediate in size between the smaller *germaini* type and the larger *minensis* types, have convex posterior heads like the *germaini* type, have promesonotal sculpture varying from nearly as extensively rugose as the *germaini* type, to areolate like the *minensis* types; and some have petiolar nodes intermediate between the more abruptly arising *minensis*-like and the more obliquely arising *germaini*-like nodes.

Rogeria lirata (Figs. 28-30, 89-90) from more northern parts of South America is *germaini*'s closest relative (See *lirata* description for comparisons). *Rogeria lacertosa* (Fig. 31), also from southern Brazil, differs in size, clypeal shape, sculpture on side of head, and pilosity. *Rogeria pellecta* (Figs. 32-33), collected further south in Brazil, differs in clypeal shape, metapleural lobes, sting, and pilosity.

Distribution.—So far *germaini* is known only from southern Brazil and Paraguay. Most specimens have come from Winkler apparatus collecting by expeditions from the MHN in Geneva. Specimens were extracted from rotting leaf litter and wood in forests.

Material Examined.—BRAZIL: Minas Gerais State, Passa Quatro (Reichensperger); Mato Grosso State; São Paulo State, Anhembi [= Pirambóia, 29 km E Botucatu] (Kempf et al.). PARAGUAY: Alto Paraná Province, Puerto Santa Teresa; Misiones Province, Panchito Lopez; Itapua Province, San Benito Island [2 workers: whole specimen; mouthparts, sting]; Itapua Province, Santa María; Central Province, Asunción (F. Baud et al.). 15 workers, 1 queen [BMNH, CKC, MCSN, MCZ, MHN, NMB].

Rogeria lirata new species

Figs. 28-30, 89-90

Diagnosis.—As in *germaini* but: 1) metapleural lobes larger, triangular, and 2) rugae on promesonotum more rounded and thicker than on head; one ruga begins near anteroventral corner of pronotum and continues unbroken to the metanotum.

Holotype and Paratype Workers.—TL 2.6-3.4 (3.3), HL 0.63-0.80 (0.78), HW 0.53-0.70 (0.67), SL 0.45-0.56 (0.55), EL 0.05-0.08 (0.08) (6-12 facets),

PW 0.39-0.51 (0.51), WL 0.65-0.87 (0.86), SpL 0.12-0.20 (0.175), PetL 0.31-0.47 (0.44), PpetL 0.17-0.23 (0.21) mm, CI 0.83-0.88 (0.86), OI 0.09-0.12 (0.12), SI 0.79-0.85 (0.82), PSI 0.19-0.23 (0.20). N=10

Dentition as in *germaini*. Nuchal groove forms a weak notch in lateral view. No clear angle between anterior and dorsal faces of pronotum. Spiracle faces slightly caudad, posterior edge within one diameter of nearest edge of propodeum. Petiolar peduncle with a sharp, but not lamellate keel. Petiolar node profile angular. Postpetiolar node in dorsal view shaped as in Figs. 24 or 49; sternum flat. Sting apparatus as described for *germaini*.

Divergent longitudinal rugae on frontal lobes grade into areolate sculpture at level of eyes. Sculpture of posterior head transversely arching rugose to rugose-areolate. Laterodorsa and sides of head longitudinally rugose-areolate; sides may be effaced to nearly smooth. Head microsculpture vestigial; intervals nearly smooth, quite shiny. Anterior face of pronotum areolate, becoming vermiculate-rugose on disc (Fig. 90). Thick, rounded rugae of promesonotum may merge, but are rarely joined by cross-ridges. Rugae on meso- and metapleura sharper and more separated. Anterior and dorsal faces of petiolar node smooth. Sides and posterior faces of node in holotype longitudinally rugose-areolate, but weaker and more rugose in Trinidad specimen and nearly smooth in specimens from Peru. Microsculpture weak or absent; integument shiny.

Scapes with decumbent to suberect hair (holotype) or with short, uniformly subdecumbent hair. Head dorsum with subdecumbent to erect hair.

In most, mandibles, frontoclypeal region, antennae and legs brownish-yellow; other parts rusty-brown, becoming darker, almost black, on dorsa of mesosoma and petiole. Trinidad and Guyana specimens lighter on all parts.

Queens.—TL 3.6-3.7, HL 0.76-0.80, HW 0.69-0.70, SL 0.52-0.57, EL 0.14-0.15, PW 0.58-0.60, WL 0.95-1.00, SpL 0.18-0.20, PetL 0.46-0.52, PpetL 0.23-0.24 mm, CI 0.88-0.90, SI 0.76-0.81, PSI 0.18-0.21. N=4.

Besides the usual features of an alate female, differing from the worker in the following ways. Mandible with 7 teeth or 3 teeth and 5 denticles. Parapsidal furrows not distinct from furrows in sculpture. Propodeal spines project caudad or posteroventrad. Rugae on sides of pronotum almost vertical to shoulder, then bend across the

anterior face of the pronotum. Mesonotal rugae longitudinal with occasional fusions and cross-ridges. Wing venation (Fig. 30) most similar to that of *stigmatica*. Radial sector and median veins long, nearly reaching wing margin; r-m vein present.

Discussion.—See the *tonduzi* discussion for comparisons with that species. The name *lirata* refers to the characteristic rugae of the mesosoma, which resemble the ridges thrown up by a plow.

Material Examined.—**Holotype locality**. COLOMBIA: 7km N Leticia, forest litter, 10-25-II-1972, #B-230 (S. and J. Peck) [MCZ].

Paratype localities. TRINIDAD: 3 workers, #191 (N. A. Weber) [MCZ, MZSP]; 1 worker, Mayaro, Trinity Hills Reserve, 5-VIII-1976 (J. Noyes) [BMHN]. GUYANA (British Guiana): 1 worker, R. Mazaruni Forest Settlement, 20-VIII-1935, #304 (N. A. Weber) [MCZ]. COLOMBIA: 2 workers, holotype locality [mouthparts, sting; one coated for electron microscopy] [CKC, MCZ]. PERU: 2 workers, Loreto Department, 15km WSW Yurimaguas, 5.59S 76.13W, 200m, 22-VII-1986, #8701-24 and #8701-25 (P. S. Ward) [mouthparts, sting] [LACM, MCZ].

Nontype localities. TRINIDAD: 1 queen, Nariva Swamp, 23-IV-1935, #140 (N. A. Weber) [MCZ]. BRAZIL: 3 queens, Mato Grosso State, Sinop, 55.37W 12.31S, X-1974 #12314 (Alvarenga), #12576 (Alvarenga and Roppa) [MZSP]; 2 queens, Goiás State, Jataí, XI-XII-1972, #8857, #8939 (F. M. Oliveira) [MZSP].

Rogeria lacertosa Kempf

Fig. 31

Rogeria lacertosa Kempf 1963:194, Figs 5-6. Holotype and paratype workers, BRAZIL: Rio Grande do Sul State, Sinimbu (F. Plaumann) [MZSP] [All 4 paratypes examined; holotype not examined].

Additions to *germaini*-group diagnosis. WL 0.93-1.05mm. Clypeal apron with median notch. Metanotal groove weak to strong. Petiolar keel with single lamellate carina. Sting shaft apex has dorsal flange; lancets acute; both weak. Macrosculpture not effaced on side of head below eye. Promesonotal rugae sharp and narrow like those on head. Sides of both nodes distinctly macroareolate. Erect hairs on scapes. No decumbent hair on gaster; little if any on mesosoma dorsum.

Workers.—TL 3.6-4.0, HL 0.83-0.91, HW 0.72-

0.81, SL 0.59-0.61, EL 0.10-0.11 (19-20 facets), PW 0.52-0.60, WL 0.93-1.05, SpL 0.17-0.20, PetL 0.43-0.45, PpetL 0.23-0.26mm, CI 0.87-0.88, OI 0.13-0.14, SI 0.75-0.79, PSI 0.18-0.20. N=4

The following supplements Kempf (1963). All specimens at hand with 6 mandibular teeth decreasing in size basad, except for a large basal tooth. Eyes elliptical. Nuchal groove forms a notch in in lateral view of head. Anterior edge of propodeum not marked by a transverse carina. Metapleural lobes low and broadly rounded or triangular with more narrowly rounded apex. Postpetiolar node from above like that of *pellecta* (Fig. 32). Sting apparatus as *inermis* (Fig. 42), but sting shaft and lancets are less sclerotized (easily twisted) and the lancets lack the barbule.

Laterodorsa of head predominantly rugose to rugose-areolate. Back of head areolate in a transversely arched pattern. Microsculpture vestigial; intervals with a shiny, effaced granular appearance. Anterior face of pronotum transversely areolate; disc with diverging, longitudinal, vermiculate rugae with variable number of cross-ridges imparting a rugose-areolate appearance in places. Sides of mesosoma predominantly longitudinally rugose, but with occasional cross-ridges making elongate cells. Intervals in mesosoma macrosculpture shiny, nearly smooth, especially on sides. Anterior and sometimes dorsal faces of nodes weakly sculptured. Nodes slightly dulled by vestigial microsculpture.

Head dorsum with erect-suberect hairs in addition to the typical decumbent pilosity.

Color yellowish-brown; gaster slightly darker. Legs and, sometimes, antennae lighter, more yellowish. Mandibles often slightly darker than head capsule.

Discussion.—Because *minensis* has been synonymized with *germaini*, some of Kempf's (1963) list of characters that distinguish *lacertosa* are no longer valid, however, *germaini* and *lacertosa* are still distinguishable on the basis of a number of characters (see *germaini* discussion). *Rogeria pellecta* (Figs. 32-33), also from southern Brazil, differs in petiole keel, sting and lancets, promesonotal sculpture, and pilosity.

Distribution.—*Rogeria lacertosa* is known only from the type material collected from 100-200m elevation in southern Brazil. No ecological data are available.

Material Examined.—BRAZIL: Rio Grande do

Sul State, Pardinho (F. Plaumann), Sinimbu (F. Plaumann) [mouthparts, sting]. 4 workers [MZSP].

Rogeria plecta Kempf

Figs. 32-33

Rogeria plecta Kempf 1963:191, Figs. 3-4. Holotype worker, BRAZIL: Santa Catarina State, Nova Teutônia (F. Plaumann) [MCZ, MZSP] [6 of 28 paratype workers examined, including 4 from holotype locality; holotype not examined].

Diagnosis.—WL 0.90-0.99mm. Clypeus with median notch. Metanotal groove distinct. Metapleural lobes prominent, triangular. Petiolar node arises gradually from peduncle. Sting and lancets strong, acute; sting shaft with dorsal flange; lancet with barbule. Laterodorsa of head longitudinally rugose. Promesonotum coarsely areolate to rugose-areolate. Back of petiolar node strongly areolate; postpetiole vestigially areolate. Scapes lack erect hair. Dorsa of head, mesosoma, nodes and gaster with erect and decumbent pilosity. Mandibles, palpal formula, eye, propodeal spines, postpetiole, other aspects of petiole, sculpture, and pilosity as in *germaini*-group diagnosis.

Workers.—TL 3.4-3.7, HL 0.81-0.89, HW 0.71-0.78, SL 0.55-0.60, EL 0.09-0.11 (16-21 facets), PW 0.50-0.55, WL 0.90-0.99, SpL 0.17-0.21, PetL 0.39-0.46, PpetL 0.20-0.22mm, CI 0.87-0.88, OI 0.12-0.14, SI 0.77-0.79, PSI 0.19-0.22. N=6

The following supplements Kempf (1963). Palpal formula 3,2. Anterior edge of clypeus weakly emarginate. Eyes oval. Metanotal groove may be bordered behind by a transverse costa. Posterior face of petiolar node vertical or slightly concave in lateral view. Postpetiole widest anteriorly, as in Fig. 32, or evenly convex, as in Fig. 53. Sting apparatus like that of *inermis* (Fig. 42), except for the sting (Fig. 33), which has larger anterolateral processes on sting base, a stronger, relatively thicker sting shaft, and a lower dorsal flange.

Posterior head sculpture is rugose-areolate, with rugae longitudinally diverging or transversely arching across back of head. Rugae of laterodorsa sometimes broken and with lateral spurs. Sides of head areolate around eye, but effaced and nearly smooth ventrad. Dorsal face of propodeum transversely carinate to coarsely areolate. Petiolar node with areolate macrosculpture that becomes weaker and less defined anteriorly. Ventral petiole with a pair of longitudinal carinae arising from an anterior keel. Head and mesosoma

microsculpture vestigial, leaving nearly smooth, shiny intervals in macrosculpture. Sides of petiolar peduncle microareolate; nodes roughened by obscure microsculpture and not as shiny as head and mesosoma.

Color yellowish-brown; gaster slightly darker. Legs, and sometimes antennae, lighter, more yellowish. Mandibles often slightly darker than head capsule.

Gynecoid Workers.—As described by Kempf (1963).

Discussion.—In the southern Brazil/Paraguay area occur related species *germaini*, *lacertosa*, and *sicaria*. Comparisons with these species are found in the "Species Groups" section and in the *germaini* and *lacertosa* discussions.

Distribution.—*Rogeria plecta* is known only from the 33 type specimens taken in southern Brazil from berlesate of leaf litter.

Material Examined.—BRAZIL: Santa Catarina State, Nova Teutônia (F. Plaumann) [mouthparts, sting]. 6 workers, 1 gynecoid [MCZ, MZSP].

Rogeria sicaria Kempf

Fig. 34

Rogeria sicaria Kempf 1962b:22, Figs. 20, 21. Holotype worker, BRAZIL: São Paulo, Agudos [19km SSE Bauru] (W. W. Kempf) [MZSP] [Holotype examined].

Diagnosis.—WL 0.75mm. Eye very small. Clypeal apron convex. Metanotal groove strong. Propodeal spines very long, strongly inclined dorsal and divergent. Petiole long (PetL/PW 0.95), with prominent keel. Sting apex strong, with dorsal flange. Sides of head below eye, mesosoma, and petiolar node areolate; coarsely so on mesosoma. No erect hair on scapes. Head, mesosoma dorsum, nodes, and gaster T1 with stiff, erect-suberect hairs and shorter, more abundant, appressed-decumbent hair.

Holotype Worker.—TL 2.8, HL 0.67, HW 0.56, SL 0.48, EL 0.03 (8 facets), PW 0.37, WL 0.75, SpL 0.22, PetL 0.35, PpetL 0.17mm, CI 0.83, OI 0.05, SI 0.86, PSI 0.29.

The following supplements Kempf (1962b). Mandible triangular, with 5 teeth decreasing in size to base. Clypeal apron evenly convex; body of clypeus projecting over mandibles. Frontal lobes narrow (FLW/HW 0.29). Eyes small, circular, somewhat sunken in head. Petiolar peduncle long (PetL/PW 0.95), with strong keel and dentate

inferior process. Postpetiole highest in caudal half; dorsal view subtrapezoidal as in Fig. 49.

Posterior head areolate and more coarse than elsewhere on head. Intervals shiny, but dulled somewhat by vestigial microsculpture. Areolate sculpture on petiolar node not as well defined as on head and mesosoma and even more effaced on postpetiolar node. Nodes roughened by vague microsculpture.

Color uniformly golden-brown.

Discussion.—This species is still known only from the holotype. It seems related to *germaini*, *pellecta*, and *lacertosa*, also from southern Brazil. See the "Species Groups" section for comparisons.

Creightoni-Group and Related Species

Rogeria merenbergiana new species Figs. 46-48

Additions to *creightoni*-group diagnosis. WL 0.69-0.83mm. Palpal formula 3,2. Clypeal apron with median concavity. Eye small, elliptical; EL/SpL 0.67-0.86. Anterior edge of pronotal disc without a strong transverse carina. MHI 0.91-1.01. Promesonotum and metanotum with distinct profiles—promesonotum convex, metanotum usually flat. Propodeal spines short, straight. Postpetiole from above subtrapezoidal. Mesosoma and sides of head rugose (sides of head sometimes effaced rugose-areolate). Erect hair on scapes and middle and hind tibiae.

Holotype and Paratype Workers.— TL 2.7-3.1 (3.0), HL 0.69-0.71 (0.71), HW 0.57-0.62 (0.61), SL 0.46-0.52 (0.50), EL 0.07-0.09 (0.08) (8-14 facets), PW 0.42-0.47 (0.45), WL 0.74-0.83 (0.80), SpL 0.10-0.14 (0.12), PetL 0.28-0.36 (0.335), PpetL 0.15-0.18 (0.16)mm, CI 0.83-0.88 (0.85), OI 0.13-0.15 (0.13), SI 0.80-0.84 (0.83), PSI 0.13-0.17 (0.15), MHI 0.91-1.00 (0.93). N=6

Mandibles with 6-7 teeth decreasing in size basad and basal tooth as large or larger than penultimate basal. If 6 teeth, may have 1-2 additional denticles among basal teeth. Body of clypeus not strongly produced. Nuchal groove weak. Posterior outline of head evenly convex. Propodeal spiracle one diameter, or slightly less, from edge of infradental lamella. Metapleural lobes low; edges perpendicular. Petiolar node with a more or less distinct angle between dorsal and posterior faces. Petiolar peduncle with weak keel. Postpetiole with

longer anterior face and short posterior face meeting at a narrow apex. Postpetiolar node from above as in *unguispina* (Fig. 49). Postpetiolar sternum short, weakly concave; anterior edge square.

Laterodorsa of head longitudinally rugose-areolate. Posterior head with rugae diverging from midline or transversely arching; few if any cross ridges. Sides of head longitudinally rugose. Anterior pronotal disc transversely rugose to rugose-areolate; rest of promesonotal dorsum longitudinally rugose. Dorsal face of propodeum areolate-rugose. Lateral mesosoma rugose; less regularly so on meso- and metapleura. Microsculpture on head and mesosoma effaced; intervals quite smooth and shiny, especially on sides and back of head. Petiole distinctly microareolate; sides of node vaguely rugose to vaguely areolate; posterior face with strong ridges. Postpetiole effaced microareolate and very sparsely and vaguely rugose.

Color very dark reddish brown to yellowish brown; appendages and often sides of mesosoma and gaster lighter.

Nontype Workers.— TL 2.6-3.0, HL 0.63-0.71, HW 0.53-0.60, SL 0.43-0.49, EL 0.08-0.09 (12-15 facets), PW 0.40-0.43, WL 0.69-0.77, SpL 0.10-0.13, PetL 0.29-0.33, PpetL 0.16-0.18mm, CI 0.84-0.85, OI 0.14-0.15, SI 0.79-0.82, PSI 0.14-0.17, MHI 0.95-1.01. N=3

Little difference from types. Some slightly smaller, but with slightly larger eye for size. Generally higher mesosoma height index. Posterior head sometimes transversely arching rugose-areolate. Sides of head rugose-areolate, but effaced posterior to eye. Promesonotal dorsum longitudinally rugose to rugose-areolate. Lateral mesosoma rugose-areolate.

Paratype And Nontype Queens.— TL 3.3-3.7, HL 0.70-0.75, HW 0.61-0.64, SL 0.48-0.52, EL 0.16-0.17, PW 0.58-0.60, WL 0.98-1.15, SpL 0.15-0.17, PetL 0.34-0.39, PpetL 0.19-0.20mm, CI 0.86-0.88, SI 0.78-0.80, PSI 0.14-0.16, MHI 1.13-1.19. N=3

Mandible with 6-7 teeth; if 6, basal larger than penultimate tooth. Clypeus evenly convex to weakly emarginate. Posterior outline of head strongly convex. Mesosoma and waist habitus shown in Fig. 48. Sculpture mostly like worker. Anterior pronotum areolate, becoming more rugose on sides. Half to nearly all of ventral half of mesopleura smooth; the rest of meso- and metapleura and meso- and metanota longitudi-

nally rugose-carinate. Dorsal face of propodeum transversely rugose. Intervals on mesosoma nearly smooth; shiny. Petiole and postpetiole more strongly microareolate and weakly areolate.

Discussion.—*Rogeria unguispina* (Fig. 49) from the mountains of Venezuela (1100-2000m) is also very similar in size, sculpture, pilosity and color to *merenbergiana*, and the two species intergrade with respect to mesosoma shape and petiole shape. It is quite possible that these are geographic variants of the same species, but all *unguispin*a specimens presently available have more elongate eyes and have a strong carina running across the shoulders, and specimens dissected differ in palpal formula. Most *unguispin*a specimens also have downcurved propodeal spines, concave posterior face of petiolar node, and a broad, shallow metanotal groove. See also the *nevadensis* discussion for comparisons with that species from high elevations in Colombia.

Rogeria alzatei occurs in Colombia, but so far has not been found above 1000m. These ants are usually smaller than *merenbergiana* (WL 0.51-0.68mm), lack erect hair on the scapes, and lack a distinct metanotal profile.

Rogeria creightoni, so far only known from North and Central America, is related to *merenbergiana*, but generally has: 1) longer, less inclined propodeal spines, 2) less distinct metanotum, and 3) stronger, rugose-areolate sculpture on sides of head (Figs. 51-54, 95-96).

Rogeria belti from Central America is the same size and also generally has a more or less definite step in mesosoma profile at metanotal groove, but has: 1) larger eye, 2) longer propodeal spines, 3) more rounded postpetiolar node, 4) more areolate pronotum, and 5) mesosoma dorsum without two distinct types of hairs.

This species is named in honor of Gunther Buch and his family, who have heroically maintained part of their farm, Finca Merenberg, as a nature preserve and permitted the collection of these and other ants.

Distribution.—*Rogeria merenbergiana* is found at high elevations (1300-2300m) in the Andes of Ecuador and southern Colombia. It has been taken in litter samples in moist broadleaf forest and bamboo-moss forest. A nest was found in a rotten log in a pasture.

Material Examined.—**Holotype locality.** COLOMBIA: 14 workers, 1 queen, Huila, 12km W

Belén, Santa Leticia, Finca Merenberg, 2300m, 9-13-I-1978, rotten log in pasture (C. Kugler and J. Hahn) [1 mouthparts; 4 stings] [MCZ].

Paratype localities. COLOMBIA: 13 workers, 1 queen, holotype locality [BMNH, LACM, MCZ, MZSP, USNM]; 2 workers, Huila, Las Cuevas de los Guacharos National Park, 1900-2300m, near Palestina, about 20km S Pitalito, 15-17-I-1978 (C. Kugler and J. Hahn) [whole specimen slide mounted] [MCZ].

Nontype localities. ECUADOR: 2 workers, Pichincha Province, 16km E Tandapi, 2000m, in litter, 20-VI-1975, B-302 (S. and J. Peck); 3 workers, 2 queens, Pichincha Province, 3km E Tandapi, 1300m, litter in wet ravine, VI-1975 (S. and J. Peck); 4 workers, Pichincha Province, 20-30km ENE Alluriquin on Chiriboga Road, 1400-1800m, 1975, B-301 (S. and J. Peck) [CKC, MCZ].

Rogeria unguispina new species

Fig. 49

Additions to *creightoni*-group diagnosis. WL 0.64-0.83mm. Palpal formula 2,2. Clypeal apron with median concavity. Eye moderately large, elongate-oval. Strong carina across shoulders. Metanotal groove broad and shallow. Propodeal spines usually with downcurved tips. Postpetiole from above subtrapezoidal. Sculpture on side of head vestigial, leaving a small or extensive smooth area. Pronotal disc and sides with weakly undulating rugae and nearly smooth, shiny interrugal spaces. Erect-suberect hair on scapes, and middle and hind tibiae.

Holotype and Paratype Workers.— TL 2.4-3.1 (3.0), HL 0.60-0.72 (0.71), HW 0.50-0.61 (0.60), SL 0.40-0.49 (0.47), EL 0.10-0.11 (0.11) (15-19 facets), PW 0.36-0.46 (0.46), WL 0.64-0.83 (0.81), SpL 0.09-0.13 (0.13), PetL 0.26-0.34 (0.34), PpetL 0.14-0.19 (0.19)mm, CI 0.82-0.86 (0.84), OI 0.12-0.16 (0.13), SI 0.79-0.82 (0.78), PSI 0.14-0.16 (0.15). N=7

Mandibles with 5-6 teeth, basal larger than penultimate tooth; some with a denticle between basal and penultimate teeth. Body of clypeus not projecting over apron. Nuchal groove makes a notch in side of head. Pronotum rounded on front and sides. Propodeal spiracle large (Fig. 49) to moderate; less than one-half diameter from nearest edge of propodeum. Free edges of metapleural lobes form an oblique angle. Posterior face of petiole concave in holotype and some paratypes.

Petiolear peduncle lacks a distinct keel. Postpetiolear node highest in posterior half. Postpetiolear sternum with a short, flat profile and square anterior corner.

Laterodorsa of head rugose, sometimes areolate caudad (holotype). Posterior head rugose-areolate in a more or less transversely arching pattern. Interstices on head vaguely roughened by effaced microsculpture; especially shiny on sides and back of head. Promesonotal dorsum longitudinally rugose in front, becoming more vermiculate with partial or complete cross-ridges behind. Pronotal sides longitudinally rugose with few cross-ridges. Meso- and metapleura with broken, irregular macrosculpture. Dorsal face of propodeum transversely areolate. Interstices on disc and sides of pronotum shiny, nearly smooth; rest of mesosoma vaguely microareolate and quite shiny. Petiolear node weakly to vestigially microareolate; posterior face of node with longitudinal carinulae. Postpetiolear node nearly covered with vague microsculpture to nearly smooth; always weaker than on petiole.

Color blackish-brown with yellowish-brown mandibles, flagellum of antennae, legs, and terminal segments of gaster.

Discussion.—*Rogeria nevadensis* is a similar ant from the mountains of northeastern Colombia, but *nevadensis*: 1) is usually smaller, 2) has smaller eyes, 3) has straight propodeal spines, 4) has more effaced sculpture, and 5) lacks erect hair on the scapes and tibiae. See also the *merenbergiana* discussion.

The name *unguispina* refers to the claw-like shape of the propodeal spines.

Distribution.—So far, *unguispina* is known only from Venezuelan rain forest between 200m and 2000m elevation.

Material Examined.—**Holotype locality.** VENEZUELA: Miranda state, Río Capaya at Quebrada El Bagre, near Salmerón, E of Caracas, 200m, nest beneath log on forest floor in limestone gorge, 8-II-1982, #238 (J. Lattke) [MCZ].

Paratype localities. VENEZUELA: 9 workers, holotype locality [mouthparts, sting] [BMNH, CKC, LACM, MCZ, MZSP, USNM]; 1 worker, Falcón State, Sierra de San Luis [mountain range just south of Paraguaná Peninsula], Haitoncitos, near Curimagua, 1180m, primary forest, 3-VIII-1982, #271 (J. Lattke) [MCZ]; 1 worker, Aragua State, Rancho Grande, 15-VI-1960, 4563a (J. Ojasti)

[MCZ]; 1 worker, Aragua State, Rancho Grande, 14-VIII-1967, 1100m (R. W. Poole) [MCZ]; 2 workers, Lara State, vicinity of Caspo, 18km S Sanare, 1620m, forest rotten wood, 6-XII-1985 (J. Lattke and W. L. Brown) [MIZA].

Rogeria brunnea Santschi

Figs. 50, 93

Rogeria curvipubens brunnea Santschi 1930:79. Syntype workers, CUBA: Pinar del Río, Sierra de los Organos, Ránger (A. Bierig) [NMB] [Both syntypes examined]. **N. comb.**

Rogeria scabra Weber 1934:27, Fig. 2. Syntype workers, queen, CUBA: Cienfuegos, Soledad, Limones Seboruco (Darlington and Weber) [MCZ] [Queen and 1 of 2 worker syntypes examined]. **N. syn.**

Rogeria caraiba Santschi 1936:198, Fig. 5. Syntype workers, CUBA: Habana, Playa de Marianao [NMB] [All 8 syntypes examined]. **N. syn.**

Rogeria cubensis Santschi 1936:199, Figs. 3-4. Holotype worker, CUBA: Pinar del Río, Sierra del Rosario (A. Bierig) [NMB] [Holotype examined]. **N. syn.**

Rogeria cubensis habanica Santschi 1936:200. Holotype worker, CUBA: Playa de Marianao (Bierig) [NMB] [Holotype examined]. **N. syn.**

Additions to *creightoni*-group diagnosis. WL 0.61-0.91mm. Clypeal apron convex. Eye small, elliptical. Nuchal groove weakly visible in lateral view. MHI 0.84-0.99. Pronotal shoulders well rounded. Propodeal spines straight, inclined. Propodeal spiracle less than 1 diameter from edge of infradental lamella. Postpetiole long (PpetL/PW 0.42-0.49), subtrapezoidal in dorsal view; sternum with long, flat profile and receding anterior edge (except Dominican Republic). Both macro- and microsculpture weak overall (stronger in Dominican Republic). Rugae fine, low on head and mesosoma (Fig. 93); vestigial on petiole. Erect hair sometimes sparse and only slightly longer than decumbent hair. Scapes have erect hairs; extensor surfaces of legs do not.

Workers.—TL 2.3-3.3, HL 0.57-0.80, HW 0.45-0.70, SL 0.36-0.52, EL 0.06-0.09 (9-18 facets), PW 0.35-0.49, WL 0.61-0.91, SpL 0.09-0.15, PetL 0.25-0.34, PpetL 0.15-0.22mm, CI 0.79-0.87, OI 0.12-0.16, SI 0.73-0.89, PSI 0.15-0.17, MHI 0.84-0.94. N=16

Mandibles with 5-7 teeth; basal tooth equal to or slightly larger than penultimate basal; a denticle may occur between basal teeth. Body of clypeus not projecting over apron. Posterior outline of head convex to weakly concave. Mesosoma with broadly rounded shoulders; metanotal groove

a weak impression or absent; no ridge at anterior of propodeum. Propodeal spines narrow, moderately long; a bisecting line passes dorsal to propodeal spiracle and through or below anteroventral corner of pronotum. Metapleural lobes low, angular. Petiolar peduncle with strong keel; node large and somewhat bulbous. Postpetiolar node with long, low profile and weakly defined posterior and anterior faces (more distinct in Dominican Republic).

Laterodorsa and sides of head rugose-areolate; in most Cuban specimens ridges become very weak on sides, even absent in spots. Posterior head with transversely arching rugose-areolate macrosculpture. Anterior pronotal disc transversely rugose to rugose-areolate; rest of pronotum longitudinally rugose, usually with incomplete cross-ridges between rugae. Mesonotum more rugose-areolate. Pronotal sides basically rugose (areolate-rugose in Dominican Republic); meso- and metapleura confused rugose-areolate with some smooth patches. Dorsal face of propodeum transversely rugose. Vague rugosities on sides and/or posterior petiolar node; postpetiolar node smooth.

Color brown to yellowish-brown, with lighter, more yellowish appendages and frontoclypeal region.

Queens.—TL 2.8-3.4, HL 0.59-0.74, HW 0.52-0.65, SL 0.39-0.50, EL 0.11-0.15, PW 0.45-0.52, WL 0.81-0.95, SpL 0.10-0.16, PetL 0.26 (estimated)-0.40, PpetL 0.17-0.22mm, CI 0.86-0.89, SI 0.74-0.78, PSI 0.13-0.16, MHI (Cuban only; could not measure in Bahamian) 0.97-1.06. N=3

Apparently collected as strays, so not definitely associated with workers described above. The Bahamian queen distinctly smaller (all of the smallest measurements above); Cuban queens nearly identical in size. Mandible with 6 teeth; basal and penultimate tooth subequal in size. Clypeus evenly convex. Posterior outline of head medially concave. Mesosoma of Cuban queens robust, shaped like that of *scobinata* (Fig. 62), but larger and with more prominent, angular metapleural lobes. Mesosoma of Bahamian queen seems like that of Cuban queens, but is obscured by legs. Waist as in workers, except for lack of keel

on the petiolar peduncle in Cuban specimen. PpetW/PpetL 1.05-1.14. Sculpture much as in workers. Macrosculpture on sides of head weak. Most of ventral half of mesopleura smooth. Pilosity and color as in workers.

Discussion.—Workers of this species have two disjunct sizes. In the smaller size range (WL 0.62-0.70mm) are three specimens from Pinar del Río Province (including *brunnea* syntypes), one from Soledad (*scabra* syntype), one from I. Pinas, three from Dominican Republic, and one from Bahamas. The larger workers (WL 0.80-0.91mm) are from Sierra del Rosario (*cubensis* holotype), Soledad, Playa Marianao (*habanica* holotype), Sierra Maestra, and Sierra Anale. Aside from size, the smaller workers show little consistent difference from the larger workers, and in ways that often vary within *Rogeria* species: 1) slightly more macrosculpture on petiolar node, and 2) slightly more extensive microareolate sculpture on sides of mesosoma. The specimens from Dominican Republic differ from the rest in having a more compact mesosoma, more distinct postpetiolar node and sternum in side view, and slightly stronger sculpture.

Workers of *creightoni* from San José, Costa Rica have the same size as larger *brunnea* and much the same pilosity, nuchal groove, and shape of mesosoma and petiole. *Rogeria creightoni* specimens from Yucatán and Chiapas have size, eye size, postpetiole, and pilosity like the larger *brunnea*, and the Yucatán specimen has similar mesosoma shape. But *brunnea* workers can be distinguished by the combination of characters in the diagnosis.

Material Examined.—CUBA: Pinar del Río Province, Sierra de los Organos, Sierra del Rosario (Bierig), Las Acostas (E. O. Wilson), San Vicente (E. O. Wilson); Habana Province, Playa Marianao (Bierig); Cienfuegos Province, Soledad (P. J. Darlington; N. A. Weber; E. O. Wilson; D. Bates and G. Fairchild); Las Villas Province, Caibarién (E. O. Wilson); Sierra Anale (Bierig); Sierra Maestra, Uvero (L. Armas). I. Pinas, S. Casas (L. B. Zayas). DOMINICAN REPUBLIC: 16km ENE Pedernales (P. S. Ward). BAHAMAS: Andros Island, Nassau Island (W. M. Wheeler). 20 workers, 3 queens [LACM, MCZ, NMB].

Rogeria creightoni Snelling

Figs. 51-54, 95-96

Rogeria creightoni Snelling 1973:2, Fig. 1. Holotype and paratype worker, UNITED STATES: Texas, Cameron County, La Feria (W. S. Creighton) [LACM] [Holotype and paratype examined].

Additions to *creightoni*-group diagnosis. WL 0.63-0.93mm. Clypeal apron usually with weak to distinct median notch. Eyes small, oval to circular (EL/SpL 0.29-0.64). Metanotal groove weak or absent. MHI usually 0.90-1.06. Propodeal spines long (PSI usually > 0.17), often nearly horizontal. Postpetiolar node from above usually subtrapezoidal, sometimes subrectangular; anterior edge of sternum not prominent. Sides of head distinctly rugose-areolate. Pronotal disc transversely rugose-areolate on anterior edge and longitudinally rugose-areolate behind (Fig. 96). Scapes and extensor surfaces of tibiae with erect-suberect hairs.

Workers.— TL 2.4-3.5, HL 0.58-0.81, HW 0.51-0.72, SL 0.38-0.55, EL 0.05-0.10 (8-16 facets), PW 0.37-0.52, WL 0.63-0.93, SpL 0.11-0.20, PetL 0.27-0.40, PpetL 0.14-0.22mm, CI 0.85-0.91, OI 0.08-0.17, SI 0.68-0.80, PSI 0.16-0.28, MHI 0.87-1.08. N=21

Mandibles with 5-7 teeth, if 5, may have 1-2 additional basal denticles. Basal tooth subequal or larger than penultimate basal. Palpal formula 3,2. Body of clypeus projecting to anterior edge of apron or beyond. Nuchal groove weak to strong. Posterior margin of head weakly concave to convex. Mesosoma habitus variable (Figs. 51-53). Propodeal spines moderately long and angled to very long and nearly horizontal, a bisecting line usually passes well above anteroventral corner of pronotum. Propodeal spiracle not especially large or prominent; located < 1/2 diameter to almost one diameter from edge of infradental lamella. Metapleural lobes moderately to very prominent; corner broadly to narrowly rounded. Petiolar node more or less distinct (Figs. 51, 53). Petiolar keel absent to moderately well developed. Sting apparatus of specimens from four localities like that of *inermis* (Fig. 42), except for less angular anteroventral corner of spiracular plate, somewhat lower valve chamber height, and in Belize and Oaxaca specimens the sting shaft is higher and slightly upturned.

Laterodorsa of head longitudinally rugose to

areolate; posterior head transversely arched areolate-rugose. Pronotal sides longitudinally rugose to areolate-rugose; meso- and metapleura confused rugose (Fig. 95). Dorsal face of propodeum marked anteriorly by a distinct transverse carina, then areolate and/or transversely rugose. Head and mesosoma microsculpture obscure; intervals in macrosculpture moderately shiny. Top and sides of petiolar node effaced microareolate with very weak, indistinct macrosculpture; posterior face with weak longitudinal rugulae. Postpetiolar node with vague microsculpture on sides; smooth dorsally.

Color brownish-yellow to brownish-yellow; dorsa of head and gaster slightly darker, appendages lighter.

Queen.— Uncertain; see discussion.

Discussion.—This species becomes quite heterogeneous with this revision. Ants from almost every locality are different from the others in some conspicuous way. Specimens from Belize have the longest propodeal spines (PSI 0.24-0.28), more prominent metapleural lobes, weak or absent petiolar keel and thicker ridges in macrosculpture. The Texas specimens have similar habitus, but have somewhat shorter propodeal spines (PSI 0.21-0.23), less prominent metapleural lobes, more distinct petiolar keel and less thickened macrosculpture. A Tamaulipas specimen is similar to the Texas specimens, but has longer, distinctly inclined propodeal spines. Specimens from Yucatán, and Chiapas (Fig. 52) are the largest (WL 0.78-0.93mm), have a prominent clypeal body, somewhat longer scapes, small circular eye, strong nuchal groove, relatively shorter propodeal spines (PSI 0.19-0.22), and head macrosculpture with sharp ridges and unusually large areolae. Specimens from La Selva, Costa Rica are similar, but have normal clypeus and sculpture. Others from Costa Rica (Fig. 53) have shorter, more inclined propodeal spines (PSI 0.16-0.20), a more distinct petiolar node and keel, and subrectangular postpetiolar node. One specimen from Oaxaca is more like those from Belize; another is more like the San José specimens. With little material from most localities, I did not feel confident naming a new species for each variant, but as collections improve, I will not be surprised if this species undergoes fission.

At one time during the revision I also considered describing *cornuta*, *innotabilis*, *leptonana*, and

alzatei as variants of *creightoni*. But now I believe they can be delineated. Comparison of *creightoni* with *leptonana* is found in key couplet 40; comparisons with *cornuta* and *alzatei*, in their respective discussions. All known specimens of *innotabilis* fall within the geographic range of *creightoni* and the two species are sympatric in at least one locality. All specimens of *creightoni* differ from *innotabilis* (Figs. 55-57, 97-98) in several ways: 1) erect hair on scapes and tibiae, 2) palpal formula 3,2,3) clypeal apron with weak to distinct median notch, and 4) postpetiolar sternum not prominent. The regional variants differ in additional, but inconsistent ways.

A single queen from Trinidad (N. A. Weber #129) is very much like the three Costa Rican and Colombian queens provisionally assigned to *innotabilis* (Fig. 57) in size, general habitus, triangular mandibles, convex clypeus, robust mesosoma (MHI 1.28), propodeal spine size and shape, and subrectangular postpetiolar node, but differs in having erect hair on scapes and tibiae, little or no keel on petiolar peduncle, undulate ventral profile of postpetiole, and longitudinally oriented sculpture on the posterior head. On the basis of the pilosity, I provisionally assign the Trinidad queen to *creightoni*, but because of its great similarity in other respects to the *innotabilis*-like queens, and because neither set of queens is from an area where workers of *creightoni* or *innotabilis* have been collected, I do not feel confident of these assignments.

See also discussions of *alzatei*, *belti*, *brunnea*, and *cornuta*.

Distribution.—*Rogeria creightoni* ranges from southern Texas to Costa Rica; from about 1,500m in parts of Chiapas and Costa Rica to sea level. Types were collected in a residential area formerly mesquite-acacia savannah. Other specimens come from riparian woodland, palm-thorn forest, rain forest, pine-oak forest, cecropia forest, and cacao plantation. Most were taken in leaf litter on the ground. Some Belize specimens were under a termite nest; another in orchids.

Material Examined.—UNITED STATES: Texas, Cameron County (W. S. Creighton) [LACM]; Live Oak County (P. S. Ward) [mouthparts, sting] [MCZ]. MEXICO: Tamaulipas, Antiguo Morelos (S. & J. Peck); Vera Cruz, Pueblo Nuevo (E. O. Wilson); Oaxaca, 1 mi. E Reforma, nr. Tuxtepec (A. Newton) [mouthparts, sting]; 9 mi. E El Cameron (A. Newton); Chiapas, 12 mi. NW Ocozocoautla

(A. Newton); Yucatán, Chichén Itzá [MCZ]. BELIZE: Intercepted in Brownsville, Texas on orchids (Heinrich); nr. Belmopan (S. & J. Peck); Caves Branch (S. & J. Peck) [mouthparts, sting] [BMNH, CKC, MCZ, MZSP, USNM]. COSTA RICA: Heredia Province, La Selva (Talbot & VanDevender) [sting] [LACM], (D. M. Olson) [DMOC]; San José (H. Schmidt) [MZSP]; Jurrucarres (A. Bierig) [MZSP]; no locality (F. Nevermann) [MZSP]. 32 workers.

Rogeria innotabilis new species

Figs. 55-57, 97-98

Additions to *creightoni*-group diagnosis. WL 0.66-0.73mm. Mandibles triangular to slightly subtriangular. Palpal formula 2,2. Clypeal apron convex or slightly flattened medially. Eye small, elliptical. Nuchal groove clearly visible in lateral view, but not notching ventral outline of head. Mesosoma with nearly flat dorsal profile; a strong carina marks anterior edge of propodeum; MHI 0.90-1.00. Propodeal spines straight, wide. Petiolar keel moderate to large. Postpetiole subrectangular in dorsal view; sternum weakly to strongly prominent. Spiracular plate of sting apparatus with long spine on posteroventral corner. Sides of head areolate-rugose; mesosoma predominantly rugose; microareolate sculpture distinct on mesosoma sides. No erect hair on scapes or extensor surfaces of tibiae.

Holotype and Paratype Workers.— TL 2.4-2.7 (2.7), HL 0.60-0.65 (0.65), HW 0.50-0.57 (0.54), SL 0.40-0.45 (0.43), EL 0.06-0.08 (0.08) (7-13 facets), PW 0.37-0.41 (0.41), WL 0.66-0.73 (0.72), SpL 0.10-0.15 (0.13), PetL 0.26-0.30 (0.29), PpetL 0.14-0.16 (0.16)mm, CI 0.83-0.87 (0.84), OI 0.11-0.15 (0.15), SI 0.76-0.80 (0.78), PSI 0.15-0.20 (0.18), MHI 0.90-1.00 (0.98) N=10

Mandible with 5-7 teeth. If 5 or 6 teeth, it may have 1-3 denticles among proximal teeth. If 7 teeth, 4 proximals small. Basal tooth equal to or larger than penultimate tooth. Body of clypeus not projecting to anterior edge of apron. Eye small, elliptical. Posterior outline of head strongly to weakly convex. Metanotal groove absent or weak. Propodeal spines wide, straight; a bisecting line passes through or below anteroventral corner of pronotum. Petiolar keel weak or absent. Petiolar node evenly rounded from front to back, or apex somewhat flattened (Fig. 55). Postpetiolar node

highest in posterior half; node in dorsal view much as in Fig. 53. Sting apparatus like that of *inermis* (Fig. 42), except for spiracular plate shape (Fig. 56).

Head macrosculpture areolate on laterodorsa; areolate to transversely arching rugose-areolate on posterior head. Areolae on posterior head are larger and ridges sharper than elsewhere on head. Head dorsum slightly dulled by vestigial microsculpture; intervals smooth and shiny on sides and back. Anterior pronotal disc with 1-2 transverse rugae; rest of promesonotal dorsum longitudinally rugose with lateral spurs (Fig. 98) to rugose-areolate. Lateral pronotum areolate; meso- and metapleura mixed rugose and rugose-areolate. Anterior edge of propodeum marked by weak to strong transverse carina; dorsal face crossed by one or more transverse, sometimes branching, rugulae. Dorsum with vestigial microsculpture, but ventral sides quite distinctly microareolate (Fig. 97). Macrosculpture on sides and back of petiolar node very weakly areolate; microsculpture vague and effaced. Postpetiolar node shiny, almost completely smooth.

Color golden brown with yellowish appendages to brown with slightly lighter frontoclypeal area, mandibles, mesosoma sides, gaster, and legs.

Possible Queens.—TL 2.6-2.9, HL 0.59-0.61, HW 0.52-0.54, SL 0.40-0.41, EL 0.11-0.13, PW 0.44-0.50, WL 0.72-0.83, SpL 0.13-0.14, PetL 0.28-0.31, PpetL 0.14-0.17mm, CI 0.88-0.89, OI 0.21-0.24, SI 0.75-0.77, PSI 0.16-19, MHI 1.15-1.22. N=3

Collected outside known range of *innotabilis* workers, but have *innotabilis* traits: shapes of clypeus, nuchal groove, and postpetiole, and lack of erect/suberect hair on scapes and tibiae.

Differing from the worker by normal caste differences and the following. Parapsidal furrows indistinguishable from furrows in sculpture. Pronotum with 2-3 transverse rugae mesad, becoming longitudinally rugose to rugose-areolate on mesosoma sides; anterior katepisternum smooth. Mesonotum longitudinally rugose. Venation nearly identical to that of *belti* (Fig. 37).

Discussion.—For comparison with related species, see *creightoni*, *leptonana*, and *alzatei* discussions. Remarks about the queens are found in the *creightoni* and *curvipubens* discussions.

The name *innotabilis* (L., not remarkable) reflects my inability to identify any one salient feature on which to base the name for this species.

Distribution.—If the queens truly belong to *innotabilis*, this species ranges from Chiapas to northern Colombia, but workers have not been collected south of Nicaragua. Workers come from moist forest litter at 1000-1200m elevation. Collection sites for queens range from 10-1200m.

Material Examined.—**Holotype locality**. MEXICO: Chiapas State, 12 mi. NW Ocozocoautla, 3200 ft., 4-5-IX-1973, forest leaf litter (A. Newton) [MCZ].

Paratype Localities. MEXICO: 7 workers, holotype locality [mouthparts, sting, 1 coated for SEM] [BMNH, MCZ, MZSP]; 10 workers, Chiapas, 6-XII-1951, #51 11574 (Cary) [2 mouthparts, stings] [USNM]. NICARAGUA: 2 workers, Km 139 near Matagalpa, Hotel Selva Negra, ca. 1200m, 18-VI-1978, forest leaf litter (C. Kugler & J. Hahn) [mouthparts, sting] [LACM, MCZ].

Nontype localities. COSTA RICA: Puntarenas Province, Monteverde, 1200m, 23-V-1979, #3496 (P. Ward) [MCZ]. COLOMBIA: Magdalena Department, Parque Tayrona, 210m, 1-X-76 (C. Kugler) [MCZ]; Guajira, Don Diego, 25-50m, 22-VI-76 (W. L. Brown & C. Kugler) [queen mouthparts, sting] [MCZ]. 3 queens.

Rogeria alzatei new species

Figs. 58-60, 99

Diagnosis.—WL 0.51-0.70mm, most < 0.65mm. Mandibles subtriangular (usually) to triangular. Clypeus usually truncate. Eye usually moderately large, oval (10-14 facets, OI 0.17-0.20 in types), but occasionally half as large and elliptical. Nuchal groove weak to strong. Mesosoma compact (MHI 0.90-1.07). Propodeal spines usually slender, inclined. Petiolar peduncle with little or no keel. Postpetiolar node from above usually subrectangular; anterior edge of sternum not prominent. Macrosculpture areolate on head sides. Posterior head transversely rugose-areolate (Fig. 99). Pronotal disc rugose to rugose-areolate. No erect hair on scapes or legs.

Holotype and Paratype Workers.— TL 1.9-2.2 (2.2), HL 0.51-0.56 (0.54), HW 0.45-0.48 (0.47), SL 0.32-0.36 (0.35), EL 0.07-0.09 (0.09) (11-14 facets), PW 0.32-0.37 (0.35), WL 0.51-0.61 (0.59), SpL 0.10-0.12 (0.11), PetL 0.21-0.26 (0.23), PpetL 0.12-0.14 (0.13)mm, CI 0.87-0.88 (0.87), OI 0.17-0.20 (0.19), SI 0.72-0.74 (0.74), PSI 0.19-0.21 (0.19), MHI 1.01-1.07 (1.05). N=11

Mandible subtriangular; 5-6 teeth, two basal teeth small, subequal. Palpal formula 2,2. Clypeal apron truncate, with distinct corners; body of clypeus does not project to edge of apron. Posterior outline of head continuously convex. Nuchal groove indistinct in lateral view. Mesosoma's evenly convex dorsal profile ends abruptly fore and aft by rather sharp angles and by transverse sculpture. Metanotal groove weak or absent. Propodeal spines straight, narrow; a bisecting line passes through or just above anteroventral corner of pronotum. Corner of metapleural lobes a narrowly rounded right angle. Petiolar node evenly rounded front to back. Pygidium in the five specimens dissected with no piligerous tubercles.

Head laterodorsa rugose-areolate to areolate; sides more coarsely areolate. Microsculpture vestigial, producing irregular intervals on head dorsum and nearly smooth intervals on sides and posterior (Fig. 99). Anterior edge of pronotal disc with two transverse rugae. Promesonotal dorsum longitudinally rugose with numerous lateral spurs that sometimes connect, forming areolae. No macrosculpture on dorsal face of propodeum. Lateral pronotum longitudinally rugose-areolate. Meso- and metapleura with scattered, irregular rugae. Vestigial rugae on sides and back of petiolar node. Vague microsculpture makes roughened intervals on mesosoma, petiole and much of postpetiole; apex of postpetiolar node smooth.

Body yellowish-brown to reddish-brown with slightly darker head and gaster dorsa (black to naked eye); legs and antennae lighter, more yellowish or yellowish-brown.

Nontype Workers.— TL 1.9-2.5, HL 0.50-0.66, HW 0.42-0.56, SL 0.31-0.46, EL 0.05-0.10 (4-21 facets), PW 0.29-0.39, WL 0.51-0.70, SpL 0.09-0.13, PetL 0.21-0.28, PpetL 0.11-0.15mm, CI 0.81-0.88, OI 0.08-0.20, SI 0.71-0.85, PSI 0.15-0.21, MHI 0.90-1.07. N=32

Specimens from Guyana, French Guiana, and the Caribbean coast of Colombia extend the description as follows: Mandibles triangular with 3-4 teeth plus 4 basal denticles. Clypeal apron evenly convex, sometimes with medial emargination. Some with only 7-8 facets in the eyes. Some with wider propodeal spines (Fig. 60) or slightly downturned tips. Petiolar keel sometimes distinct (Fig. 60). Macrosculpture on head or pronotum more areolate.

Dominican Republic specimens have a con-

vex clypeus, a distinct metanotal groove as in Fig. 46, and subtrapezoidal postpetiolar node as in Fig. 51.

Specimens from Peru, Brazil, and Paraguay extend the description somewhat differently: Palpal formula 3,2. Clypeal apron usually truncate with rounded corners; occasionally convex. Several specimens with a somewhat prominent clypeal body (Fig. 59). Generally with smaller, elliptical eyes (OI of most 0.10-0.16), but the four workers from the Puerto Maldonado vicinity of Peru possess both the smallest eyes (Fig. 59) and largest eyes of the species (4 and 21 facets, OI 0.08 and 0.20). Nuchal groove forms a distinct notch in the head of one Peruvian worker (Fig. 59). Mesosoma generally less compact (MHI 0.93-1.03). Petiolar keel weak to distinct (Fig. 59). Some with postpetiolar node slightly wider in anterior half and shape similar to Fig. 66. Posterior pygidium with small tubercles in a Paraguayan specimen dissected. Sting apparatus with reduced anterodorsal corner of quadrate plate in a Brazilian worker.

Paratype and Nontype Queens.—TL 2.4-2.8, HL 0.56-0.60, HW 0.51-0.53, SL 0.35-0.38, EL 0.13-0.14, PW 0.44-0.49, WL 0.70-0.79, SpL 0.14-0.15, PetL 0.26-0.30, PpetL 0.15-0.16mm, CI 0.88-0.92, OI 0.25-0.26, SI 0.70-0.72, PSI 0.19-0.20, MHI 1.17-1.18. N=2

Both collected in the same localities as *alzatei* workers (BCI, Panama; Quebrada Susumuco, Colombia), but not in nest series. They most resemble *alzatei* workers in characteristic shapes of clypeus, mandible, mesosoma, propodeal spines, petiole and postpetiole, as well as sculpture and pilosity. Mesoscutellum projects slightly beyond posterior edge of metanotum. Posterior head rugose-areolate; no tubercles. Middorsum of head covered with erect hairs.

Discussion.—The extent of variation within this species makes me question whether this is a single species, but external characters that can be used in a key are either not marked enough to discount individual variation or not concordant. Further complicating the picture is the surprising amount of variation within four specimens from the same region of Peru, and unique sets of features found in single specimens from northern Colombia, Rio de Janeiro, and Peru. Specimens from Dominican Republic strongly resemble *creightoni* workers from the same localities, but differ in lacking erect hair on the scapes and tibiae

and in having narrower propodeal spines.

Given the geographic variation within *alzatei*, the species as a whole is difficult to distinguish clearly from *creightoni*, *innotabilis*, and *leptonana*. But if one compares only those specimens of *alzatei* that are in sympatry or parapatry with those three species, the differences are clear. The Panamanian *alzatei* workers differ from Central American *creightoni*, *innotabilis*, and *leptonana* in having: 1) subtriangular mandibles, 2) truncate clypeal apron, 3) larger, elongate-oval eye (OI 0.17-0.20), 4) more compact mesosoma (MHI 1.01-1.07), and 5) petiolar peduncle without a keel. They are also smaller than *creightoni* and *innotabilis* workers (WL 0.51-0.61mm vs. 0.66-0.93mm in *creightoni* and 0.66-0.73mm in *innotabilis*). Additional differences from *leptonana* are palpal formula (2,2 vs. 3,2 in *leptonana*), longer propodeal spines (PSI 0.19-0.20 vs. <0.16 in *leptonana*), and lack of erect hair on scapes.

See also the description of sibling species *scobinata* and the discussions of *belti*, *curvipubens*, *micromma*, *tribrocca* and *merenbergiana*.

The species is named in honor of a courageous Colombian intellectual and friend, Isaac Alzate.

Distribution.—The range of *alzatei* is from Panama to Paraguay, from western slopes of the Andes in Colombia to the Eastern coast of Brazil. All specimens were apparently taken as strays or in Berlese or Winkler sampling in moist forests from sea level to 1000m.

Material Examined.—**Holotype locality**. PANAMA: Canal Zone, Barro Colorado Island (BCI), 2-VII-79, W. L. Brown [MCZ].

Paratype localities. PANAMA: 3 workers, 1 queen from holotype locality [mouthparts, sting, 1 worker coated for SEM] [CKC, MCZ]; 2 workers, BCI, IV-V-1942, #4953 (J. Zetek) [USNM]; 2 workers, BCI, VI-X-1943, #5105 (J. Zetek) [whole specimen slide mounted] [USNM]; 1 worker, BCI, I-1960 (W. L. Brown & E. S. McCluskey) [MCZ]; 1 worker, BCI, 7-III-1975, FP#10 (C. Toft & S. Levings) [LACM]; 1 worker, Punta de los Chivos, W side Gatun Lake, 3km SW Gatún, 100m, 3-9-VII-1979 (W. L. Brown) [MCZ]; 1 worker, Bocas del Toro, Pipeline Road, 300m, 8.53N 82.10W, 18-VII-1987, #633 (D. M. Olson) [MZSP].

Nontype localities. DOMINICAN REPUBLIC: 16km ENE Pedernales, 800m (P. S. Ward). COLOMBIA: Guajira, Rio Don Diego (W. L. Brown & C. Kugler); Magdalena Department, San Pedro, 550m (P. Ward) [MCZ]; Chocó Department, 10km

SW San José del Palmar, Río Torito, Finca los Guadales, 800m (C. Kugler) [mouthparts, sting] [CKC, MCZ, MZSP]; Antioquia Department, Providencia, Estación Biológico, 600-800m, (C. Kugler) [MCZ]; Cundinamarca Department, Bogotá to Villavicencio, Km 79 (W. L. Brown & I. del Polania) [MCZ]; Meta Department, Bogotá to Villavicencio, 23km NW Villavicencio, Quebrada Susumuco, 1000m (S. & J. Peck; C. Kugler) [1 mouthparts, 2 stings, 1 whole specimen] [MCZ]. GUYANA (British Guiana): Oronque River (N. A. Weber) [MCZ]. BRAZIL: São Paulo State, Agudos (W. Kempf; C. Gilbert) [mouthparts, sting] [MZSP, USNM]; Rio de Janeiro (T. Borgmeier) [MZSP]; Federal District (C. A. C. Seabra) [MZSP]. PERU: Madre de Dios Department, Puerto Maldonado vicinity, 260m (C. Kugler) [CUIC, MCZ]. PARAGUAY: Central Province (F. Baud, et al.) [mouthparts, sting] [BMNH, MCZ (voucher), MHN]; Concepción, and Paraguari Provinces (F. Baud, et al.) [BMNH, MHN]. 62 workers, 1 queen.

Rogeria scobinata new species

Figs. 61-62, 100

Diagnosis.—As in *alzatei*, except the following: Clypeal apron truncate (none emarginate). MHI 0.96-1.14. Posterior head with tuberculate macrosculpture (Fig. 100). Erect hair usually absent from head dorsum; if present, it is short and usually confined to posterior margin.

Holotype and Paratype Workers.— TL 1.9-2.5 (2.2), HL 0.50-0.60 (0.55), HW 0.42-0.52 (0.475), SL 0.31-0.40 (0.35), EL 0.06-0.09 (0.07) (10-14 facets), PW 0.30-0.40 (0.35), WL 0.50-0.67 (0.585), SpL 0.08-0.12 (0.095), PetL 0.19-0.26 (0.23), PpetL 0.12-0.16 (0.14)mm, CI 0.82-0.86 (0.86), OI 0.14-0.18 (0.15), SI 0.74-0.78 (0.74), PSI 0.16-0.19 (0.16), MHI 0.96-1.09 (1.00). N=5

Nontype Workers.— TL 1.9-2.5, HL 0.50-0.61, HW 0.44-0.52, SL 0.31-0.40, EL 0.06-0.09 (7-15 facets), PW 0.30-0.40, WL 0.51-0.68, SpL 0.08-0.13, PetL 0.19-0.28, PpetL 0.12-0.17mm, CI 0.84-0.88, OI 0.14-0.18, SI 0.70-0.78, PSI 0.16-0.20, MHI 1.00-1.14. N=32

Mandibles subtriangular, 5-toothed (sometimes with 1-2 additional basal denticles), decreasing in size basad; basal tooth small. Palpal formula 2,2. Median clypeus of some nontype workers from Colombia like that of *alzatei* (Fig. 58), but type specimens with less prominent corners (Fig. 61)

and other nontypes (Bolivia, some Brazil) have an almost evenly convex clypeal apron. Body of clypeus not projecting over clypeal apron. Posterior outline of head weakly concave medially to weakly convex. Nuchal groove clearly visible in side view. Eye oval to elliptical. Anterior and dorsal faces of pronotum may join smoothly, or in a weak angle (Fig. 61). Metanotal groove broad, slightly less to slightly more impressed than shown in Fig. 61, bordered behind by a transverse carina. Propodeal spines inclined. Metapleural lobes moderately prominent; corner varies from sharply angular (Ecuador, some Peru) to rounded as in Fig. 44 (some Paraguay). Ventral petiolar peduncle usually with a weak, nonlamellate keel, but some Ecuadorian specimens with distinct keel. Postpetiolar node in dorsal view subrectangular as in Fig. 58. Pygidium with a pair of median, columnar, piligerous tubercles near caudal edge (barely visible in dissection microscope at 50X).

Laterodorsa and sides of head densely areolate. Posterior head with short triangular, blunt tubercles in more or less distinct rows (Fig. 100). Tuberculate sculpture usually extends across posterior quarter of head, but in a few specimens from Leticia, Benjamin Constant, and Paraguay, the ridges between the tubercles are not always completely lost, so the posterior head appears mostly fragmented-rugose, with only a few of the triangular tubercles. Interstices on most of head somewhat dulled by indistinct areolate microsculpture, but smoother and quite shiny between tubercles on back of head; sides sometimes rather strongly microareolate. Anterior edge of pronotal disc with 1-4 more or less transverse rugae. Rest of pronotum longitudinally rugose with frequent incomplete lateral spurs. Mesosoma sides weakly and sparsely rugose to rugose-areolate, but more strongly microareolate than on pronotal disc. Dorsal face of propodeum usually lacking macrosculpture, but rather strongly microareolate. Rest of mesosoma with indistinct microareolate sculpture. Petiolar node with broken vestigial macrosculpture. Postpetiole without macrosculpture; nearly smooth on top. Sides of nodes with weak microareolate sculpture that imparts a granular appearance; microsculpture usually weaker on postpetiole.

Workers from Leticia have 8-10 erect hairs along posterior rim of head and those from Benjamin Constant have sparse, short erect hairs on

the posterior rim and along the midline.

Color brown to golden brown. Legs and antennae generally lighter than rest of body; gaster sometimes darker.

Queens.—TL 2.4-2.6, HL 0.55-0.58, HW 0.46-0.52, SL 0.34-0.38, EL 0.11-0.13, PW 0.41-0.45, WL 0.68-0.74, SpL 0.11-0.14, PetL 0.25-0.27, PpetL 0.14-0.16mm, CI 0.84-0.90, SI 0.70-0.75, PSI 0.16-0.19, MHI 0.64-0.69. N=7

Habitus shown in Fig. 62. Parapsidal furrows indistinguishable from grooves in sculpture. Anterior pronotum transversely rugose to rugose-areolate, becoming longitudinal on sides. Mesoscutum with longitudinal, often diverging rugae; mesoscutellum rugose or rugose-areolate.

Discussion.—*Rogeria alzatei* is a sibling species of *scobinata*, with which it is sympatric in Peru, Brazil, and Paraguay, but can be distinguished by characters in the diagnosis and key. The pair of columnar tubercles on the pygidium may also be distinctive.

The name *scobinata*, meaning having the nature of a rasp, refers to the sculpture on the posterior head, which has rows of teeth like a rasp.

Distribution.—*Rogeria scobinata* ranges from the north coast of South America to Paraguay at elevations below 1000m. All specimens were taken as strays in tropical forest, mostly by Berlese or Winkler sampling of leaf litter, rotten wood, or moss.

Material Examined.—**Holotype locality**. PERU: Madre de Dios Department, 3km N Puerto Maldonado, 260m, primary forest remnant by side of road, berlesate of leaf litter and rotten wood, 13-16-VI-1981 (C. Kugler and R. R. Lambert) [MCZ].

Paratype localities. PERU: 2 workers, 1 queen, holotype locality [MCZ]; 22 workers, 2 queens, 5km E Puerto Maldonado on Río Tambopata, Finca Medina, 260m, primary forest berlesate, 13-16-VI-1981 (C. Kugler and R. R. Lambert) [mouthparts, sting, 1 worker coated for SEM] [BMNH, CKC, LACM, MCZ, MZSP, MHN, USNM].

Nontype localities. TRINIDAD: Nariva Swamp (N. A. Weber) [MCZ]. SURINAM: La Poulle, Vank, and Tambahredjo (J. van der Drift) [MZSP]. COLOMBIA: 7km N Leticia (S. and J. Peck) [MCZ]. ECUADOR: Napo Province, Limoncocha and 20km S Tena (S. and J. Peck); Pastaza Province, 25km N Puyo, (S. and J. Peck) [MCZ]. PERU: Loreto Department, Ramon Castillo (S. and J. Peck), 15km WSW Yurimaguas (P. S.

Ward) [PSWC]; Pasco Department, near Pozuzo, (C. Kugler and R. R. Lambert); Madre de Dios Department, Puerto Maldonado vicinity near Lake Sandoval (C. Kugler and R. R. Lambert) [CKC, CUIC, MCZ]. BOLIVIA: La Paz Department, Caranavi (C. Kugler and R. R. Lambert) [MCZ]. BRAZIL: Pará State, (collector name unreadable); Amazonas State, Benjamin Constant and vicinity (W. L. Brown); Mato Grosso State, Utiariti, Rio Sauêruinã [=R. Papagaio] (Lenko and Pereira); São Paulo State, Piraçununga Municipality, Cachoeira das Emas (EEBP) (W. L. Brown); Rio de Janeiro (T. Borgmeier) [MCZ, MZSP]. PARAGUAY: Alto Paraná, Amambay, Caaguazú, Canendiyu, and Concepción Provinces (F. Baud et al.). 122 workers, 13 queens.

Rogeria tribrocca new species

Fig. 63

Additions to *creightoni*-group diagnosis. WL 0.62mm. Eye small, elliptical. Clypeal apron with three acute processes. Metapleural lobes very low, broadly rounded. Postpetiolar node widest in anterior half. Posterior edge of gaster T3 with median spine that seems to arise from a weak concavity. Sides of head smooth. Promesonotal dorsum with fine rugae diverging and branching from anterior pronotum, becoming weak on meso- and metanota; interrugal spaces rather wide. No erect hair on scapes or legs.

Holotype Worker.— TL 2.3, HL 0.61, HW 0.51, SL 0.40, EL 0.05 (7 facets), PW 0.36, WL 0.62, SpL 0.10, PetL 0.26, PpetL 0.13mm, CI 0.83, OI 0.10, SI 0.78, MHI 0.93, PSI 0.16.

One mandible with six teeth; the other with the penultimate basal replaced by two denticles (Fig. 63). Nuchal groove forms a weak notch in lateral view of head. Pronotal shoulders seen from above subangular. Propodeal spiracles 1 diameter from nearest edge of infradental lamella. Ventral petiole somewhat obscured by glue, but probably with distinct keel and dentate process. Petiolar node narrow; nearly symmetrically rounded in lateral view. Postpetiolar node with broadly confluent anterior and dorsal faces and short posterior face. Postpetiolar sternum with perpendicular anterior corner and flat ventral profile (Fig. 63); node in dorsal view widest in anterior half, as in Fig. 74. Sting shaft projecting from gaster acute, with low dorsal flange.

Laterodorsa of head longitudinally rugose-areolate. Posterior head with transversely arching rugae. Intervals with weak microsculpture. Dorsal face of propodeum with 3 weak transverse rugulae. Mesosoma sides with sparse, indistinct, longitudinal rugulae. Microsculpture on mesosoma even weaker than on head; interrugal spaces shiny, nearly smooth. Petiolar and postpetiolar nodes nearly smooth, shiny.

Mesosoma dorsum with eight pairs of erect hairs (some matted down); nodes each with two pairs of posterodorsally projecting hairs.

Color of body and appendages brownish-yellow; dorsum of gaster T1 slightly darker.

Discussion.—Both *curvipubens* (Figs. 74-76, 101-102) and *alzatei* (Figs. 58-60, 99), have also been collected in Quebrada Susumuco or nearby Villavicencio environs. But they do not have a three-toothed clypeal apron or a median spine on the third tergum of the gaster.

The name *tribrocca* (*brocca* L., projection of teeth) refers to the three tooth-like projections of the clypeal apron.

Material Examined.—**Holotype locality**. COLOMBIA: Meta Department, Quebrada Susumuco [or Susumuco], 23km NW Villavicencio, 1000m, forest litter, 5-III-1972, #B-234 (S. and J. Peck) [MCZ].

Rogeria carinata new species

Fig. 64

Rogeria curvipubens: M. Smith 1937:851. Misidentification.

Additions to *creightoni*-group diagnosis. WL 0.53-0.67mm. Clypeal apron convex. Eye small. Propodeal spines small. Mesosoma low (MHI 0.86-0.96). Postpetiole subrectangular in dorsal view; sternum with distinct, but not projecting anterior lip. Sides of head rugose. Promesonotal dorsum carinate, with broad, shiny intervals. Short erect-suberect hairs on scapes, but not on extensor surfaces of legs.

Holotype and Paratype Workers.— TL 2.0-2.5 (2.2), HL 0.51-0.61 (0.55), HW 0.44-0.54 (0.46), SL 0.35-0.42 (0.38), EL 0.05-0.06 (0.06) (7-10 facets), PW 0.31-0.41 (0.34), WL 0.53-0.67 (0.57), SpL 0.05-0.10 (0.08), PetL 0.19-0.24 (0.22), PetW 0.10-0.13 (0.11), PpetL 0.11-0.14 (0.12), PpetW 0.14-0.18 (0.15)mm, CI 0.86-0.89 (0.86), OI 0.11-0.12 (0.13), SI 0.78-0.80 (0.83), PSI 0.09-0.15 (0.14), MHI 0.86-0.96 (0.92). N=15

Mandibles with 5 teeth and 0-2 denticles between the two basal teeth; basal tooth larger than penultimate basal. Eyes oval to elliptical. Nuchal groove weak. Posterior outline of head weakly convex to weakly concave. Mesosoma from above broad, angular at shoulders, but strongly constricted behind; metanotum half as wide as shoulders. Propodeal spiracle small, one diameter from posterior edge of propodeum. Metapleural lobes small, rounded. Ventral petiole with weak keel. Postpetiole highest in posterior half. Sting apparatus with slightly lower valve chamber than that of *inermis* (Fig. 42).

Laterodorsa of head rugose-areolate in Puerto Rican specimens. Posterior head transversely arched areolate-rugose. Interrugal spaces on head weakly and irregularly roughened on dorsum; smoother on sides and posterior. Anterior face of pronotum with transverse carinules that continue onto shoulders and curve dorsad. Meso- and metapleura with irregular longitudinal rugae; intervals smooth dorsally, but vestigially microareolate below level of propodeal spiracle. Dorsal face of propodeum mostly smooth with 0-3 transverse rugulae. Petiolar node vaguely microareolate; macrosculpture absent or indistinct on sides. Postpetiole vaguely microareolate on venter; smooth and shiny on dorsum. Gaster smooth and shiny.

Mesosoma dorsum with 10 pairs of erect hairs.

Color brownish-yellow; head and mesosoma slightly darker than rest of body. Some Puerto Rican specimens slightly darker, with reddish hue to head and mesosoma.

Discussion.—The carinate macrosculpture of the promesonotum with very shiny intervals serves to differentiate *carinata* from others of the *creightoni*-group. See also the discussion of *nevadensis*, which has similar sculpture.

Material Examined.—**Holotype locality.** BRITISH VIRGIN ISLANDS: Tortola, Long Bay, berlesate from soil and leaves, 25-VII-1965 (I. Proj. Staff) [MCZ].

Paratype localities. 1 worker, holotype locality [MCZ]. PUERTO RICO: 3 workers, Guanica, 7-IV-1982, #75 (J. A. Torres) [LACM]; 1 worker, Cayo Ratones, 17-VII-1982, #77 (J. A. Torres) [LACM]; 8 workers, Cayo L. Peña, Humacao, 9-X-1982, #91 (J. A. Torres) [2 stings] [BMNH, CKC, LACM, MCZ, MZSP]; 1 worker, Ensenada, #1409, (no collector) [USNM].

Rogeria nevadensis new species

Fig. 65, 94

Additions to *creightoni*-group diagnosis. WL 0.58-0.65mm. Clypeal apron emarginate. Eye small. Shoulders rounded; promesonotum and propodeum meet without a strong angle. Postpetiolar node widest in anterior half. Sides of head largely smooth and shiny. Promesonotal dorsum longitudinally rugose, with low, rounded ridges and no lateral spurs; interrugal spaces wide and nearly smooth. No erect hair on scapes or extensor surfaces of legs.

Holotype and Paratype Workers.—TL 2.2-2.5 (2.2), HL 0.59-0.62 (0.59), HW 0.49-0.51 (0.49), SL 0.40-0.42 (0.40), EL 0.06-0.08 (0.06) (7-10 facets), PW 0.34-0.38 (0.34), WL 0.58-0.65 (0.58), SpL 0.09-0.10 (0.09), PetL 0.22-0.25 (0.22), PpetL 0.12-0.14 (0.12)mm, CI 0.81-0.83 (0.82), OI 0.13-0.15 (0.13), SI 0.82, PSI 0.15, MHI 0.93-0.95 (0.93). N=3

Mandibles with 5 teeth plus two denticles, or six teeth plus 1-2 denticles among basal teeth; basal tooth not larger than penultimate basal. Eye elliptical. Nuchal groove weak. Promesonotum slopes to join dorsal face of propodeum without an angle or transverse carina; metanotal groove weak or absent. Propodeal spines narrow; a bisecting line passes through anteroventral corner of pronotum. Propodeal spiracle within one diameter of edge of infradental lamella. Petiolar peduncle with indistinct keel. Postpetiolar node with a short vertical anterior face and long, sloping dorsal face; posterior face slightly concave in two paratypes. Postpetiole widest in anterior half as in Fig. 66. Postpetiolar sternum with flat ventral profile and somewhat prominent anterior edge. Sting shaft projecting from apex is like that of *inermis* (Fig. 42).

Laterodorsa of head rugose-areolate. Posterior head with transversely arching rugae. Head shiny with effaced microsculpture, especially on sides and back. Anterior pronotum crossed by several incomplete rugae. Lateral mesosoma (Fig. 94) with little distinct macrosculpture and smooth, shiny intervals. Dorsal face of propodeum with transverse rugae and effaced microareolate sculpture. Both nodes with weak, effaced microareolate sculpture and vague, vestigial rugose macrosculpture.

Mesosoma dorsum with 10-11 pairs of erect hairs; 2-3 pairs project posterodorsally from each node.

Color brown to dark reddish-brown (mesosoma and head dorsum may be darkest), with brownish-yellow appendages and frontoclypeal area.

Gynecoid Worker.—A nontype specimen is worker-like in most respects, but is larger (WL 0.70mm; PSI 0.19), has distinct mesonotal and metanotal sutures and partially formed wing attachments. Pronotum transversely rugose; mesoscutum longitudinally rugose. Sides of postpetiolar node from above more evenly convex.

Discussion.—*Rogeria merenbergiana* (Figs. 46-48), which is also found at high elevations in Colombia and Ecuador, has similar shapes of clypeus, mesosoma and propodeal spines, and somewhat reduced sculpture, but: 1) are a little larger than *nevadensis* (WL 0.69-0.83mm), 2) have a metanotal impression, 3) have erect hair on second and third tibiae and scapes, and 4) are more distinctly sculptured, with sides of head rugose.

Rogeria carinata (Fig. 64) from Puerto Rico and Tortola have the same size, pilosity, shape of waist, and extensive shiny spaces on mesosoma, but: 1) the metanotal-propodeal junction is more angular, 2) the sides of the head are distinctly rugose, 3) the promesonotal dorsum has straighter parallel ridges and smoother intervals, and 4) the propodeal spines are generally shorter (PSI 0.11-0.15).

Rogeria nevadensis takes its name from the Sierra Nevada de Santa Marta, site of the type localities.

Material Examined.—**Holotype locality**. COLOMBIA: Magdalena Department, SE Santa Marta, Cuchilla San Lorenzo, vicinity of El Campano, 1340m, rain forest, VI-1976 (W. L. Brown) [MCZ].

Paratype localities. 1 worker, same site as holotype [coated for SEM] [MCZ]. 1 worker, COLOMBIA: Magdalena, E Orihueca, 74.03W 10.55N, San Pedro de la Sierra, 1300m, rotten log in coffee plantation, 10-II-1977 (C. Kugler) [LACM].

Nontype locality. One gynecoid worker, berlesate at the San Pedro de Sierra site (C. Kugler) [MCZ].

Rogeria leptanana new species

Figs. 66-70

Additions to *creightoni*-group diagnosis. WL 0.54-0.66mm. Median clypeal apron concave to convex. Eyes small, nearly circular. Propodeal spines small to absent. Mesosoma low, slender (MHI 0.78-0.90; PW/WL 0.53-0.58). Petiole with moderate to large keel. Postpetiolar node from above as in Fig. 66. Anterior lip of postpetiolar sternum not prominent. Sides of head distinctly macro- or microsculptured. Mesosoma rugose, sometimes with strongly microareolate sides. Erect hair on scapes and usually on extensor surfaces of tibiae.

Holotype and Paratype Workers.— TL 2.1-2.3 (2.1), HL 0.50-0.55 (0.51), HW 0.43-0.46 (0.44), SL 0.32-0.34 (0.32), EL 0.05-0.07 (0.06) (7-10 facets), PW 0.32-0.36 (0.33), WL 0.57-0.61 (0.57), SpL 0.07-0.10 (0.07), PetL 0.20-0.23 (0.21), PpetL 0.12-0.13 (0.13)mm, CI 0.83-0.86 (0.86), OI 0.11-0.15 (0.14), SI 0.73-0.75 (0.73), PSI 0.12-0.16 (0.12), MHI 0.83-0.90 (0.83). N=4

Mandibles triangular, with 5 teeth and occasional denticle; basal tooth larger than penultimate tooth. Palpal formula 3,2. Median clypeal apron concave. Body of clypeus projecting slightly over edge of apron. Posterior outline of head very weakly concave or flat. Nuchal groove indistinct in lateral view. Mesosoma dorsal profile nearly flat. Propodeal spines short with wide base; a bisecting line passes just above anteroventral corner of pronotum. Spiracle about 1 diameter from nearest edge of infradental lamella. Petiolar node small. Postpetiole widest in anterior half (Fig. 66). Ventral profile of sternum concave; anterior lip not prominent.

Head rugose-areolate to areolate on laterodorsa and sides, transversely areolate-rugose on posterior head. Macrosculpture well defined on posterior head, weaker on dorsum and sides. Areolate microsculpture gives a granular appearance to dorsum and sides of head, where it largely obscures the weak macrosculpture; intervals on posterior head nearly smooth. Anterior edge of pronotal disc transversely rugose-areolate. Rest of promesonotal dorsum longitudinally rugose with occasional laterals; microsculpture obscure. Mesosoma sides with confused areolate macro- and microsculpture; the latter quite strong, giving a granular appearance. Petiole appears granular, with vestigial overlying macrosculpture.

Postpetiolar node smooth; sides and venter appear granular.

Mesosoma dorsum with more than 12 pairs of emergent erect hairs; nodes each with at least 2 pairs of long posterodorsally projecting hairs. Tibiae with erect hairs.

Body yellowish-brown to brownish-yellow; frontoclypeal area and appendages lighter, more yellowish.

Nontype Workers.—TL 2.2-2.5, HL 0.54-0.60, HW 0.43-0.50, SL 0.34-0.40, EL 0.04-0.08 (5-9 facets), PW 0.33-0.35, WL 0.54-0.66, SpL 0.03 (no spines)-0.11, PetL 0.21-0.26, PpetL 0.12-0.16mm, CI 0.80-0.83, OI 0.09-0.12, SI 0.77-0.83, PSI 0.05 (no spines)-0.18, MHI 0.78-0.90. N=8

Type description extended as follows. Mandibles subtriangular in Dominican Republic specimens. Clypeal apron convex in the Chiriquí, Panama specimens and truncate in Chiapas and Dominican Republic. Body of clypeus not projecting beyond clypeal apron in Chiapas specimen. Basal tooth may equal penultimate basal in size. Scapes slightly longer (SI 0.77-0.83). The Ocosingo, Mexico specimen has slightly longer spines than types (PSI 0.18); Cerro Pico Blanco, Costa Rica specimens have very short spines (PSI 0.07-0.10) those from Panama are devoid of armature (Fig. 67). Short propodeal spines of Costa Rican specimens are more inclined than in types; a bisecting line passes just below the axilla. Postpetiole of Chiapas and Pedernales, Dominican Republic specimens narrower than others (PpetW/PpetL 1.23-1.28 vs. 1.41-1.56); Pedernales postpetioles are widest in posterior half. Microsculpture on head may be less distinct than in types. Panamanian specimens lack erect hair on extensor surfaces of tibiae and have only 9 pairs of erect hairs on the mesosoma dorsum.

Possible Queens.—TL 2.6-2.8, HL 0.60-0.61, HW 0.52-0.53, SL 0.40, EL 0.12-0.13, PW 0.45, WL 0.73-0.78, SpL 0.14-0.17, PetL 0.28-0.30, PpetL 0.14-0.16mm, CI 0.86-0.88, OI 0.20-0.23, SI 0.75-0.77, PSI 0.19-0.22, MHI 0.92-0.97. N=2

Both queens collected on the north coast of Colombia. Though workers of *leptonana* are unknown from South America, these queens (Fig. 68) have strongest affinities to *leptonana* workers: Mandible with 5 teeth; basal as large as or larger than penultimate basal. Clypeal apron emarginate. Posterior outline of head flat. Propodeal spines wide. Propodeal spiracle 2 diameters from edge of

infradental lamella. Mesosoma low. Petiolar peduncle with prominent lamellate keel; node short. Pygidium and sting apparatus as in workers.

Sculpture also as in workers. Microsculpture present but indistinct on head and mesosoma. Pronotum with 1-2 transverse rugae medially; laterally rugose. Meso- and metanota longitudinally rugose, with nearly smooth, shiny intervals. Meso- and metapleura longitudinally rugose, except for smooth, shiny mesokatepisterna. Dorsal face of propodeum smooth. Petiole, including peduncle, and postpetiole nearly smooth.

There are differences, however. Palpal formula 2,2 in the dissected Guajiran queen (vs. 3,2 in workers). One queen has a nearly subrectangular postpetiole. Neither has erect hair on the tibiae.

Males.—TL 2.9, HL 0.51-0.53, HW 0.55-0.56, SL 0.32-0.34, EL 0.25, PW 0.50-0.53, WL 0.91-0.95, PetL 0.32-0.33, PpetL 0.15-0.16mm, CI 1.04-1.10, SI 0.58-0.61. N=4.

All four specimens from a nontype nest series, Cerro Pico Blanco, near San José, Costa Rica. Mandible with 4 teeth. Clypeal margin convex. Antennal flagellomeres 2-11 subequal in length and width; not twisted. Lateral habitus shown in Fig. 69. Mayrian and parapsidal sutures present. Forewing venation as in Fig. 30 hind wing as in Fig. 37. Genitalia shown in Fig. 70. Mandibles smooth; clypeus nearly so. Head dorsum areolate; sides behind eyes rugose; posterior head rugose-areolate. Mesosoma longitudinally rugose on lateral pronotum and dorsal meso- and metapleura. Anterior and ventral mesopleura smooth. Ventral metapleura diagonally rugose. Anterior portion of mesonotum with vague effaced microsculpture; longitudinally rugose macrosculpture begins at level of wing and continues onto mesoscutellum. Propodeum areolate. Petiole microareolate, with a few weak, fine longitudinal rugae. Postpetiole and gaster smooth. Abundant erect and decumbent pilosity on scapes, head, mesosoma, waist, and gaster. Head brown, except for yellowish-brown frontoclypeal area and yellow mandibles. Rest of body and appendages brownish-yellow; gaster T1 and S1 darker.

Discussion.—The nontype specimens from the high elevations of Costa Rica may belong to a distinct species defined by the complete absence of propodeal spines, but presently they seem linked to the types by the two specimens from Panama, which have intermediate spine length.

The different palpal formula of the workers and queens and the fact that workers and queens specimens come from different countries cause doubt about whether the queens are correctly assigned. But most morphological characters fit *leptonana* better than any other species. See also the *curvipubens* discussion.

The range *innotabilis* (Figs. 55-57, 97-98) overlaps that of *leptonana* at least in southern Mexico and Nicaragua, perhaps more, if queens are correctly assigned. Workers of *innotabilis* differ as follows: 1) no erect hair on scapes, 2) generally larger (WL 0.66-0.73mm), 3) clypeus evenly convex, 4) palpal formula 2,2, 6) postpetiolar node widest midlength and sternum moderately to strongly prominent.

See also *creightoni*, *curvipubens*, *alzatei*, *inermis*, and *neilyensis* discussions.

The name from *leptos* (G., slender) and *nanus* (L., dwarf) describes the habitus of this species.

Distribution.—Specimens range from Chiapas, Mexico to the northern coast of Colombia; from sea level to 1750m. Type specimens come from lowland rain forest, Colombian specimens from forest receiving about 2m strongly seasonal annual precipitation. Montane specimens from Costa Rica were taken under large rocks in a pasture; those from Panama were collected in debris under a stump in unknown habitat.

Material Examined.—Holotype and paratype locality. PANAMA: Canal Zone, Barro Colorado Island; 2 workers including holotype, II-III-1943, #5059 (J. Zetek) [USNM, lot 43 3035]; 5 workers, VI-X-1943, #5105 (J. Zetek) [1 whole specimen slide mounted] [USNM, lot 43-16534]; 4 workers, 14-II-1976 (A. Newton) [MCZ]; 1 worker, 27-II-1976 (A. Newton) [MCZ]; 1 worker, I-1960, #B-9 (W. L. Brown & E. S. McCluskey) [mouthparts, sting] [MCZ]; 2 workers, 7-III-1975, FP#6 (C. Toft & S. Levings) [LACM].

Nontype localities. MEXICO: 1 worker, Chiapas, Ocosingo Valley, Finca El Real, 1-7-VII-1950 (Goodnight & Stannard). COSTA RICA: 6 workers, 4 males, Cerro Pico Blanco, near San José, 1750m, 15-III-1987 (W. Eberhard & W. L. Brown) [2 male genitalia] [MCZ]. PANAMA: 2 workers, Chiriquí Province, near Nueva California, W of Finca Palo Santo, 1550m, 5-III-1959, #B-377 (H. S. Dybas) [MCZ]. COLOMBIA: 1 queen, Guajira, near Don Diego, Quebrada Guacoche, 10m, 22-VII-1976 (W. L. Brown & C. Kugler) [queen mouth-

parts, sting] [MCZ]; 1 queen, Magdalena Department, Parque Nacional Tayrona, near Pueblito, 210m, 11-XI-1976 (C. Kugler) [MCZ]. DOMINICAN REPUBLIC: 3 workers 16km ENE Pedernales, 800m, 9-IX-1992 (P. S. Ward); 1 worker 4km NNW Villa Altagracia, 200m, 12-IX-1992 (P. S. Ward) [MCZ].

Rogeria belti Mann

Figs. 35-39, 91-92

Rogeria belti Mann 1922:31. Syntype workers, HONDURAS: Progreso (Mann) [USNM] [2 of 12 syntypes examined].

Diagnosis.—WL 0.61-0.94mm. Clypeal apron usually with median notch, sometimes convex. Eyes large, oval. Propodeal spines moderately long, inclined (bisecting line usually passes well below anteroventral corner of pronotum). Promesonotal dorsum usually strongly areolate; postpetiolar node smooth. Scapes with erect hair. Hair on mesosoma dorsum decumbent to erect; not clearly sorting into two kinds. Head dorsum and gaster T1 with short decumbent and long erect/suberect hair. No erect hair on extensor surfaces of tibiae.

Workers.—TL 2.4-3.4, HL 0.56-0.80, HW 0.48-0.69, SL 0.39-0.55, EL 0.10-0.14 (20-36 facets), PW 0.34-0.51, WL 0.61-0.94, SpL 0.11-0.20, PetL 0.25-0.39, PpetL 0.13-0.21mm, CI 0.82-0.89, OI 0.18-0.25, SI 0.76-0.89, PSI 0.14-0.24. N=31

Mandibles with 5-6 teeth; typically 5 teeth evenly decreasing in size basad followed by a large basal tooth, or 4 teeth are followed by 1 or 2 denticles and a large basal tooth (Fig. 35). A few specimens in scattered localities have an additional denticle between the third and fourth teeth. Palpal formula 3,2. Clypeal apron medially emarginate in most, but evenly convex in specimens from Miami, Costa Rica. Body of clypeus not projecting over clypeal apron. Posterior outline of head weakly convex, sometimes with a slight median concavity. Eyes sometimes narrower than shown in Fig. 35; widest in Miami, Costa Rica specimens (Fig. 36). Pronotum from the side usually subangular at junction of anterior and dorsal faces; from above, shoulders well rounded. Metanotal groove either hardly visible, or a distinct narrow groove, or a small step in mesosoma profile; usually marked behind by a transverse ridge (Fig. 35). Propodeal spiracles small, slightly more than 1 diameter from posterior edge of propodeum, facing slightly caudad. Metapleural lobes nar-

rowly to broadly rounded. Petiolar keel not lamellate. Petiolar node usually dome-shaped (Fig. 35), but sometimes slightly flattened on top. Postpetiolar node highest in posterior half; dorsal view subtrapezoidal as in Fig. 49; sternum long and flat. Sting apparatus as in *creightoni*-group diagnosis.

Longitudinal rugae on frontal lobes become rugose-areolate by midlength of head; middle pair of rugae usually remain free of cross-ridges until posterior head. Cheeks and laterodorsa areolate to rugose-areolate. Sides of head strongly areolate in most, but nearly smooth in Miami, Costa Rica specimens. Posterior head areolate with no clear transverse pattern in most, but transversely arching rugose to rugose-areolate in ants from Miami, Costa Rica and Colombia. Promesonotum generally coarsely areolate to areolate-rugose (Figs. 91-92), but lower in relief and more rugose in specimens from Miami, Costa Rica and some from Colombia. Meso- and metapleura confused areolate to rugose. Dorsal face of propodeum predominantly transversely rugose, except for Boquete, Panama specimens, in which dorsal face is indistinctly areolate. Petiolar node not as heavily sculptured as mesosoma, but distinctly areolate to weakly rugose-areolate; dorsal and anterior faces often free of macrosculpture. Intervals irregular and usually shiny. Microsculpture generally weak and indistinct, producing quite shiny intervals in macrosculpture, especially on sides of head, mesosoma, and on petiolar node. Head dorsum and petiolar node of Miami, Costa Rica specimens with more pronounced microsculpture, lending a granular appearance.

Most dark reddish-brown with yellowish-brown mandibles, antennae and legs. Specimens from Boquete, Panama and Miami, Costa Rica lighter, with more yellowish appendages and end of gaster. Mexican specimens reddish-black with brown appendages.

Queens.—TL 3.0-3.4, HL 0.68-0.74, HW 0.58-0.64, SL 0.48-0.52, EL 0.18-0.20, PW 0.48-0.59, WL 0.88-1.00, SpL 0.13-0.21, PetL 0.29-0.37, PpetL 0.18-0.20mm, CI 0.84-0.85, SI 0.77-0.86, PSI 0.14-0.21. N=5

Like the worker except for normal queen structures and the presence of predominantly rugose sculpture on the mesonotum. Parapsidal furrows indistinguishable from furrows in sculpture. Habitus similar to that of *merenbergiana* queen

(Fig. 48), but mesonotum slightly more convex and propodeal spines longer and narrower. Wings as in male (Fig. 37).

Males.—TL 3.4-3.5, HL 0.59-0.61, HW 0.65-0.70, SL 0.32-0.35, EL 0.32, PW 0.71-0.72, WL 1.12-1.19, PetL 0.40-0.41, PpetL 0.19-0.20mm, CI 1.11-1.15, SI 0.50. N=2

All five specimens from La Ceiba, Honduras. Mandibles with 5 teeth. Clypeus weakly emarginate. Flagellomeres 2-11 straight, subequal in length and width. Wings, habitus and genitalia as shown in Figs. 37-39. Rs vein curves away from leading edge of wing; r-m vein lost; M vein short. Mandibles smooth except for piligerous punctures. Face very finely areolate, opaque. Posterior head longitudinally rugose. Pronotum weakly punctate. Mesonotum and posterior face of propodeum finely rugulose and densely punctured. Mesopleura longitudinally striate right under wing, otherwise smooth and shiny with piligerous punctures. Metapleura and sides of propodeum longitudinally rugose. Posterior face of propodeum rugose-areolate. Petiolar node finely punctate to smooth. Postpetiole and gaster smooth and shiny. Hair as in worker, but more dense. Color brownish-black, with brown legs and antennae and brownish-yellow mandibles.

Discussion.—The 18 specimens from Miami, Costa Rica (Fig. 36) differ from typical *belti* in having: 1) an evenly convex clypeus, 2) a larger eye (31-36 facets vs. 20-30 in typical *belti*), 3) smaller propodeal spines (PSI 0.15-0.18 vs. 0.19-0.24 in typical *belti*), 4) generally narrower head, 5) head and mesosoma more rugose than areolate, and 6) weaker macrosculpture in general, but microsculpture stronger on head and petiolar node. Queens from Miami, Costa Rica like their workers have narrower heads, shorter propodeal spines and weaker sculpture than the four from Guatemala, Panama and the Osa Peninsula of Costa Rica. I considered these Miami ants a new species until the arrival of new specimens from Costa Rica and Colombia. One worker from Heredia, Costa Rica has a convex clypeus like the Miami ants, but eye and propodeal spine size just within the typical *belti* range. Other workers from Colombia have eyes as large as any of the Miami specimens, but an emarginate clypeus like typical *belti*, and they have intermediate sculpture. While it is still possible that the Miami population represents a different species, I am not confident of that at present.

Some *alzatei* (Figs. 58-60, 99) specimens strongly resemble specimens of *belti* from Costa Rica in size, habitus, spine length, and sculpture, but *alzatei*: 1) is smaller (WL 0.52-0.65mm), 2) has a truncate clypeal apron in Central America, 3) has smaller eyes (11-14 facets), and 4) lacks erect hair on the scapes.

The geographic ranges of *creightoni* (Figs. 51-54, 95-96) and *belti* overlap in much of Central America and some members look quite similar in size, sculpture, and pilosity. Workers of *creightoni* can be distinguished by: 1) generally smaller, elliptical eyes with longer propodeal spines (< 19 facets; EL/SpL 0.29-0.64 vs. 0.62-1.23 in *belti*), 2) more horizontal propodeal spines, 3) promesonotal dorsum rugose to rugose-areolate, and 4) hair on mesosoma dorsum clearly sorting into two distinct kinds.

See discussions of *inermis*, *tonduzi*, *merenbergiana*, and *exsulans* for comparisons with other similar species.

Distribution.—*Rogeria belti* is so far known from southern Mexico to the Canal Zone and southwest Colombia. Elevations range from 200m to 1500m in Mexico and 50m to 950m in Panama. Labels with ecological data show them collected in rain forest "in Philodendron," "frond sheaths on ground," leaf litter, around an epiphyte mat on a fallen branch, rotten wood, and in dead trees or branches on the ground. Jack Longino found a colony "nesting under loose bark of a still solid log fallen across trail." On another rotten log he lured workers from under the bark to a freshly killed tabanid (Longino, unpublished field notes).

Material Examined.—MEXICO: Vera Cruz State, Los Tuxtlas (P. S. Ward); Chiapas State, El Bosque (A. Newton). GUATEMALA: Bobas (W. M. Mann). BELIZE [=British Honduras]: Caves Branch (S. and J. Peck). HONDURAS: Progreso [or El Progreso] (W. M. Mann), Lancetilla and La Ceiba (W. L. Brown) [mouthparts, sting; 2 male genitalia]. EL SALVADOR: between Apopa and Nejapa (W. L. Brown). COSTA RICA: Miami (unknown collector) [mouthparts, sting] [USNM]; Heredia Province, (J. Longino); Santa Clara [=Limón?] Province, Hamburg Farm and Parismina Br. (F. Nevermann); Puntarenas Province, Manuel Antonio National Park and Reserva Biológica Carara (P. S. Ward), Osa Peninsula, Corcovado National Park (J. Longino; P. S. Ward). PANAMA: Chiriquí Mountains, Boquete (F. M.

Gaige); Cerro Campana (A. Newton); El Valle (H. S. Dybas); Canal Zone, Barro Colorado Island (J. Zetek; A. Newton). COLOMBIA: Nariño Department, La Guayacana (P. Silverstone) [LACM]. 117 workers, 15 queens, 5 males [CUIC, JTLC, LACM, MCZ, MZSP, USNM].

Rogeria inermis Mann

Figs. 40-42

Rogeria inermis Mann 1922:32, Fig. 15. Syntype workers, HONDURAS: Progreso, Lombardia (Mann) [MCZ] [3 of 5 syntypes examined].

Diagnosis.—WL 0.60-0.85mm. Clypeal apron medially emarginate. Eye oval, moderately large. Nuchal grooves weakly visible in lateral view. Propodeal spines short to absent. Propodeal spiracles rather large, prominent, face somewhat caudad, usually < 1/2 diameter from edge of infradental lamella. Promesonotal dorsum rugose to areolate-rugose; pronotal sides rugose, shiny. Scapes with erect hair. Head dorsum with erect hairs and shorter, decumbent pilosity. Hair on mesosoma and gaster T1 subdecumbent to erect; not two distinct kinds. Pilosity on gaster rather sparse. Extensor surfaces of tibiae with decumbent to suberect hairs.

Workers.— TL 2.2-3.0, HL 0.55-0.71, HW 0.48-0.63, SL 0.38-0.50, EL 0.09-0.13 (15-28 facets), PW 0.34-0.47, WL 0.60-0.85, SpL 0.03(no spines)-0.10, PetL 0.25-0.37, PpetL 0.14-0.20mm, CI 0.82-0.91, OI 0.18-0.22, SI 0.73-0.88, PSI 0.04(no spines)-0.14. N=15

Mandibles with 5 or 6 teeth, usually five decreasing in size basad then a large basal tooth. Palpal formula 3,2. Median clypeal apron weakly to strongly emarginate. Posterior outline of head convex. Metanotal groove weak to absent. Anterior edge of propodeum sometimes marked by a transverse ridge. Propodeal spines usually short and acute (Fig. 40), but may also be quite long (Fig. 41), blunt, or absent. Petiole (Fig. 40) with a distinct, rounded node; peduncle slender, venter with strong tooth, but little or no keel. Postpetiolar node highest in posterior half; shape in dorsal view subtrapezoidal as in Fig. 49. Anterior lip of postpetiolar sternum square, not protruding. Pygidium as in *creightoni*-group diagnosis.

Sting apparatus as in Fig. 42. Spiracular plates with incomplete medial connection; spiracle not enlarged. Anterodorsal corner of quadrate plate

prominent, with medial and lateral lobes. Oblong plate anterior apodeme long, slender; ventral arm tall, with with long, slender fulcral arm. Gonostylus with dorsoterminal and companion setae; no gap between these and other sensilla. Lancets strong, acute, with a single minute apical barb. Sting shaft slender, straight; apex strong, acute, with low dorsal flange. Valve chamber and sting bulb large, subequal in height and length. Sting base much lower than bulb height, with weak anterolateral processes. Furcula an inverted Y-shape. See Kugler (1978b) for a more complete description.

Microsculpture on head and mesosoma reduced to vague irregularities in otherwise smooth and shiny interrugal spaces. Middorsum of head longitudinally rugose with lateral spurs, grading to areolate-rugose on laterodorsa and sides. Sculpture below and behind the eye sometimes vestigial, leaving a shiny area. Posterior head in most specimens transversely arching rugose (with lateral spurs) to areolate-rugose, but longitudinally rugose in two workers from the Osa Peninsula of Costa Rica. Rugae on mesosoma are sharp, with broad interrugal spaces that are even smoother and shinier than on the head. Anterior pronotum with 1-3 transverse rugae; disc with longitudinal rugae; meso- and metanotum vermiculate-rugose or areolate-rugose. Pronotal sides, mesopleura, and metapleura predominantly rugose; intervals very shiny. Dorsal face of propodeum transversely rugose to areolate. Sides of petiolar node weakly rugose to rugose-areolate, producing an uneven, shiny surface; apex smooth. Postpetiolar node largely smooth and shining with only slight unevenness of surface on sides.

Color varies from a reddish-brown (almost black) body with yellowish brown appendages to a yellowish-brown body with darker gaster and brownish-yellow appendages.

Queens.—TL 2.9-3.0, HL 0.62-0.64, HW 0.55-0.57, SL 0.41-0.45, EL 0.15-0.16, PW 0.47-0.48, WL 0.81-0.84, SpL 0.09, PetL 0.32-0.36, PpetL 0.18-0.19mm, CI 0.89, SI 0.74-0.79, PSI 0.11. N=3

Mandibles with 6 teeth, or 5 teeth and 2 denticles. Parapsidal furrows not discernible. Sculpture on posterior head of Panamanian specimens transversely rugose-areolate; more longitudinally oriented in Costa Rican specimens. Pronotum transversely rugose-areolate. Mesonotal sculpture predominantly rugose, with some closed cells. Dorsal face of propodeum transversely rugose.

Petiolar node with weak macrosulpture, postpetiole smooth.

Discussion.—The two specimens from the Osa Peninsula of Costa Rica differ from the other specimens in having noticeably longer propodeal spines and longitudinal, rather than transverse sculpture on the back of the head. These may be members of a sibling species, but spine length is quite variable in *inermis* (e.g. PSI 0.04-0.09 in one Berlese sample). Thus, I hesitate to name a new species until more specimens show consistent differences.

Rogeria leptonana (Figs. 66-70) from Cerro Pico Blanco, Costa Rica and Nueva California, Panama have reduced or absent propodeal spines, but differ from *inermis* in: 1) generally smaller size (WL 0.57-0.66mm; only 1 of 49 *inermis* workers with WL < 0.67mm), 2) smaller eye (6-8 facets; OI 0.11-0.12), and 3) mesosoma and gaster T1 dorsa with 2 distinct types of pilosity. *Rogeria belti* (Figs. 35-39, 91-92), often collected with *inermis*, has longer propodeal spines and more areolate head and pronotal sculpture. See also the *neilyensis* discussion.

Distribution.—All specimens are from Guatemala to Panama, at elevations from 10m to 1250m. Some were collected in fruit bat guano; others, in Berlese samples from rain forest leaf litter.

Material Examined.—GUATEMALA: Alta Verapaz Department, Lanquín (S. and J. Peck). HONDURAS: Progreso [or El Progreso]; Lombardia (W. M. Mann). COSTARICA: (A. Bierig; F. Nevermann); Heredia Province, Puerto Viejo, La Selva Field Station (C. Kugler; Talbot & VanDevender) [2stings]; Limón Province, Cahuita (P. S. Ward); Puntarenas Province, Osa Peninsula (S. Peck), Manuel Antonio National Park (P. S. Ward), Carara Biological Reserve (P. S. Ward); Cartago Province, Turrialba vicinity (A. Bierig) (W. L. Brown) [mouthparts, sting]. PANAMA: Bocas del Toro, 3 localities (D. M. Olson); Barro Colorado Island (W. L. Brown and E. S. McCluskey [mouthparts, whole specimen]; N. A. Weber; J. Zetek); Gamboa (P. S. Ward); Panama City (W. L. Brown). 49 workers, 3 queens [CKC, CUIC, LACM, MCZ, MZSP, USNM].

Rogeria neilyensis new species

Fig. 43

Diagnosis.—WL 0.75-0.76mm. Clypeal apron convex, with weak median angle. Eye small.

Nuchal groove makes a deep notch in lateral view of head. Propodeal spines short, wide. Propodeal spiracles ≥ 1 diameter from edge of infradental lamella. Postpetiolar sternum not enlarged. Terminal segments of gaster rotated ventrad. Sides of head with distinct areolate-rugose to rugose macrosculpture; mesosoma predominantly rugose. Scapes and legs lack erect hairs. Head dorsum with short, dense, decumbent pilosity and longer, more sparse, erect-suberect hairs. Mesosoma hairs range continuously from short, decumbent to long, erect (i.e. not sorting into two distinct kinds as on head.). Hair on gaster T1 dense, subdecumbent-suberect (decumbent hairs few or absent).

Holotype and Paratype Workers.— TL 2.8-2.9 (2.8), HL 0.66-0.68 (0.67), HW 0.58-0.60 (0.59), SL 0.45, EL 0.06-0.07 (0.06) (9-13 facets), PW 0.42-0.43 (0.42), WL 0.75-0.76 (0.75), SpL 0.08-0.10 (0.08), PetL 0.30-0.34 (0.30), PpetL 0.18-0.19 (0.18)mm, CI 0.88-0.89 (0.88), OI 0.10-0.12 (0.10), SI 0.76-0.77 (0.76), PSI 0.11-0.13 (0.11), MHI 0.96-1.00 (0.96). N=2

Mandible 6-toothed; basal tooth larger than penultimate tooth. On left mandible, fifth tooth replaced by 2 denticles. Body of clypeus slightly prominent. Frontal lobes rather wide (FLW/HW 0.43-0.44). Anteroventral corner of pronotum projecting tooth-like. No distinct metanotal groove. Propodeal spiracles moderately large, weakly bulging from sides. Metapleural lobes low, broadly rounded. Petiolar peduncle with large ventral keel and tooth. Postpetiolar node lacking a distinct posterior face; subtrapezoidal from above, as in Fig. 50.

Longitudinal rugae on frontal lobes become areolate-rugose half way to back of head. Posterior head transversely areolate-rugose. Laterodorsa areolate-rugose. Intervals in macrosculpture of head shiny, but wrinkled by vague, irregular microsculpture. Anterior edge of pronotal disc areolate; rest of promesonotal dorsum longitudinally rugose-areolate; more rugose mesad, more areolate laterad. Dorsal face of propodeum transversely rugose. Intervals on mesosoma generally wider and smoother than on head. Petiolar node vaguely areolate; posterior face and peduncle with longitudinal carinae. Surface of postpetiolar node uneven, but predominantly smooth and shiny. Gaster T1 and S1 smooth and shiny, but other segments progressively dulled caudad by dense microareolate sculpture.

Color yellowish-brown, with slightly more yellowish appendages and anterior of head; first tergum of gaster dark brown.

Discussion.—This species is similar in size and reduced petiolar spines to another Central American species, *inermis* (Figs. 40-42), which differs as follows: 1) clypeal apron medially emarginate, 2) nuchal groove weak, 3) eyes larger (OI 0.18-0.22; 15-28 facets), 4) propodeal spiracle ≤ 1 diameter from edge of propodeum, 5) scapes with erect hair, and 6) mesosoma and gaster T1 with little, if any, decumbent hair.

The *leptonana* (Figs. 66-70) specimens from Cerro Pico Blanco, Costa Rica, have low, wide propodeal spines like *neilyensis*, but *leptonana* has: 1) an emarginate clypeus, 2) weak nuchal grooves, 3) lower lower mesosoma profile (MHI 0.84-0.90), and 4) scapes with erect hair.

The name *neilyensis* refers to the type locality.

Material examined.—**Holotype locality.** COSTA RICA: Puntarenas Province, 3km N Ciudad Neily [=Villa Neily], 8.41N 82.57W, 210m, 31-VII-1985, #7771-5 (P. S. Ward). From sifted litter (leaf mold and rotten wood) in second-growth rain forest [MCZ].

Paratype locality. 2 workers, holotype locality [LACM, MCZ].

Rogeria exsulans Wilson and Taylor

Fig. 44

Rogeria exsulans Wilson and Taylor 1967:74, Fig. 60. Holotype worker, SAMOA: Upolu (T. E. Woodward) [Holotype MCZ; paratypes ANIC, MCZ] [Holotype and 30 paratypes examined].

Diagnosis.—WL 0.68-0.84mm. Eye fairly large, oval. Propodeal spiracle faces posterolaterally. Petiole with lamellate keel and dentate inferior process. Terminal segments of gaster rotated ventrad. Sides of head areolate-rugose; posterior head and promesonotum strongly areolate. Scapes with decumbent and a few short, suberect hairs. No erect hair on extensor surfaces of legs. Mostly abundant decumbent to subdecumbent hair on dorsa of head, mesosoma, nodes and gaster T1 (sparse erect hair on head and mesosoma); not sorting into two distinct kinds of pilosity.

Workers.— TL 2.5-3.0, HL 0.62-0.71, HW 0.52-0.64, EL 0.08-0.11 (20-26 facets), PW 0.37-0.45, WL 0.68-0.84, SpL 0.10-0.15, PetL 0.26-0.33, PpetL 0.15-0.17mm, CI 0.84-0.90, OI 0.19-0.21, SI 0.81-0.85, PSI

0.14-0.19. N=4

Some mandibles with 6 teeth (5 decreasing in size then a large basal), but usually the small penultimate basal tooth is replaced by 2 denticles, or by a gap and 1 denticle. Palpal formula 3,2. Clypeal apron medially emarginate. Back of head in dorsal view convex or flat medially; temples broadly rounded (Wilson and Taylor's Fig. 60). Promesonotal profile may be evenly rounded, but more often angular (Fig. 44). Metanotal groove usually distinct, producing a step between promesonotum and propodeum, but weak in two specimens. Propodeal spiracles more than one diameter from nearest edge of infradental lamella. Node short, evenly convex. Postpetiolar sternum relatively long, flat; postpetiole from above subtrapezoidal, as in Fig. 51. Sting apparatus as in *creightoni*-group diagnosis.

Longitudinal rugae of frontal lobes and median head gradually change to strongly areolate on posterior head. Cheeks and laterodorsa longitudinally areolate-rugose. Intervals on head dorsum vaguely undulate, but shiny; intervals on sides and posterior head smooth and shiny. Promesonotum for the most part strongly areolate, but several elongate cells may occupy the midline of the pronotal disc, and often the pronotal sides have weaker areolate sculpture. Meso- and metapleura confused areolate-rugose. Mesosoma microsculpture reduced; intervals in macrosculpture uneven, but very shiny. Petiolar node with weak to vestigial areolate macrosculpture and vague microareolate background. Postpetiolar node shiny, nearly smooth throughout.

Head, mesosoma dark reddish-brown, waist and anterior and posterior ends of gaster somewhat lighter. Mandibles, clypeus, antennae, and legs yellowish-brown.

Discussion.—The only other Pacific species, *stigmatica* and *megastigmatica* are easily distinguished from *exsulans* by their lack of a petiolar keel and inferior process, as well as other features listed in the diagnoses.

The species most similar to *exsulans* is Central American. *Rogeria belti* has some members with similar size, habitus, eye size, clypeus shape, a distinct petiolar keel, strong areolate sculpture, and intergrading types of hairs on mesosoma. However, *belti* workers still differ in having generally longer propodeal spines (PSI 0.19-0.24), less prominent petiolar keel, and distinct long/erect

and short/decumbent pilosities on the gaster.

Distribution.—*Rogeria exsulans* has been collected only at 600-700m on a single island in the middle of the South Pacific. Most collections specify a rain forest habitat, where it has been found under dead bark, in rotten logs, in moss and ferns on trees and in berlesate of moss on logs and tree trunks.

Material Examined.—WESTERN SAMOA: Upolu, Afiamalu (T. E. Woodward; R. W. Taylor; E. C. Zimmerman) [2 mouthparts, stings]. 31 workers [MCZ].

Rogeria cornuta new species

Fig. 45

Diagnosis.—WL 0.93-1.02mm. Eye relatively small. Nuchal groove makes strong notch in lateral view of head. Propodeal spines very long (EL/SpL < 0.50); not inclined dorsad; distal portions subparallel with midline. Propodeal spiracles prominent, less than 1/2 diameter from edge of infradental lamella. Metapleural lobes prominent. Petiole with little or no keel. Sides and posterior head strongly areolate; mesosoma predominantly rugose. Erect hair on scapes. Gaster T1 lacks decumbent hair.

Holotype and Paratype Workers.— TL (3.5)-3.8, HL (0.80)-0.89, HW (0.73)-0.78, SL (0.55)-0.58, EL 0.10 (16-18 facets), PW (0.55)-0.60, WL (0.93)-1.02, SpL (0.25)-0.27, PetL (0.42)-0.45, PpetL (0.21)-0.24mm, CI 0.88-(0.92), OI 0.13-(0.14), SI 0.74-(0.75), PSI 0.26-(0.27), MHI (0.98)-1.02.

Mandible with 6 teeth; basal larger than penultimate basal. Clypeal apron medially emarginate; body of clypeus projecting slightly over apron. Posterior outline of head broadly and weakly concave. Sides of pronotum with anterior grooves for insertion of corners of head; shoulders from above angular. No meso- or metanotal grooves. Paratype promesonotal dorsum less convex and more angular in front and back than shown for holotype (Fig. 45). Propodeal directed caudad so that a bisecting line would extend just below shoulder; distal half of spines curve inward, almost paralleling the midline. Postpetiolar node somewhat flattened on top; subtrapezoidal in dorsal view. Postpetiolar node of paratype lower in front than behind. Postpetiolar sternum long, not projecting anteriorly.

Head macrosculpture coarse (especially be-

hind), with sharp ridges and shiny interstices. Longitudinal rugae on front breakup at midlength of head and give way to a transversely arching areolate-rugose pattern on the posterior head. Laterodorsa confused rugose-areolate. Mesosoma macrosculpture also coarse with smooth interstices, but ridges are rounded. Anterior face of pronotum transversely rugose-areolate, pronotal disc longitudinally rugose to vermiculate-rugose (holotype). Mesonotum vermiculate-rugose with some cross-ridges. Pronotal sides areolate-rugose (holotype) or broken and confused; rest of sides confusedly longitudinally rugose with few connecting ridges. Anterior edge of propodeum marked by a sharp transverse ridge. Petiolar node weakly areolate on sides and posterior; smooth along anterior and dorsal midline. Postpetiolar node weakly areolate on sides; smooth along midline.

Scapes, head dorsum and tibiae with short decumbent and long erect-suberect hair. Hair on mesosoma and waist ranges from decumbent to erect and varies in length, but not clearly segregated into two distinct types. Hair on gaster erect-suberect.

Color dark reddish-brown, with lighter frontoclypeal area and ends of gaster; legs and antennae yellowish-brown.

Discussion.—Some *creightoni*, also from Belize, have the same habitus as *cornuta*, including long, horizontal propodeal spines, but these *creightoni* members are much smaller (WL 0.63-0.71mm) and have abundant decumbent pilosity on the gaster T1. Other *creightoni* from La Selva, Costa Rica are the same size as the *cornuta* holotype, but have shorter propodeal spines, slightly smaller eyes, and abundant decumbent pilosity on the gaster T1.

The name *cornuta* means horned, referring to the long, horn-like propodeal spines.

Material Examined.—**Holotype locality.** BELIZE (British Honduras): 2.5 mi. S Belmopan, 4-VIII-1972, S. and J. Peck, #242 [MZSP].

Paratype locality. 1 worker, MEXICO: Chiapas State, Ocosingo, 2-VI-1967, J. M. Campbell [MCZ].

Curvipubens-Group and Related Species

Rogeria curvipubens Emery

Figs. 74-76, 101-102

Rogeria curvipubens Emery 1894:190. Worker and queen syntypes, U. S. VIRGIN ISLANDS: St. Thomas (Eggers) [MCSN] [Worker syntype examined].

Additions to *curvipubens*-group diagnosis. Postpetiolar node strongly vaulted and with small posterior peduncle. Anterior edge of postpetiolar sternum not strongly produced; junction of posterior and ventral edges angular (Fig. 75). Sting shaft and lancets weak, spatulate. Sides of head smooth and shiny. Promesonotum with vestigial microsculpture, making interrugal spaces nearly smooth and weakly to strongly shiny. Dorsal face of propodeum usually with 1-5 transverse rugulae.

Workers.— TL 1.9-2.3, HL 0.48-0.58, HW 0.38-0.49, SL 0.32-0.39, EL 0.04-0.07 (4-11 facets), PW 0.28-0.38, WL 0.50-0.63, SpL 0.05-0.11, PetL 0.20-0.24, PpetL 0.10-0.13mm, CI 0.80-0.86, OI 0.10-0.15, SI 0.77-0.81, PSI 0.13-0.18, MHI 0.84-1.05. N=22

Mandibles typically with 6 teeth, but occasionally with an additional denticle or tooth; basal tooth little if any larger than penultimate basal. Haitian specimens with 5 teeth. Anterior edge of clypeus evenly convex or with median concavity (Haiti). Body of clypeus, though not especially prominent, is generally the anteriormost point of the head in full dorsal view; little or no shelf-like apron. Posterior outline of head generally broadly convex, but sometimes with a weak median concavity (Fig. 74). Nuchal groove weak. Eye small, elliptical. Pronotum weakly angular or rounded in front and on sides. Metanotal groove absent or suggested by a broad, very shallow impression. Anterior propodeum marked by transverse carinula that often does not interrupt mesosoma profile. Propodeal spines short, wide, with curved (Fig. 74) or straight edges; a bisecting line passes below the anteroventral corner of pronotum. Metapleural lobes low, subangular to rounded. Sting apparatus like that of *inermis* (Fig. 42) in most respects, but lancets and sting shaft are weak and the lancets are blunt and spatulate. Though twisted in all preparations, the sting shaft does seem to have a dorsoterminal flange.

Posterior head transversely arching rugose to rugose-areolate, intervals shiny (Fig. 101). Most of

head with vague microsculpture. Anterior edge of pronotal disc areolate to rugose-areolate; disc longitudinally rugose (Fig. 102), sometimes effaced on meso- and metanota. Pronotal sides with one or more weak longitudinal rugae; meso- and metapleura confused rugose to rugose-areolate. Petiole and postpetiole microareolate and devoid of macrosculpture, except for small carinulae on petiolar peduncle of some specimens. Microsculpture weaker on apices of nodes, especially postpetiolar node, which is shiny and nearly smooth.

Head with 0-6 short suberect hairs; mesosoma dorsum with 2-7 pairs. Extent of erect pilosity on gaster T1 variable; usually covering whole surface, but may cover as little as the posterior third.

Color uniformly yellow, to golden or light brown body with lighter appendages, frontoclypeal region and ventral gaster.

Queens.—TL 2.3-2.6, HL 0.51-0.59, HW 0.44-0.51, SL 0.34-0.39, EL 0.09-0.12, PW 0.38-0.45, WL 0.63-0.71, SpL 0.11-0.14, PetL 0.22-0.27, PpetL 0.12-0.15mm, CI 0.83-0.90, SI 0.73-0.78, PSI 0.16-0.19, MHI 0.96-1.17. N=6

Queens (Fig. 76) vary like workers in shapes of head, propodeal spines, petiole and postpetiole. Mandibles have 6 teeth in most; plus 2 denticles in the Guatemalan specimen. Parapsidal furrows weak or indistinguishable. Wing venation as in *belti* (Fig. 37). Sting apparatus of a queen from the north coast of Colombia like that of workers from the region, including spatulate lancets. Sculpture, pilosity, and color also vary similarly. Sides of head may be partly rugose, but some portion smooth. Pro-, meso-, and metanota rugose. Meso- and metapleura longitudinally rugose dorsad; anterior half of mesokatepisterna very smooth and shiny. Microsculpture as in workers. Numbers of erect hairs on various parts range as in workers, except for one queen with 10 pairs on mesosoma dorsum.

Queens from Mexico and Guatemala are not associated with workers. Moreover, the Guatemalan specimen lacks a postpetiole and gaster. Both have the side of the head rather strongly rugose-areolate, but I am guessing that they are *curvipubens*, rather than *cuneola* on the basis of the strongly shiny mesokatepisterna and shape of the postpetiolar sternum of the Mexican specimen.

Discussion.—Workers come from the Caribbean Islands and northern South America. How-

ever, if the two queens from Mexico and Guatemala are in fact *curvipubens*, the range of *curvipubens* broadly overlaps that of sister species *cuneola*. The two species are distinguished by characters in the *cuneola* diagnosis and description.

Rogeria alzatei (Figs. 58-60, 99) and *leptonana* (Figs. 66-70) are very similar to *curvipubens* and *cuneola* and have been considered *curvipubens* in the past, but I believe they can be distinguished, usually by general habitus, but especially by more abundant erect pilosity than described in the *curvipubens*-group diagnosis. Moreover, side-by-side comparisons of sympatric specimens from the Villavicencio vicinity of Colombia and from Barro Colorado Island reveal more differences: the *alzatei* specimens have a truncate clypeal apron, narrower propodeal spines, and generally stronger sculpture. The *leptonana* specimens have an emarginate clypeal apron, lower mesosoma, and larger petiolar keel. The only question of identity arises on the north coast of Colombia, where a single specimen has wider propodeal spines and convex clypeus like *curvipubens*, which are common in the area, but has the abundant pilosity and stronger macrosculpture of *alzatei*. I call that specimen *alzatei*, since spine and clypeal shapes vary in that species.

Assigning stray queens has also been problematic. In two localities on the north coast of Colombia (Pueblito, Tayrona Park; Don Diego, Guajira) I collected three distinct kinds of queens. One set has a distinctly lower mesosoma (MHI 0.92-0.97) and larger petiolar keel than the other two and has abundant erect pilosity on scapes, whole head, mesosoma, waist, and gaster. These and other characters suggest those are *leptonana* queens. The other two kinds of queens have a more compact mesosoma (MHI 1.05-1.22), but one set has no erect hair on scapes, head, waist, or first tergum of gaster, little or no erect hair on the mesosoma dorsum, more effaced sculpture with nearly smooth sides of head and transversely arching rugae on posterior head, and spatulate lancets, just like the *curvipubens* workers that are common in both areas. The third set of queens have distinct macrosculpture, distinctly areolate sides and posterior head, short erect hair on the whole head dorsum and more abundant erect/suberect hair on mesosoma, waist and gaster and acute lancets. I have tentatively assigned them to *innotabilis* because of their evenly convex clypeus and

posteroventral spine on the spiracular plate of the sting apparatus.

See also *micromma*, and *tribrocca* discussions.

Distribution.—*Rogeria curvipubens* has been collected in by Berlese sampling in tropical rain forest, secondary growth forest, and dry tropical forest. Collection sites have all been below 500m elevation.

Material Examined.—VIRGIN ISLANDS: St. Thomas (Eggers; Balzan); St. Croix (I. Proj. staff). HAITI: Aquin (no collector). JAMAICA: St. Elizabeth Parish, Black River (no collector). MEXICO: Vera Cruz, Cuatutlan (M. Abarca). GUATEMALA: Alta Verapaz, Trece Aguas (Schwarz and Barber). PANAMA: Barro Colorado Island (N. A. Weber; W. L. Brown). COLOMBIA: Guajira, Serrania de Macuira and vicinity Río Don Diego (W. L. Brown and C. Kugler) [1 mouthparts, 2 stings, 1 whole specimen slide mounted]; Magdalena Department, Tigrera near Santa Marta (W. L. Brown and C. Kugler), Tayrona National Park (C. Kugler) [worker and queen mouthparts, sting]; Meta Department, Caño El Buque near Villavicencio (Kugler). VENEZUELA: Bolivar State, Campamento Río Grande (P. S. Ward); Monagas State, Parque de Laguna Grande (P. F. Kukuk). SURINAM: Tambahredjo [queen sting], Sidoredjo [sting], Dirkshoop, and La Poulle (I. van der Drift). 57 workers, 13 queens [BMNH, CKC, CUIC, LACM, MCZ, MZSP, USNM].

***Rogeria cuneola* new species**

Figs. 77-78, 103

Additions to *curvipubens*-group diagnosis. Postpetiolar node weakly vaulted and with no posterior peduncle. Anterior edge of sternum strongly produced; posterior and ventral edges merge insensibly (Fig. 78). Sting shaft and lancets strong, acute; sting shaft with dorsal flange; lancet with barbule. Sides of head and mesosoma with strong microareolate sculpture that obscures weak macrosculpture and makes intervals opaque. Dorsal face of propodeum without transverse rugulae.

Holotype and Paratype Workers.— TL 2.0-2.1 (2.0), HL 0.50-0.54 (0.51), HW 0.43-0.46 (0.43), SL 0.32-0.35 (0.33), EL 0.05-0.06 (0.05) (6-7 facets), PW 0.31-0.33 (0.31), WL 0.51-0.56 (0.52), SpL 0.07-0.09 (0.08), PetL 0.20-0.22 (0.20), PpetL 0.10-0.12 (0.11)mm, CI 0.84-0.87 (0.84), OI 0.10-0.13 (0.13), SI 0.73-0.78 (0.77), PSI 0.15-0.17, MHI 0.94-1.02 (1.02). N=7

Nontype Workers.—TL 2.0-2.3, HL 0.50-0.56, HW 0.43-0.48, SL 0.31-0.36, EL 0.04-0.06 (5-10 facets), PW 0.30-0.37, WL 0.52-0.60, SpL 0.07-0.10, PetL 0.21-0.24, PpetL 0.11-0.13mm, CI 0.83-0.86, OI 0.10-0.13, SI 0.72-0.78, PSI 0.14-0.17, MHI 0.93-1.03. N=9

Like *curvipubens*, but differing in the following ways in addition to diagnosis. Relative widths of nodes with slightly different ranges (PetW/PetL 0.56-0.70); PpetW/PpetL 1.38-1.52). Sting apparatus of specimens from Oaxaca (paratypes) and Vera Cruz, Mexico with strong, acute sting shaft and lancets as in *inermis* (Fig. 42).

Posterior head with transversely arching rugose-areolate macrosculpture. Compared to *curvipubens*, rugae on mesosoma dorsum with more lateral spurs that may connect rugae and create areolae on anterior pronotum and on metanotum. Macrosculpture on mesosoma sides absent or weakly rugose-areolate. Dorsal face of propodeum lacks macrosculpture.

Head dorsum with 0-16 hairs suberect hairs; mesosoma dorsum with 1-8 pairs (usually 2-7). Erect hair on gaster T1 usually limited to posterior margin, but entirely absent from Jalisco specimen and entirely covering the tergum of the Yucatán specimen. The Yucatán specimen is also unique in having some stiff, spatulate hairs on head, mesosoma and gaster.

Paratype and Nontype Queens.—TL 2.3-2.5, HL 0.53-0.56, HW 0.45-0.50, SL 0.35-0.38, EL 0.10-0.11, PW 0.39-0.45, WL 0.65-0.72, SpL 0.11-0.14, PetL 0.22-0.25, PpetL 0.13-0.15mm, CI 0.85-0.89, SI 0.76-0.78, PSI 0.16-0.19. N=2

Queen as in *curvipubens*, except for shape of postpetiole, sting, and sculpture as in workers of *cuneola*. Mandibles with 6 or 7 teeth. Sides of head and mesokatepisterna strongly microareolate and opaque. Paratype queen with erect-suberect hair over whole gaster T1.

Discussion.—See *micromma* and *minima* discussions for comparisons with other tiny *Rogeria*. The name *cuneola* (L., small wedge) refers to the shape of the postpetiolar sternum in lateral view.

Distribution.—These tiny ants are most often taken in berlesate of leaf litter and rotten wood. Some come from siftings under termite mounds and one was collected in a *Cattelya* orchid. Habitat of most specimens is rain forest or mesic forest, either primary or secondary growth, but one specimen was found in Yucatán thorn forest.

Material Examined.—**Holotype locality.** MEXICO: Oaxaca State, 1 mi. E Reforma, 15-VIII-1973, litter, tropical evergreen forest (A. Newton) [MCZ].

Paratype localities. MEXICO: 14 workers, holotype locality [BMNH, CKC, LACM, MCZ, MZSP, USMN]; 1 worker, 1 queen, Oaxaca State, 1 mi. E Reforma, near Tuxtepec, 12-15-VIII-1973, litter forest floor (A. Newton) [3 stings, 1 worker coated for SEM] [MCZ].

Nontype localities. MEXICO: 1 worker, San Luis Potosí State, El Salto, 6-VII-1969, #B-166 (S. and J. Peck) [MCZ]; 2 workers, Vera Cruz State, Pueblo Nuevo near Tetzonapa, 17-VIII-1953, #B.F. (E. O. Wilson) [MCZ]; 2 workers, Vera Cruz State, El Palmar near Tetzonapa, 8-VIII-1953, #173 (E. O. Wilson) [sting, whole specimen] [MCZ]; 1 worker, Jalisco State, 6km N El Tuito, 31-XII-1987, #9327-6 (P. S. Ward) [MCZ]; 7 workers, 1 queen, Chiapas State, Palenque, 4-IX-1974 (E. M. and J. L. Fisher) [LACM]; 1 worker, Yucatán State, Uxmal, 27-VII-1963, #118 (E. O. Wilson) [MCZ]. BELIZE: 4 workers, Belmopan, 1-15-VIII-1972, #B-243 (S. and J. Peck). GUATEMALA: 1 worker, 14-15-V-1946[?], SF-21214, 46-6134 (no locality or collector) [USNM]. HONDURAS: 2 workers, La Lima, 4-IX-1961, UCF 217-128 (C. Evers Q.) [MZSP]. COSTA RICA: 1 worker, Guanacaste Province, Santa Rosa National Park, 14-VII-1983 (P. S. Ward) [CKC]; 3 workers, Puntarenas Province, Manuel Antonio National Park, 27-VII-1985, #7692-9 (P. S. Ward) [MCZ].

Rogeria micromma Kempf

Fig. 71

Rogeria micromma Kempf 1961:509 (Figs. 12-13). Holotype worker, SURINAM: Dirkshoop (J. van der Drift) [MZSP] [Holotype and La Poulle paratype examined].

Diagnosis.—WL 0.45-0.52mm. Clypeal apron medially flattened. Eye tiny. Postpetiolar node subrectangular in dorsal view and not strongly vaulted in side view; anterior lip of sternum not prominent, posterior edge angular in side view. Sides of head and mesosoma and dorsal face of propodeum opaque with dense microareolate sculpture. Laterodorsa and sides of head also finely macroareolate. Propodeum free of macrosculpture. No erect hair on scapes or extensor surfaces of legs. Dorsa of head, mesosoma, nodes and gaster T1 with short, appressed hairs and longer, erect to suberect hairs. Mesosoma dorsum with 8-10 pairs

of erect hair; each node with 2 pairs of posterodorsally projecting hairs.

Workers.—TL 1.7-1.8, HL 0.44-0.51, HW 0.37-0.45, SL 0.28-0.35, EL 0.02-0.04 (2-5 facets), PW 0.28-0.30, WL 0.45-0.52, SpL 0.07-0.08, PetL 0.17-0.18, PetW 0.10-0.13, PpetL 0.10-0.11, PpetW 0.13-0.15mm, CI 0.84-0.88, OI 0.05-0.08, SI 0.76-0.79, PSI 0.15-0.16, MHI 0.92-0.96. N=3

The following supplements diagnosis and Kempf (1961). Mandibles 5-toothed to 6-toothed; basal tooth not larger than penultimate basal. Mesosoma profile of holotype interrupted by a weak metanotal groove followed by two transverse carinulae, but profiles of La Poulle and Brazil specimens uninterrupted. Brazil specimen with narrower propodeal spines than in types, and propodeal spiracle closer to posterior edge of propodeum. Petiole short (PetL//WL 0.35-0.38), with ventral keel and tooth.

In Surinam specimens, vague microareolate microsculpture densely covers head, dorsum of mesosoma, dorsal face of propodeum, petiole and postpetiole of types, producing a weakly shining, granular appearance. Brazil specimen similar, except for smoother ventral petiolar peduncle and postpetiolar dorsum. Sides of mesosoma and posterior surface of head more distinctly microareolate. Anterior of pronotal disc with 1 to 2 transverse rugae followed by longitudinally rugose to areolate-rugose macrosculpture that disappears into microsculpture on meso- and metanota. Sides of mesosoma with sparse, faint longitudinal rugulae on meso- and metapleura. Nodes microareolate; more effaced on postpetiole.

Erect hairs of Dirkshoop specimen all trichoid; but thicker and stiff on the La Poulle specimen, at least some cuneate; erect hairs on the Belém specimen seem intermediate.

Color brownish-yellow; legs, mandibles and antennae sometimes slightly lighter. Frontoclypeal region not lighter than rest of head.

Discussion.—It may be that the three *micromma* specimens are just unusual *curvipubens* or *cuneola*, but at present there are enough differences to provisionally retain this species. Eighteen *curvipubens* (Figs. 74-76, 101-102) workers from other van der Drift collections in Dirkshoop and La Poulle, are very similar to *micromma* in size and shape, but differ as follows: 1) clypeal apron evenly convex, 2) sides of head and mesosoma shinier with effaced microsculpture, 3) sides of head with

rugose macrosculpture, and 4) reduced pilosity.

Some *cuneola* (Figs. 77-78, 103) specimens are also very similar to *micromma* in shape and size, and one from Yucatán has stiff erect hairs on head, mesosoma, waist and gaster T1, but *cuneola* workers differ in shape of the postpetiolar sternum, as well as in clypeal shape and pilosity.

Some *alzatei* from Panama, Colombia, Guyana, and French Guiana are only slightly larger (WL 0.51-0.68mm) than *micromma* and have the same pilosity and similar structure and sculpture, but they generally have distinctly larger eyes with more than 10 facets, have a higher, more compact mesosoma (MHI 1.00-1.04), and generally narrower propodeal spines. Several *alzatei* from northern Colombia have reduced eyes (7-8 facets) and one has wider propodeal spines, but those Colombian ants are larger, have a higher mesosoma, and more abundant erect pilosity. See also the *minima* discussion.

Material Examined.—SURINAM: Dirkshoop (J. van der Drift), La Poulle (J. van der Drift). BRAZIL: Pará, Pirelli Plantation (Iriboca) nr. Belém, (W. L. Brown). 3 workers [MCZ, MZSP].

***Rogeria minima* Kusnezov**
Figs. 72-73

Rogeria minima Kusnezov 1958:44, Figs. 1-3. Holotype dealate queen, ARGENTINA: Tucumán [FML] [Holotype examined].

Known only from a single queen mounted on a microscope slide showing dorsal head (nearly split in half lengthwise), ventral maxillae and labium, lateral mesosoma and petiole, and a mostly ventral view of postpetiole and gaster.

Diagnosis.—WL of worker probably <0.60mm. Mandibles triangular. Palpal formula 2,1. Sting shaft and lancets spatulate. Postpetiole widest in anterior half; anterior lip of sternum not prominent. Mesosoma predominantly rugose. No microsculpture on head dorsum, little on mesosoma sides; but microareolate sculpture present on gaster T1 and S1. No erect hairs on scapes or extensor surfaces of legs. Head dorsum with abundant erect hair; mesosoma dorsum with more than 12 pairs; petiolar node with 2 pair projecting posterodorsally. Most erect hairs cuneate-fimbriate.

Queen.—TL 2.3, HL 0.55, HW 0.53, SL 0.34, EL 0.10, WL 0.65, SpL 0.12, PetL 0.22, PpetL 0.11mm, CI 0.96, SI 0.64, PSI 0.18.

Mandibles with 5 teeth; basal only slightly larger than penultimate basal. Palpal formula 2,1. Clypeus torn; shape of apron unclear. Eyes moderately large, with about 20 facets. Mesosoma as shown in Fig. 72. Parapsidal furrows cannot be discerned. Petiole with ventral tooth and nonlamellate keel. Postpetiole wider (0.18mm) than long; sides of postpetiole seem to be convex in front, then tapered, as in many *curvipubens* (Fig. 74); sternum seems low and not prominent or wedge-shaped. Pygidial gland sculpture present, no tubercles on posterior surface. What is visible of the sting apparatus looks like that of *inermis* (Fig. 42), except that lancet apices lack barbules and sting shaft seems to have little, if any, terminal flange. Since both sting shaft and lancets are folded, they are probably weakly sclerotized.

Median head with diverging rugae continuing on posterior head as diverging rugose-areolate sculpture; laterodorsa areolate-rugose. No macrosculpture on median pronotum; sides weakly and incompletely areolate, especially ventrad. Mesonotum longitudinally rugose. Dorsal half of mesopleura longitudinally rugose; most of mesokatepisterna smooth, but with some weak areolate sculpture along posterior margins. Metapleural and propodeal sides confused areolate-rugose. Mesosoma lacks microsculpture, except on median pronotum, sides of propodeal spines, and metapleural lobes (metanotum and median propodeum could not be examined). All surfaces of petiole, at least venter and sides of postpetiole, and at least sterna of gaster minutely and shallowly areolate with sharp, thin partitions. Much of dorsal aspect of gaster difficult to see, but at least anterior and lateral portions of T1, and the terminal terga are also shallowly microareolate.

Body covered with appressed to decumbent setiform pilosity. In addition, dorsa of head, mesosoma nodes, and gaster T1 and S1 with erect cuneate-fimbriate hairs (Fig. 73). Mesosoma dorsum with more than 12 pairs of erect hairs; petiolar node with 2 pairs of posterodorsally projecting erect hairs (postpetiolar hairs hidden). All hair on terminal segments of gaster are setiform.

Discussion.—A worker of *micromma* from La Poulle, Surinam and a worker of *cuneola* from Uxmal, Yucatán come very close in size, sculpture, and in having cuneate pilosity, but the gasters of both are smooth except for piligerous punctures. I cannot tell if any hairs are fimbriate.

Foreli-Group***Rogeria foreli* Emery**

Figs. 79-82, 104-105

Rogeria foreli Emery 1894:191. Holotype worker, VIRGIN ISLANDS: St. Thomas (Eggers) [MHN] [Holotype examined].

Rogeria foreli gaigei Forel 1914:617. Holotype worker, COLOMBIA (Gaige) [MHN] [Holotype examined]. N. syn.

Rogeria huachucana Snelling 1973:4, Fig. 1. Holotype and paratype worker, USA: Arizona, Cochise County (Snelling) [LACM] [Holotype and 1 paratype examined]. N. syn.

Additions to *foreli*-group diagnosis. Basal mandibular teeth abruptly smaller than apical teeth. Clypeal apron convex, often with a faint median angle. Eyes usually 10 or more facets.

Workers.—TL 1.9-2.9, HL 0.50-0.71, HW 0.43-0.62, SL 0.32-0.51, EL 0.06-0.10 (7-20 facets), PW 0.30-0.45, WL 0.50-0.80, SpL 0.07-0.15, PetL 0.20-0.32, PpetL 0.12-0.19mm, CI 0.83-0.89, SI 0.74-0.85, OI 0.12-0.17, PSI 0.14-0.20. N=25

Mandibles with 4-7 teeth and 0-3 denticles. Generally teeth 1-4 decrease in size gradually, then teeth 5-7 (if present) abruptly smaller and possibly interspersed with one or more denticles. Sometimes basal tooth is distinctly larger than penultimate tooth. Body of clypeus often projecting slightly over the anterior clypeal margin. Posterior outline of head flat to weakly convex. Eyes small, oval. Nuchal grooves inconspicuous in lateral view. Pronotal shoulders well rounded. Metanotal groove generally absent (Fig. 79), but may be weakly to distinctly (Fig. 80) visible. Anterior border of propodeum not marked by a ridge. Metapleural lobes small, broadly rounded. Petiolar node shape varies between extremes shown in Figs. 79 and 81; smaller nodes are as long as wide, larger nodes are longer than wide. Postpetiolar node peaks in posterior half; subrectangular in dorsal view. Anterior lip of postpetiolar sternum small (Fig. 79), or prominent (Figs. 81, 104).

Mandibles, median clypeus, legs, posterior face of propodeum, gaster, and sometimes sides of petiolar peduncle smooth, except for minute piligerous punctures. Rest of body densely microareolate or microcolliculate, often appearing granular at low magnification. Microareolate sculpture on head is more distinct near antennal insertions and more effaced caudad, sometimes

nearly smooth on sides of head. Microareolate pattern distinct on meso- and metapleura and generally on dorsal face of propodeum; indistinct on promesonotum and petiole and vestigial on postpetiole (Figs. 104-105). Microsculpture overlain by very fine longitudinal rugulae on lateral clypeus, cheeks, frontal lobes, middorsum and sometimes laterodorsa; posterior head with very fine transverse or diverging rugulae.

Color yellow with a slightly brownish gaster to chestnut-brown with brownish-yellow or light brown appendages.

Queens.—TL 2.4-3.1, HL 0.54-0.69, HW 0.48-0.59, SL 0.36-0.49, EL 0.10-0.16, PW 0.38-0.51, WL 0.64-0.87, SpL 0.12-0.17, PetL 0.24-0.32, PpetL 0.13-0.20mm, CI 0.86-0.93, SI 0.72-0.83, PSI 0.17-0.20. N=8

Differing from the workers in the normal queen attributes and in the following. One specimen with 3 teeth and 5 denticles; the others with the same variation as in the workers. Posterior outline of head with weak median concavity in some. Parapsidal furrows are barely discernable. Mesoscutum in all specimens longitudinally rugulose; mesoscutellum vaguely rugose to areolate-rugose.

Discussion.—Side by side comparison of the types of *foreli* and *gaigei* revealed that the only difference between them is size; but the *gaigei* type is well within the size variation of *foreli* specimens. Although the types of *huachucana* come from Arizona, far from other known *foreli* specimens, and were collected in an unusual habitat, they differ from the *foreli* holotype only in having: 1) 7-8 facets in the eyes (vs. 12), and 2) a weak metanotal groove (vs. none). Since eye size and metanotal groove development vary continuously and not concordantly in *foreli* specimens from Central and South America, and since equally small eyes and even more distinct metanotal grooves are present in those specimens, I am unable to distinguish the *huachucana* specimens as a distinct species at this time.

While working in Northern Colombia for two years I regularly collected two kinds of *foreli*, which I could distinguish at a glance by the shapes of their postpetiolar sterna (Figs. 79, 81). Specimens from Barro Colorado Island, Panama, and Trinidad also have the same two types of sterna. In Colombia and Panama, both morphs have been taken from the same locality, but it is not known whether

the two morphs come from different colonies or not. I considered calling the specimens with a more prominent, shelf-like postpetiolar sternum a new species, but the difference is sometimes subtle and individuals difficult to assign. Without corroboration from another character, I decided against erecting a new species at this time.

Rogeria foreli is closely related to *bruchii*, which at present is known only from Argentina and Paraguay, much farther south than known *foreli* specimens (see the *bruchii* description).

Distribution.—*Rogeria foreli* has a disjunct distribution: Panama and northern South America, the Caribbean, and Southwestern United States. Specimens come from 0m to 610m in Panama, 0m to 240m in Colombia and Venezuela generally from berlesate of leaf mold and rotten wood. The Arizona specimens were under stones in an oak-juniper woodland at 1783-1814m.

Material Examined.—USA: Arizona, Cochise County (R. R. Snelling). PUERTORICO: Río Piedras (J. A. Torres). ST. CROIX: Buck Island. ST. THOMAS (Eggers). TRINIDAD: (N. A. Weber). PANAMA: Barro Colorado Island (W. L. Brown, W. L. Brown and E. S. McCluskey, A. Newton, N. A. Weber, J. Zetek); Gatún (W. L. Brown); Ancon (no collector) [sting]; Gamboa (P. S. Ward); Colón Province, Frijoles (J. Ventocilla); Cerro Azul (A. Newton). COLOMBIA: no locality (Gauge); Magdalena Department, Tayrona Park (C. Kugler, P. S. Ward) [mouthparts, sting]; Tigrera (W. L. Brown and C. Kugler) [queen mouthparts, whole specimen; worker mouthparts, sting]; Guajira, Don Diego (W. L. Brown and C. Kugler). VENEZUELA: Barinas State, near Ciudad Bolivia (P. Ward); Sucre State, 32km W. Campano (S. & J. Peck). 106 workers, 17 queens, 4 males [CKC, CUIC, LACM, MCZ, MCZ, MZSP, USNM].

***Rogeria bruchi* Santschi**
Fig. 82

Rogeria bruchi Santschi 1922:352. Holotype worker, ARGENTINA, Buenos Aires, Monte Veloz (C. Bruch) [NHM] [Holotype examined].

Workers.— TL 2.2-2.6, HL 0.56-0.65, HW 0.48-0.57, SL 0.38-0.46, EL 0.04-0.06 (5-7 facets), PW 0.35-0.40, WL 0.58-0.70, SpL 0.10-0.17, PetL 0.21-0.29, PpetL 0.13-0.17mm, CI 0.61-0.70, OI 0.10-0.12, SI 0.76-0.81, PSI 0.17-0.24. N=5

The five known specimens of *bruchii* are just

like the *foreli* with nonprojecting clypeus, weak or absent metanotal groove, and nonprojecting postpetiolar sternum, but differ in the following ways: 1) Mandible with five large teeth, second to fifth subequal (Fig. 82), 2) clypeus with a median notch, 3) eyes smaller than in most *foreli*.

Material Examined.—PARAGUAY: Misiones Province, 30km S. of San Juan Bautista (F. Baud et al.); Concepción Province, 50km E. of San Lazaro (F. Baud, et al.) [mouthparts, sting]. ARGENTINA: Buenos Aires Province, Monte Veloz (C. Bruch); Misiones Province, Posadas (A. Breyer). 5 workers [MCZ, MHN, MZSP, NHM].

ACKNOWLEDGEMENTS

I am very grateful to the following people for loans or gifts of specimens: Cesare Baroni Urbani (NMB), Claude Besuchet (MHN), Barry Bolton (BMNH), Carlos Roberto Brandão (MZSP), William L. Brown, Jr. (MCZ), John E. Lattke, Jack Longino, Alfred Newton (MCZ), David M. Olson, Roberto Poggi (MCSN), David Smith (USNM), Roy R. Snelling (LACM), Philip S. Ward, and E. O. Wilson (MCZ). Jack Longino also generously sent me his unpublished field collections notes.

Lily Fainter of the Virginia-Maryland Regional College of Veterinary Medicine and Bob Honeycutt of Virginia Polytechnic Institute and State University, Department of Forest Products assisted with the scanning electron microscopy. Reed R. Lambert helped collect ants in Peru and Bolivia. Richard L. Hoffman, W. L. Brown, Jr., André Francoeur, and R. W. Taylor provided valuable advice. Special thanks to Roy Snelling, who made many helpful criticisms of a draft. None of these bear any responsibility for the product.

The work was supported financially by NSF grant #DEB-8022177 and Radford University.

LITERATURE CITED

- Bolton, B. 1973. The ant genera of West Africa: A synonymic synopsis with keys (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History)*, *Entomology* 27(6):319-368.
- Bolton, B. 1982. Afrotropical species of the myrmecine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). *Bulletin of the British Museum (Natural History)*, *Entomology* 45(4):307-370.
- Bolton, B. 1987. A review of the *Solenopsis* genus-group and revision of afrotropical *Monomorium* Mayr (Hymenoptera: Formicidae). *Bulletin of the British Museum (Natural History)*, *Entomology* 54(3):263-452.
- Borgmeier, T. 1953 (1951). Algunas formigas do género *Macromischa* Roger. *Arquivos do Museu Nacional Rio de Janeiro* 42:107-112.
- Brown, W. L. 1952. Synonymous ant names. *Psyche* 58(3):124.
- Brown, W. L. 1953. Characters and synonymies among the

- genera of ants. Part II. *Breviora* no. 18:1-13.
- Brown, W. L. 1988. Data on malpighian tubule numbers in ants (Hymenoptera: Formicidae). Pp. 17-27 in: J. C. Trager (ed.) *Advances in myrmecology*. Leiden: E. J. Brill, xxvii+551 pp.
- Brown, W. L., and W. L. 1949. Wing venation and the phylogeny of the Formicidae. *Transactions of the American Entomological Society* 75(3-4):113-134.
- Emery, C. 1894. Studi sulle formiche della fauna neotropica. VI-XVI. *Bullettino della Società Entomologica Italiana* 26:137-242 + 4 pl.
- Emery, C. 1896. Studi sulle formiche della fauna neotropica. XVII-XXV. *Bullettino della Società Entomologica Italiana* 28:33-107.
- Emery, C. 1897. Formicidarum species novae vel minus cognitae in collectione musaei nationalis Hungarici quas in Nova-Guinea, colonia germanica, collegit L. Biró. *Természettudományi Közlemények* 20:571-599 + 2 pl.
- Emery, C. 1914. Les fourmis de la Nouvelle-Calédonie et des Îles Loyalty. P. 415 In: F. Sarasin and J. Roux (eds.) *Nova Caledonia recherches scientifiques en Nouvelle Calédonie et aux îles Loyalty (Zoologie)*. Wiesbaden: C. W. Kreidels Verlag, 1(4):389-436+13 pl.
- Emery, C. 1915. Noms de sous-genres et de genres proposés pour la sous-famille des Myrmicinae. Modifications à la classification de ce groupe (Hymenoptera Formicidae). *Bulletin de la Société Entomologique de France* 1915:189-192.
- Forel, A. 1899. Formicidae. *Biologia Centrali-Americana. Insecta. Hymenoptera* 3:1-160+4 pl.
- Forel, A. 1914. Einige amerikanische ameisen. *Deutsche Entomologische Zeitschrift* 1914:615-620.
- Harris, Rick A. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology, Department of Food and Agriculture, State of California* no. 28:1-31.
- Hölldobler, B. and H. Engel. 1978. Tergal and sternal glands in ants. *Psyche* 85(4):285-330.
- Hölldobler, B., R. Stanton, R., and Engel. 1976. A new exocrine gland in *Novomessor* (Hymenoptera: Formicidae) and its possible significance as a taxonomic character. *Psyche* 83(1):32-41.
- Hölldobler, B. and E. O. Wilson. 1990. *The Ants*. Cambridge, Massachusetts: Belknap Press, xii+732 pp.
- Kempf, W. W. 1961. A survey of the ants of the soil fauna in Surinam. *Studia Entomologica* 4(1-4):481-524.
- Kempf, W. W. 1962a (1961). Remarks on the ant genus *Irogera* Emery, with the description of a new species (Hymenoptera, Formicidae). *Revista Brasileira de Entomologia* 21(4):435-441.
- Kempf, W. W. 1962b. Miscellaneous Studies on Neotropical Ants. II. (Hymenoptera, Formicidae). *Studia Entomologica* 5(1-4):1-38.
- Kempf, W. W. 1963. Additions to the neotropical ant genus *Rogeria* Emery, with a key to the hitherto recorded South American species (Hym., Formicidae). *Revista Brasileira de Entomologia* 23(2):189-196.
- Kempf, W. W. 1964. Miscellaneous studies on neotropical ants. III. *Studia Entomologica* 7(1-4):45-71.
- Kempf, W. W. 1965. Nota preliminar sobre algumas formigas neotrópicas, descritas por Frederick Smith (Hymenoptera, Formicidae). *Revista Brasileira de Entomologia* 25(2):181-186.
- Kempf, W. W. 1972. Catálogo abreviado das formigas de região neotropical (Hym. Formicidae). *Studia Entomologica* 15(1-4):3-344.
- Kempf, W. W. 1975. Miscellaneous studies on neotropical ants. VI. (Hym. Formicidae). *Studia Entomologica* 18(1-4):341-380.
- Kugler, C. 1978a. Pygidial glands in the myrmicine ants (Hymenoptera, Formicidae). *Insectes Sociaux* 25(3):267-274.
- Kugler, C. 1978b. A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). *Studia Entomologica* 20:413-548.
- Kugler, C. 1980. The sting apparatus in the primitive ants *Nothomyrmecia* and *Myrmecia*. *Journal of the Australian Entomological Society* 19:263-267.
- Kugler, C. 1986. Stings of ants of the tribe Pheidologetini (Myrmicinae). *Insecta Mundi* 1(4):221-230.
- Kugler, C. 1992 (1991). Stings of ants of the tribe Ectatommini (Formicidae: Ponerinae). *Insecta Mundi* 5(3-4):153-166.
- Kusnezov, N. 1958. La posición sistemática del género *Rogeria*, con descripción de una nueva especie. *Acta Zoológica Lilloana* 15:41-45.
- Linnaeus, C. 1758. *Systema Naturae Regnum Animale* ed. 10, Tom 1. Stockholm, VI+824pp.
- Mann, W. M. 1919. The ants of the British Solomon Islands. *Bulletin of the Museum of Comparative Zoology, Harvard* 63(7):273-391 + 2 pl.
- Mann, W. M. 1921. The ants of the Fiji Islands. *Bulletin of the Museum of Comparative Zoology, Harvard* 64(5):401-499.
- Mann, W. M. 1922. Ants from Honduras and Guatemala. *Proceedings of the United States National Museum* 61(13):1-54.
- Mann, W. M. 1925. Ants collected by the University of Iowa Fiji-New Zealand expedition. *University of Iowa Studies in Natural History* 11(4):5-6.
- Mayr, G. L. 1886. Notizen ueber die Formiciden-Sammlung des British Museum in London. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 36:353-368.
- Roger, J. 1863. Die neu aufgefuehrten Gattungen und Arten meines Formicidenverzeichnisses, nebst Ergaenzungen einiger fruher gegebenenen Beschreibungen. *Berliner Entomologische Zeitschrift* 7:131-214.
- Santschi, F. 1922. Myrmicines, dolichodérines et autre formicides néotropiques. *Bulletin de la Société Vaudoise Sciences Naturelles* 54(205):345-378.
- Santschi, F. 1923. Description de quelques nouvelles fourmis du Brésil. *Revista (Museu Paulista, São Paulo, Brazil)* 13:1253-1264.
- Santschi, F. 1930. Quelques fourmis de Cuba et du Brésil. *Bulletin de la Société Royale de Botanique d'Égypte* Mai 1930(2-3):75-83.
- Santschi, F. 1936. Contribution à l'étude des fourmis de l'Amérique du Sud. *Revista de Entomologia, Rio de Janeiro* 6(2):196-218.
- Santschi, F. 1941. Quelques fourmis japonaises inédites. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 18:273-279.
- Smith, F. 1858. *Catalogue of the hymenopterous insects in the collection of the British Museum. Part VI. Formicidae*. London, 216 pp + 14 pl.
- Smith, M. 1937. The ants of Puerto Rico. *University of Puerto Rico, Journal of Agriculture* 20(4):819-875.
- Snelling, R. R. 1973. Two ant genera new to the United States. *Contributions in Science, Natural History Museum of Los Angeles County* no. 236:1-8.
- Snelling, R. R. 1989. Untitled comment. *Notes From Under-*

- ground: *A Myrmecological Newsletter*. MCZ Laboratories, Harvard, MA no. 3, pp. 7-8.
- Trager, J. C. 1989. A pitch for standardized orientation of the ant head, and related matters. *Notes from Underground: A Myrmecological Newsletter*. MCZ Laboratories, Harvard, MA. no. 1, pp. 5-7.
- Weber, N. A. 1934. Notes on neotropical ants, including the descriptions of new forms. *Revista de Entomologia, Rio de Janeiro* 4(1):22-59.
- Wheeler, G. C. 1989. Vive la myrmecologie. *Notes from Underground: a Myrmecological Newsletter*. MCZ Laboratories, Harvard, MA. no. 3, pp. 6-7.
- Wheeler, G. C. and J. Wheeler. 1953. The ant larvae of the myrmicine tribe Pheidolini. *Proceedings of the Entomological Society of Washington* 55(2):49-84
- Wheeler, G. C. and J. Wheeler. 1973. Ant larvae of four tribes: Second supplement (Hymenoptera: Formicidae: Myrmicinae). *Psyche* 80(1-2):70-82.
- Wheeler, G. C. and J. Wheeler. 1976. *Ant larvae: Review and synthesis*. (Memoires of the Entomological Society of Washington, no. 7). Washington: Entomological Society of Washington D.C. vi + 108 pp.
- Wheeler, G. C. and J. Wheeler. 1977. Supplementary studies on ant larvae: Myrmicinae. *Transactions of the American Entomological Society* 103:581-602.
- Wheeler, G. C. and J. Wheeler. 1986. Supplementary studies on ant larvae: Myrmicinae (Hymenoptera: Formicidae). *Journal of the New York Entomological Society* 94(4):489-499.
- Wheeler, G. C. and J. Wheeler. 1988. Notes on ant larvae: Myrmicinae. *Transactions of the American Entomological Society* 114:319-327.
- Wheeler, W. M. 1911. A list of the type species of the genera and subgenera of Formicidae. *Annals of the New York Academy of Sciences* 21:157-175.
- Wilson, E. O. 1955. A monographic revision of the ant genus *Lasius*. *Bulletin of the Museum of Comparative Zoology, Harvard* 113(1):1-201.
- Wilson, E. O. and R. W. Taylor. 1967. The ants of Polynesia (Hymenoptera: Formicidae). *Pacific Insects Monograph* 14:1-109

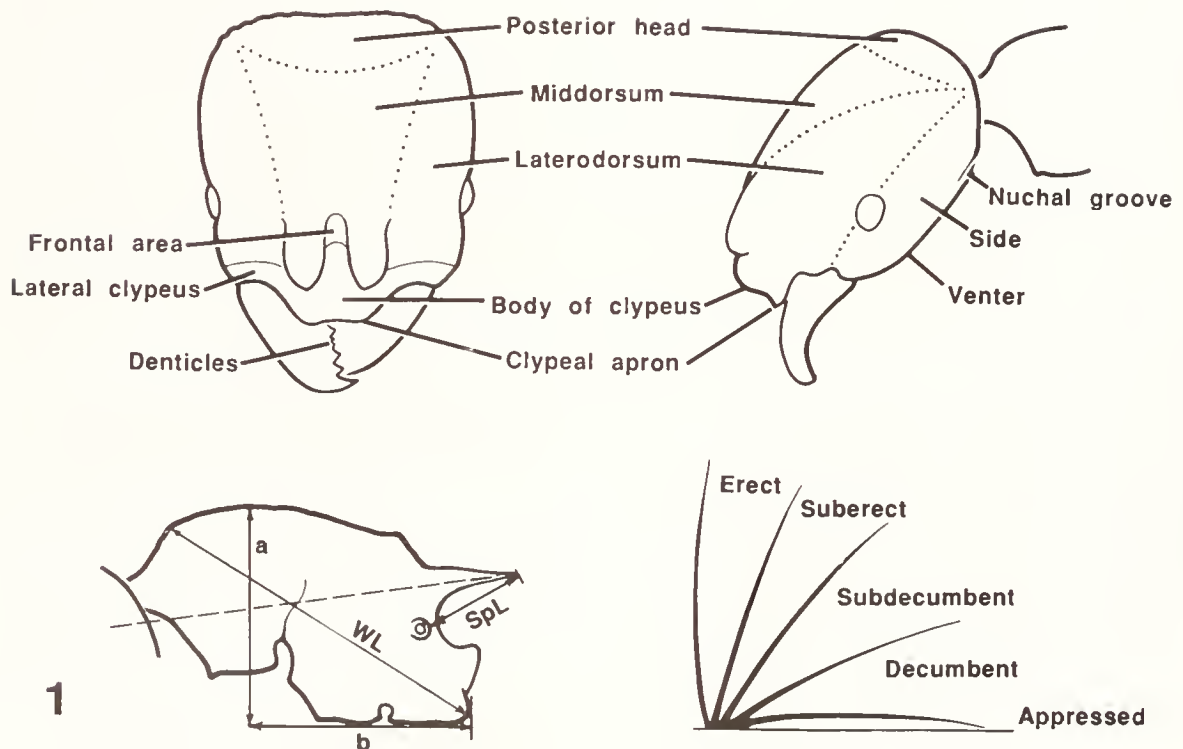
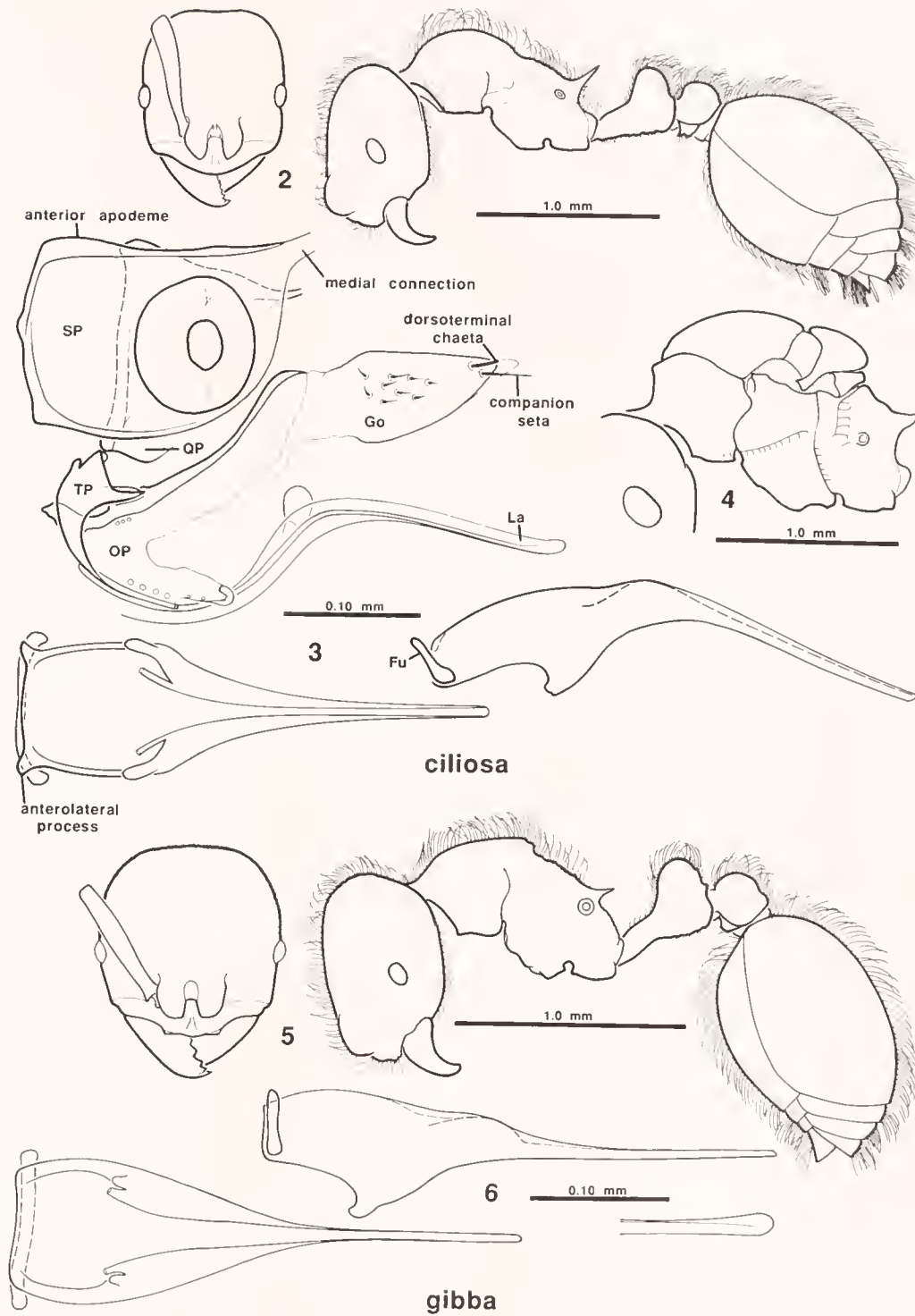
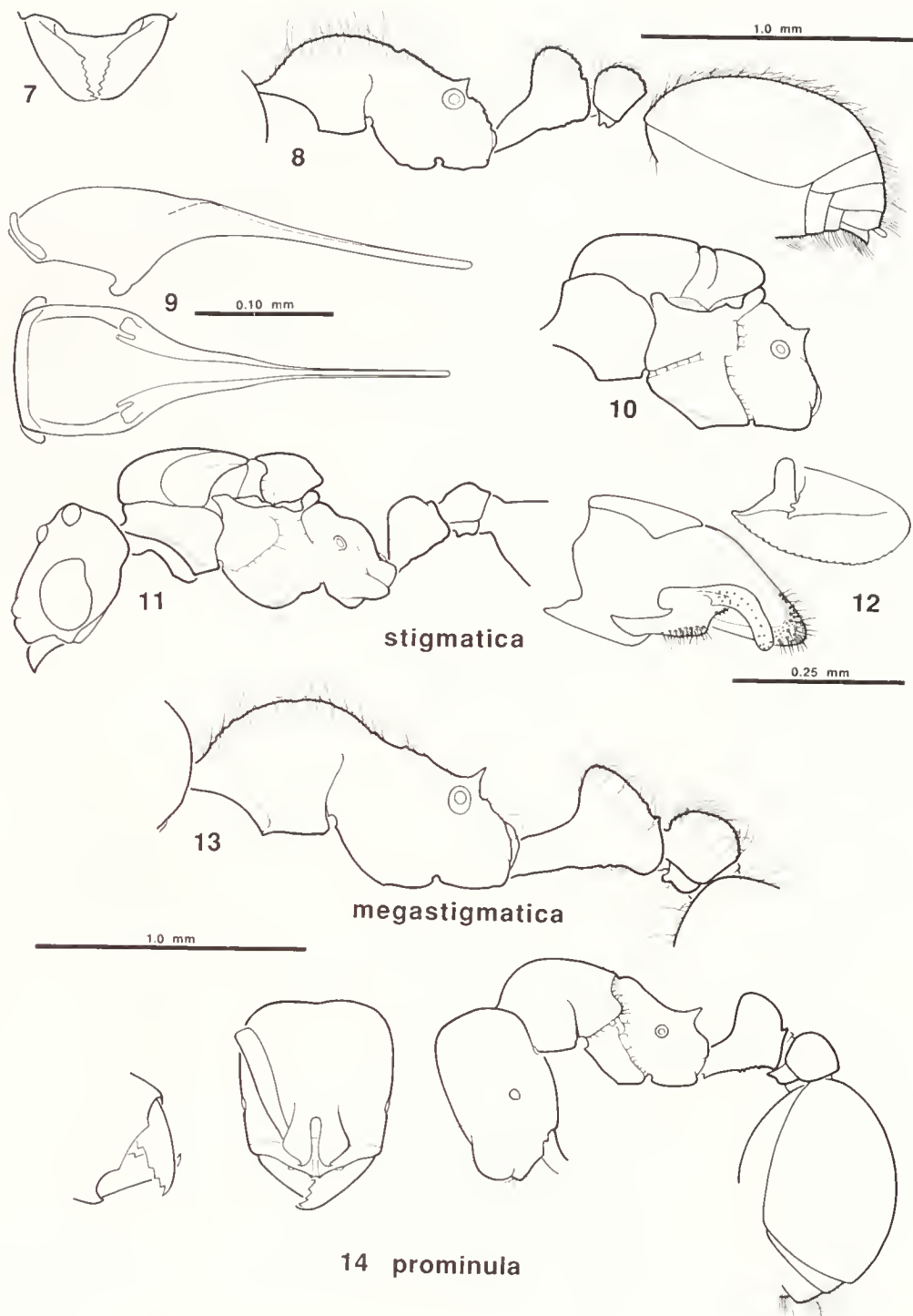


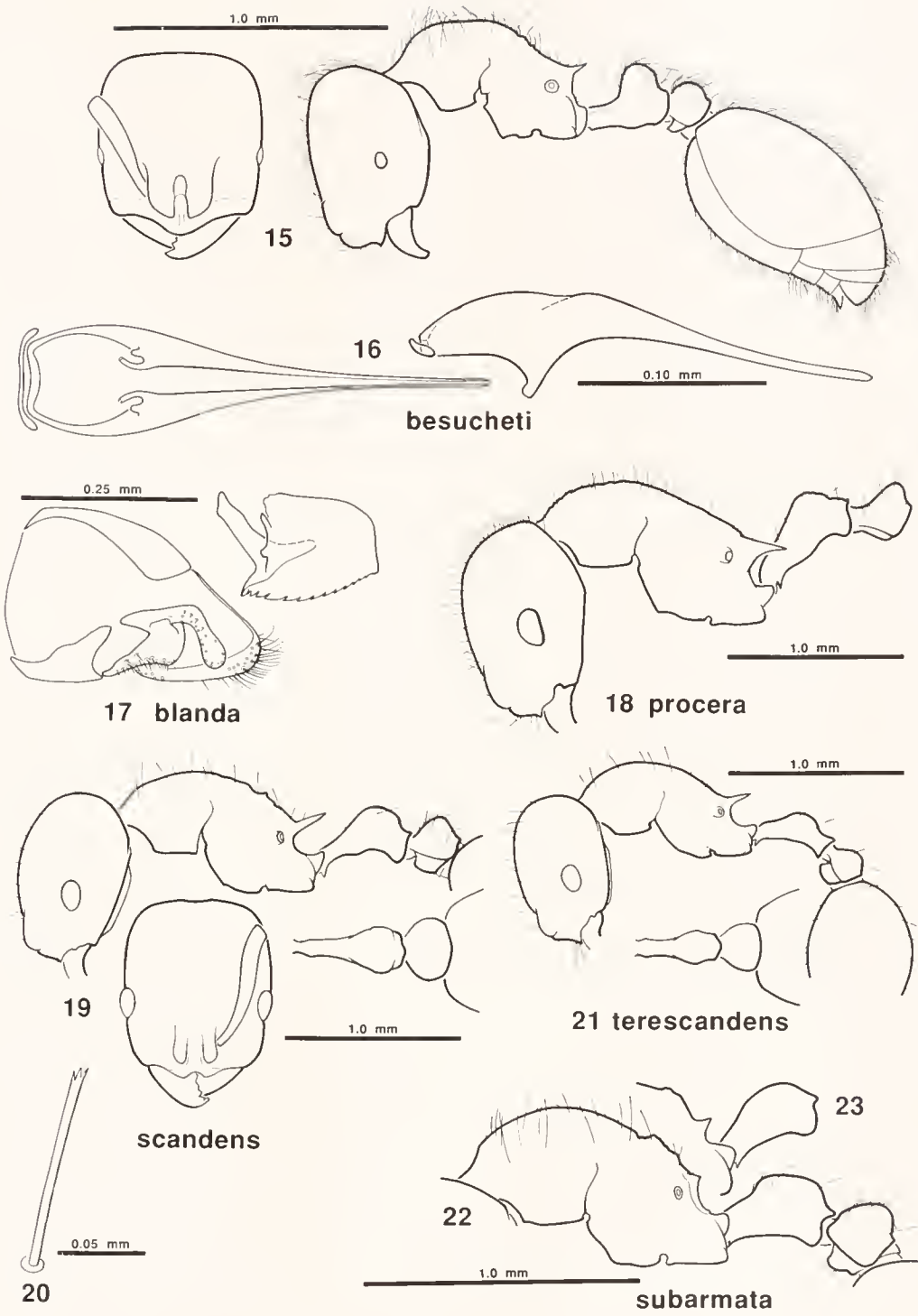
Fig. 1. Illustration of some terms and measurements used in descriptions. Dotted lines on the heads show approximate boundaries of the regions. The dashed line is an extension of a line bisecting the propodeal spines. Where it crosses the mesosoma outline gives a rough measure of spine inclination. SpL = spine length. WL = Weber's length. The mesosoma height index (MHI) is distance a (mesosoma height) divided by distance b.



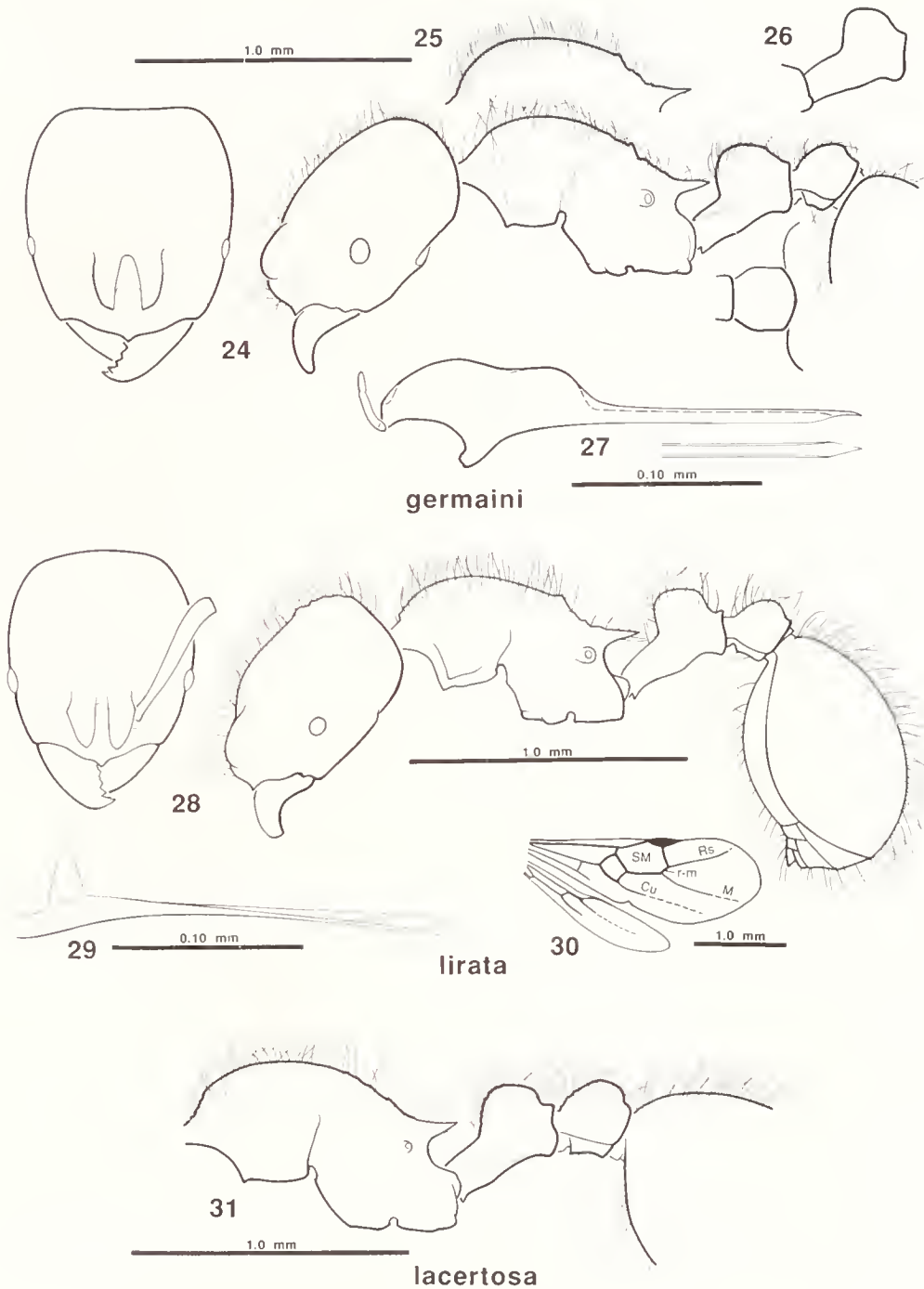
Figs. 2-6. Figs. 2-4. *Rogeria ciliosa*. 2. Holotype profile; dorsal head. 3. Paratype sting apparatus. Above: lateral views spiracular plate (SP), quadrate plate (QP), oblong plate (OP), gonostylus (Go), triangular plate (TP), and lancet (La). Below left: ventral sting, furcula. Below right: lateral sting, furcula (Fu). 4. Paratype queen lateral mesosoma. Figs. 5-6. *Rogeria gibba*. 5. Holotype profile; dorsal head. 6. Paratype sting with furcula in lateral and ventral views; lateral view of lancet apex.



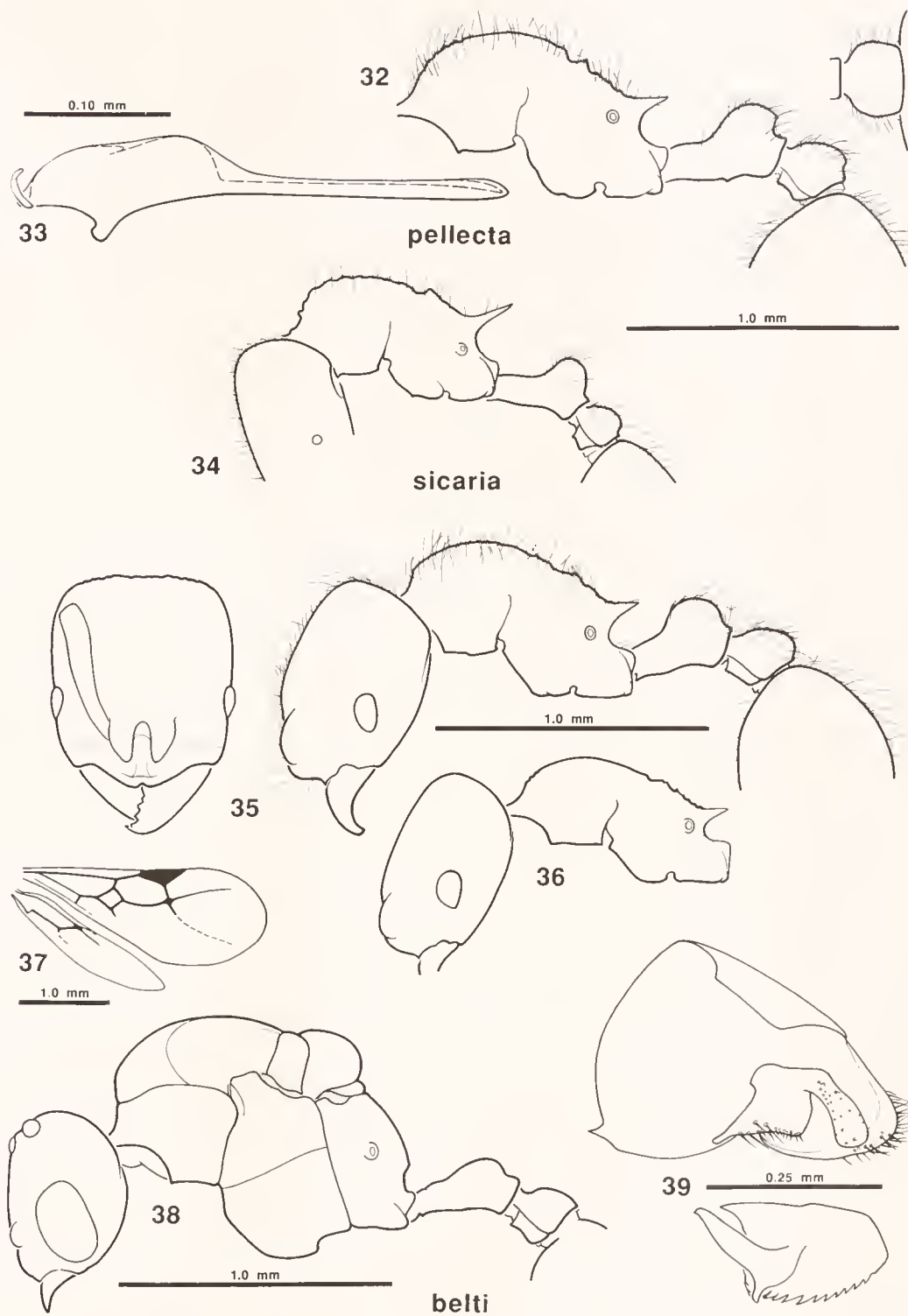
Figs. 7-14. Figs. 7-12. *Rogeria stigmatica*. 7. Syntype dorsal mandibles, clypeus. 8. Syntype profile (pilosity reconstructed by comparison with other specimens); nontype lateral gaster showing typical pilosity (Fulakora, Solomon Islands). 9. Lateral and ventral views of sting with furcula (Falepuna, Western Samoa). 10. Queen mesosoma profile (Viti Levu, Fiji). 11. Male (Sigatoka, Viti Levu). 12. Genitalia (same male). Fig. 13. *Rogeria megastigmatica* holotype profile. Fig. 14. *Rogeria prominula* holotype profile (appressed pilosity not shown); dorsolateral view mandibles and clypeal margin; dorsal head. Same scale for all external views.



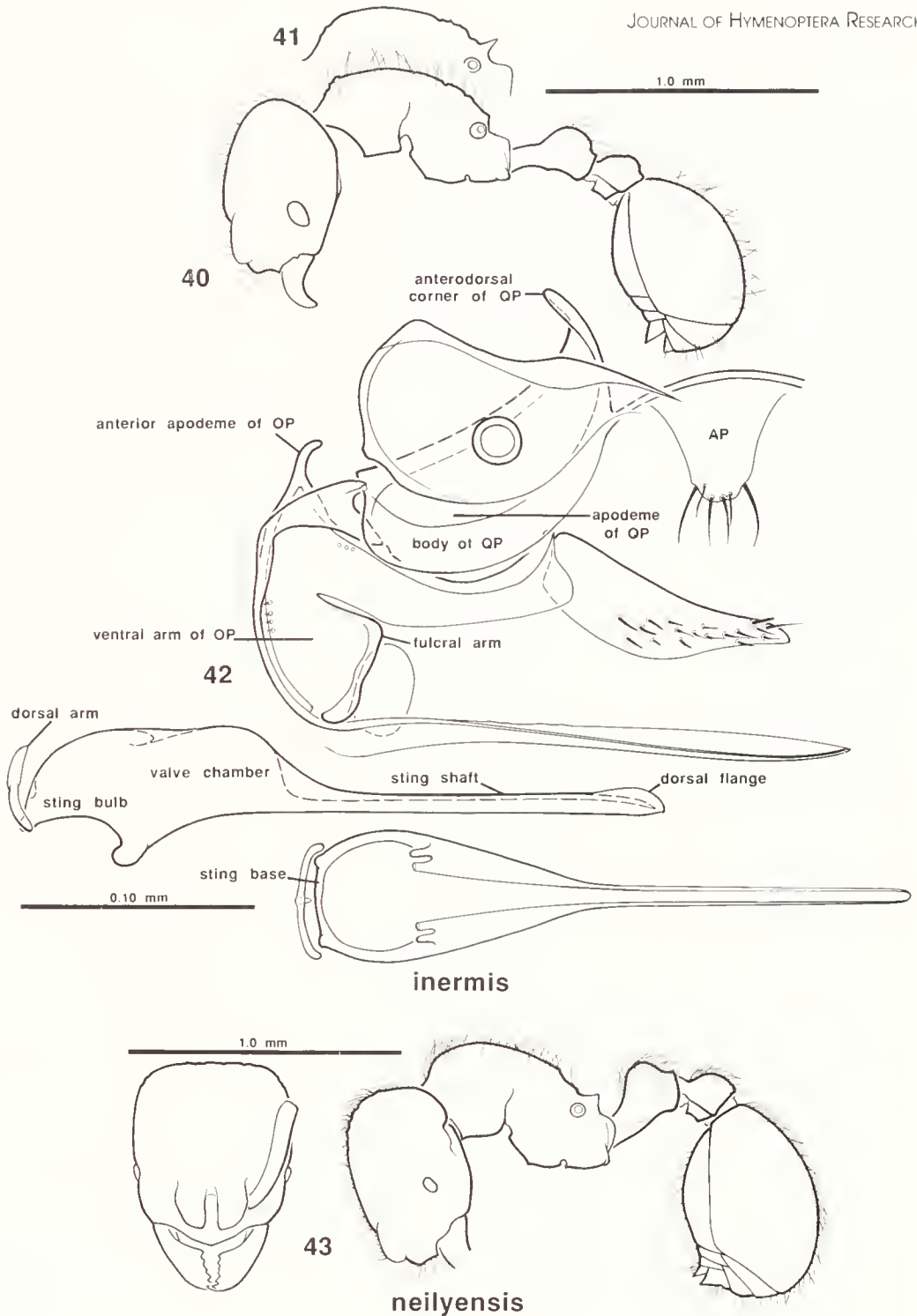
Figs. 15-23. Figs. 15-16. *Rogeria besucheti*. 15. Holotype profile; dorsal head. 16. Paratype ventral and lateral views of sting with furcula. Fig. 17. *Rogeria blanda* male genitalia (Río Akabán, Venez.). See Figs. 83-84 for worker. Fig. 18. *Rogeria procera* profile (Río Cuminá, Braz.—“*brasiliensis*” holotype). Figs. 19-20. *Rogeria scandens* syntype. 19. Profile; dorsal head; dorsal waist. 20. Erect hair. Fig. 21. *Rogeria terescandens* holotype profile; dorsal waist. Figs. 22-23. *Rogeria subarmata*. 22. Paratype profile. 23. Nontype lateral propodeum, petiole (Belém, Braz.).



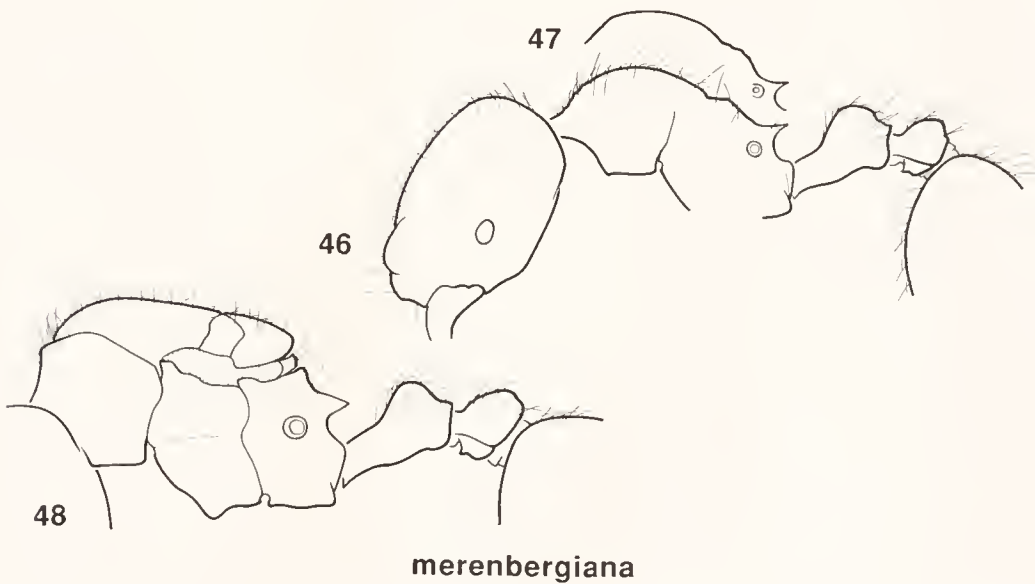
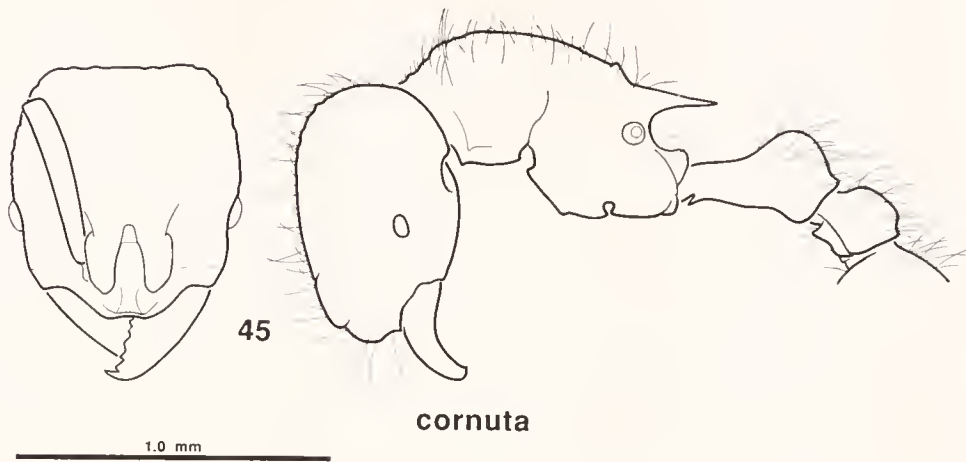
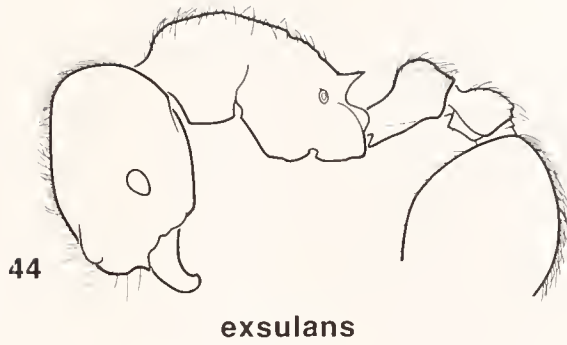
Figs. 24-31. Figs. 24-27. *Rogeria germani*. 24. Profile (mesosoma hairs had been matted down somewhat); dorsal head; dorsal postpetiole (Passa Quatro, Brazil—"minensis" lectotype). 25. Mesosoma dorsum profile showing typical pilosity (Central Prov., Para.). 26. Lateral petiole (hair omitted) (Central Prov., Para.). 27. Lateral sting, furcula; ventral sting shaft (San Benito Is., Para.). Figs. 28-30. *Rogeria lirata*. 28. Holotype profile; dorsal head. 29. Paratype lateral lancet (nr. Yurimaguas, Peru). 30. Nontype queen wings (Jatai, Braz.). Cubital vein (Cu), median vein (M), radio-medial crossvein (r-m), radial sector vein (Rs), submarginal cell (SM). Fig. 31. *Rogeria lacertosa* paratype profile. Same scale for all external views except wings.



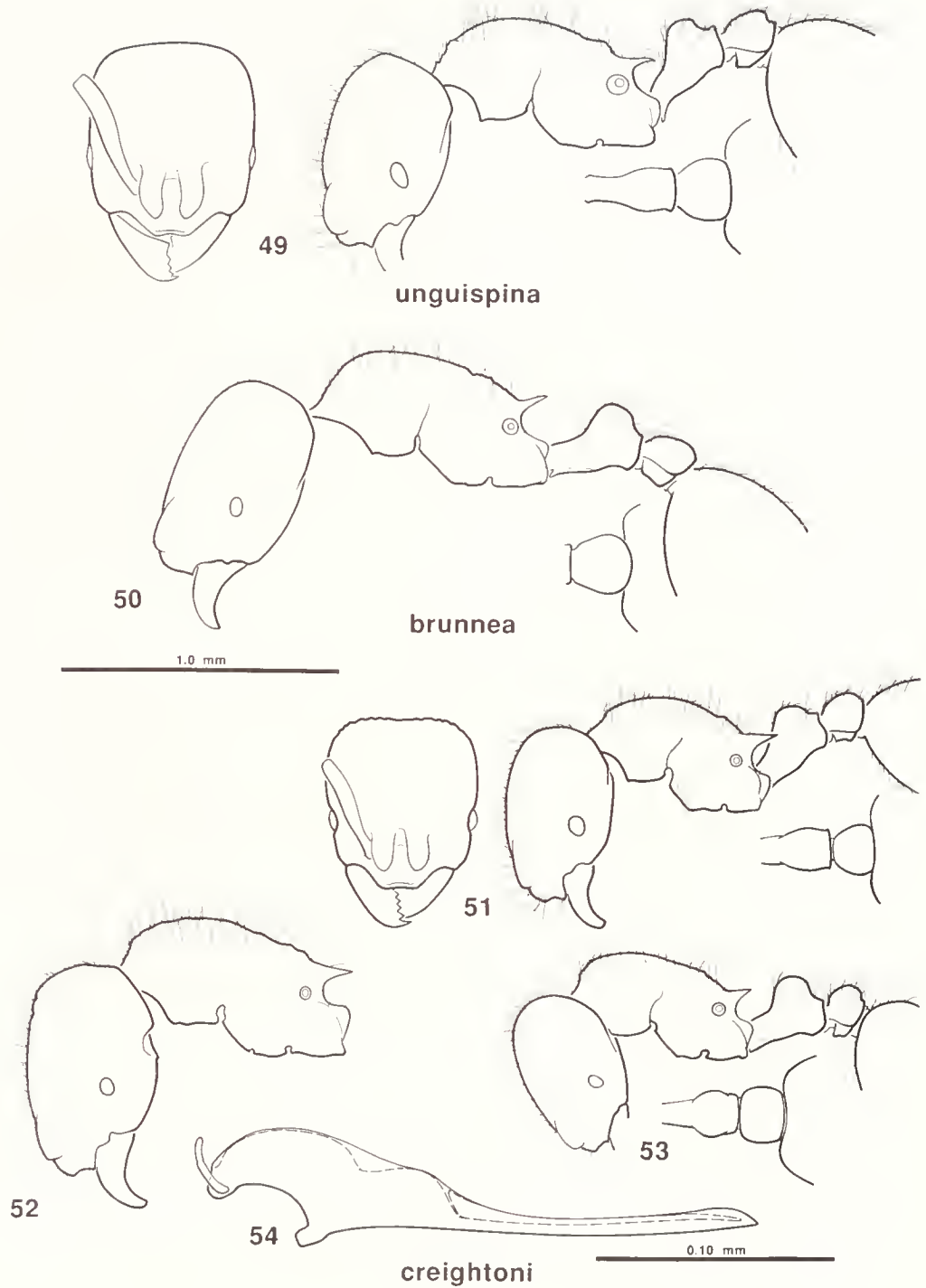
Figs. 32-39. Figs. 32-33. *Rogeria pellecta*. 32. Paratype profile; dorsal postpetiole. 33. Paratype lateral sting, furcula. Fig. 34. *Rogeria sicaria* holotype profile. Figs. 35-39. *Rogeria belti*. 35. Syntype profile; dorsal head. 36. Nontype lateral head, mesosoma (hair omitted) (Miami, C. R.). 37. Male wings (La Ceiba, Hond.). 38. Male (La Ceiba, Hond.). 39. Genitalia (same male). Same scale for all external views.



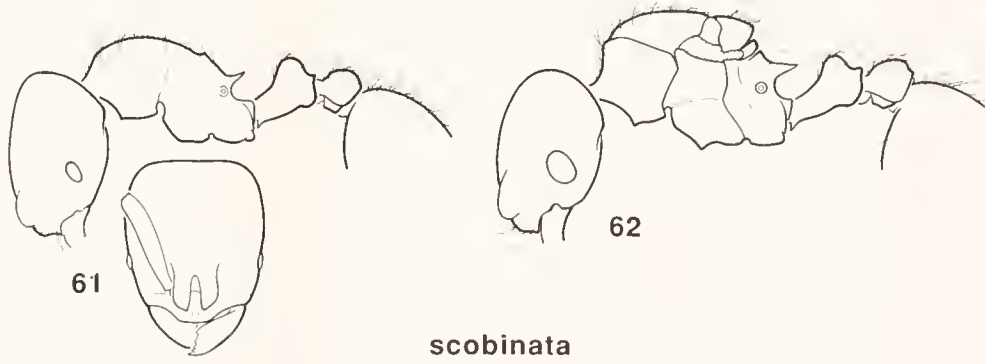
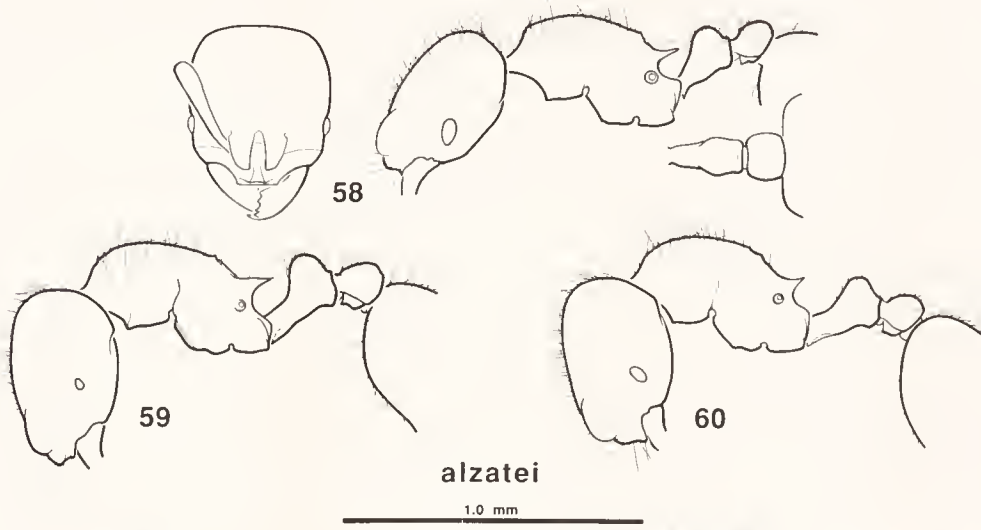
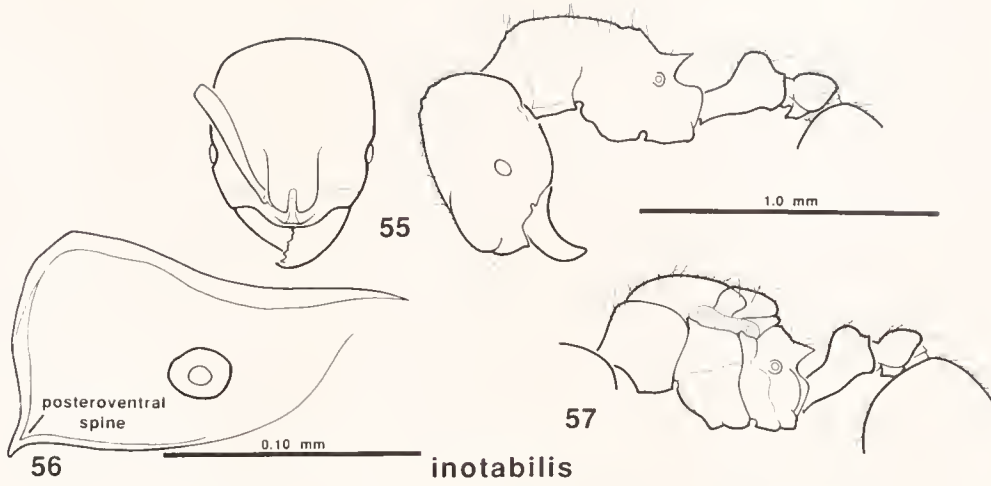
Figs. 40-43. Figs. 40-42. *Rogeria mermis*. 40. Syntype profile showing smallest propodeal spines (Osa Penin., C. R.). 41. Nontype mesosoma dorsum profile (hairs omitted) showing longest propodeal spines (Osa Penin., C. R.). 42. Sting apparatus (La Selva Station, C. R.). Right: lateral views of spiracular plate, quadrate plate (QP), oblong plate (OP), gonostylus, triangular plate and lancet; dorsal view anal plate (AP). Below: Lateral and ventral views sting, furcula. Fig. 43. *Rogeria neilyensis* holotype profile; dorsal head.



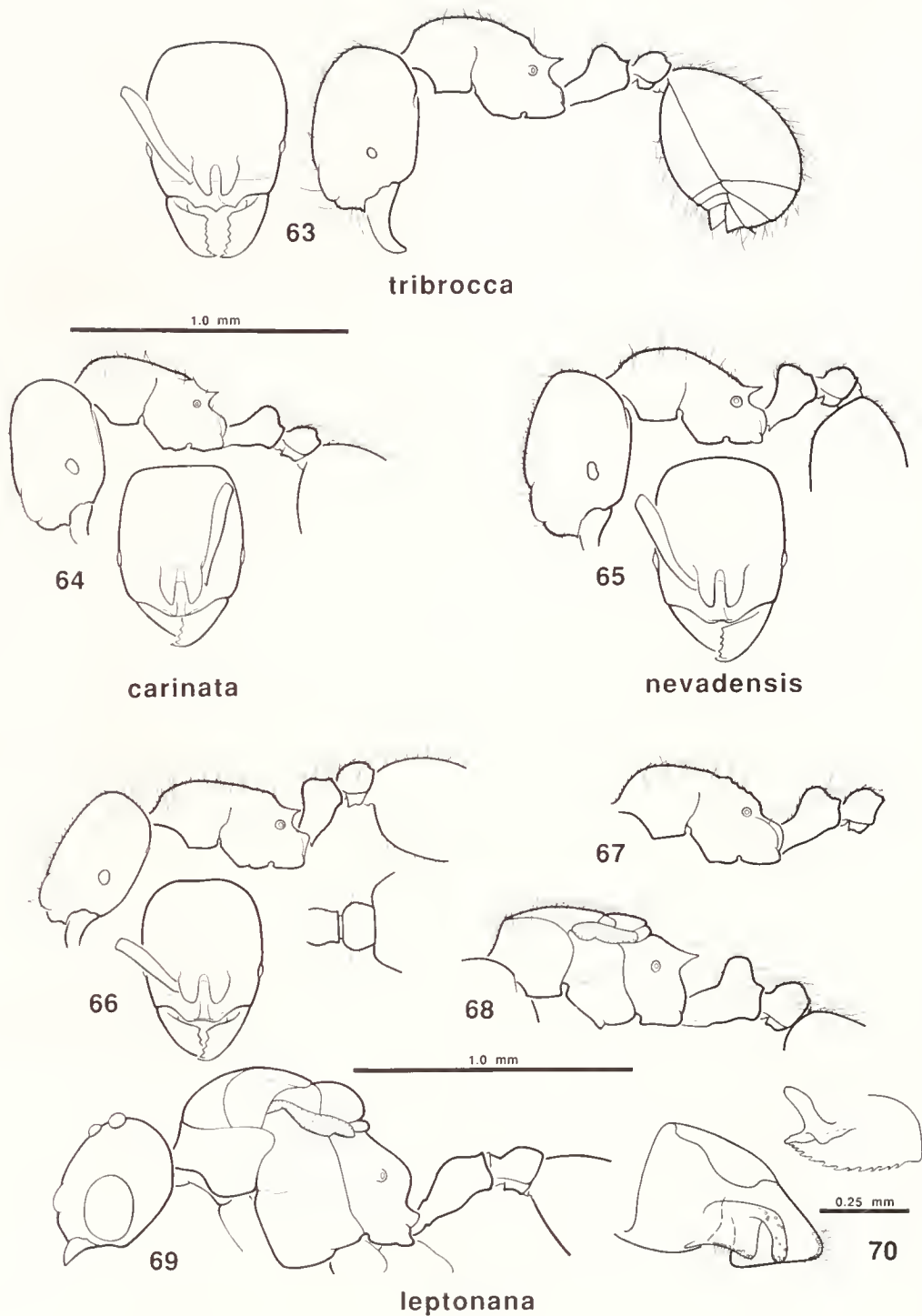
Figs. 44-48. Fig. 44. *Rogeria exsulans* holotype profile. Fig. 45. *Rogeria cornuta* holotype profile; dorsal head. Figs. 46-48. *Rogeria merenbergiana*. 46. Holotype profile. 47. Nontype mesosoma dorsum profile (hair omitted) showing the least distinct metanotum (Cuevas de los Guacharos, Col.). 48. Paratype queen lateral mesosoma and waist. Same scale for all figures.



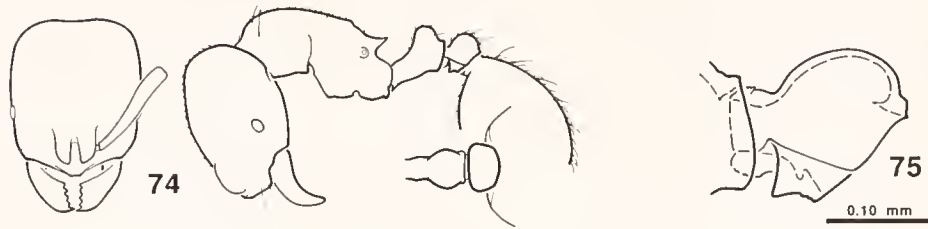
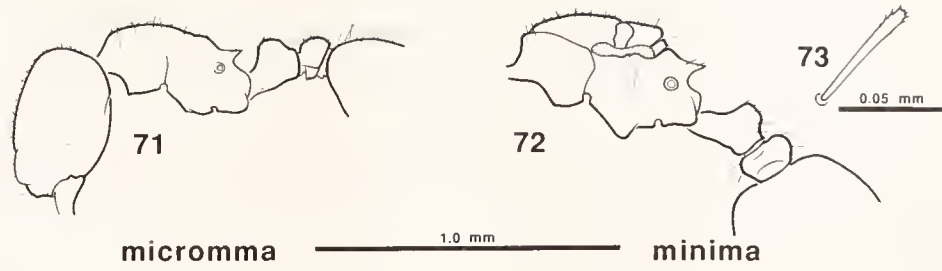
Figs. 49-54. Fig. 49. *Rogeria unguispina* holotype profile; dorsal head; dorsal waist. Fig. 50. *Rogeria brunnea* profile; dorsal postpetiole (Sierra del Rosario, Cuba—"cubensis" holotype). Figs. 51-54 *Rogeria creightoni*. 51. Paratype profile; dorsal head; dorsal waist. 52. Nontype profile (Ocozocoautla, Mex.). 53. Nontype profile; dorsal waist (Costa Rica, Nevermann leg.). 54. Lateral sting, furcula (Caves Branch, Belize). Same scale for all external views.



Figs. 55-62. Figs. 55-57. *Rogeria innotabilis*. 55. Holotype profile; dorsal head. 56. Paratype spiracular plate from sting apparatus (Chiapas, Mex). 57. Nontype queen profile (Parque Tayrona, Col.). Figs. 58-60. *Rogeria alzatei*. 58. Holotype profile; dorsal head; dorsal waist. 59. Nontype profile (Pto. Maldonado, Lake Sandoval, Peru). 60. Nontype profile (R. Don Diego, Col.). Figs. 61-62. *Rogeria scobinata*. 61. Holotype profile; dorsal head. 62. Paratype queen profile (holotype loc.). Same scale for all external views.

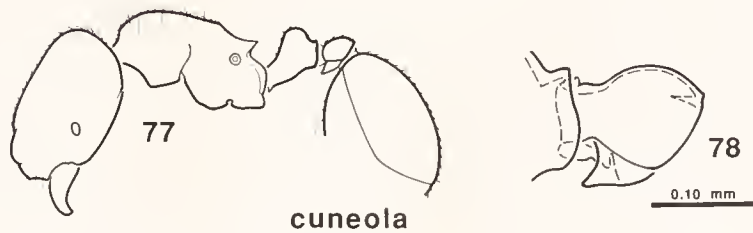


Figs. 63-70. Fig. 63. *Rogeria tribrocca* holotype profile; dorsal head. Fig. 64. *Rogeria carinata* holotype profile; dorsal head. Fig. 65. *Rogeria nevadensis* holotype profile; dorsal head. Figs. 66-70. *Rogeria leptonana*. 66. Holotype profile; dorsal head; dorsal postpetiole. 67. Nontype profile (nr. Nueva California, Pan.). 68. Nontype queen profile (Parque Tayrona, Col.). 69. Male (Cerro Pico Blanco, C. R.). 70. Male genitalia (same loc.). Same scale for all external views.

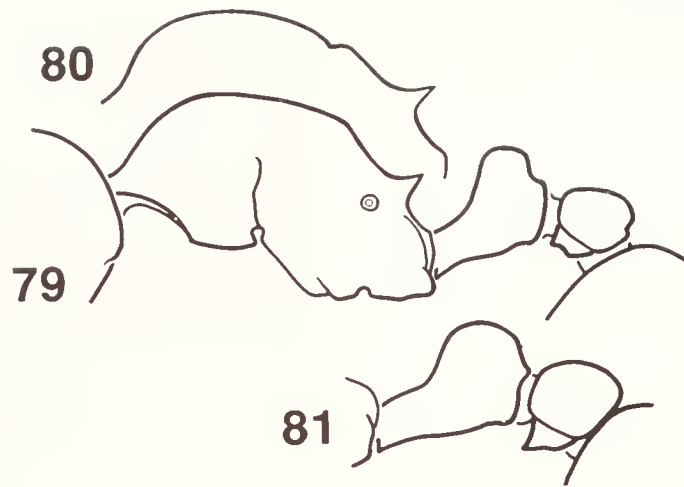


curvipubens

1.0 mm

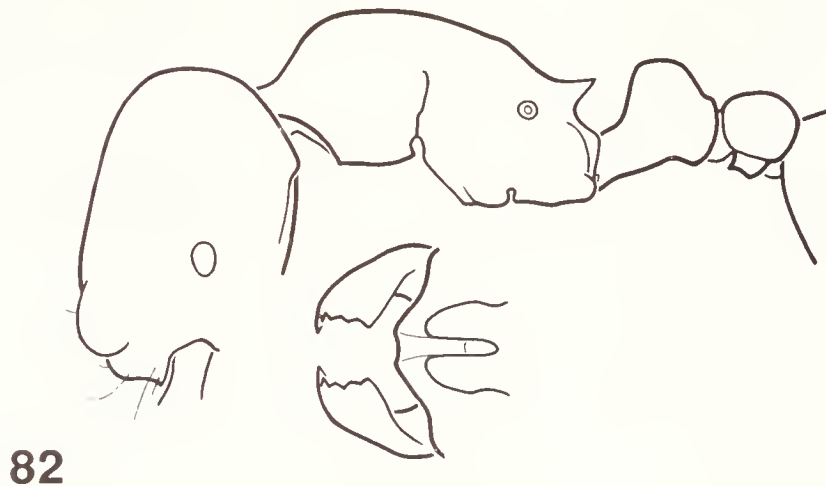


Figs. 71-78. Fig. 71. *Rogeria micromma* holotype profile. Figs. 72-73. *Rogeria minima* holotype. 72. Lateral mesosoma, petiole; ventral postpetiole, gaster. 73. Erect hair. Figs. 74-76. *Rogeria curvipubens*. 74. Nontype profile; dorsal head; dorsal waist (BCI, Pan.). 75. Slide-mounted worker lateral petiole (Parque Tayrona, Col.). 76. Queen profile (R. Don Diego, Col.). Figs. 77-78. *Rogeria cuneola*. 77. Holotype profile. 78. Slide-mounted worker lateral petiole (El Palmar, Mex.). Same scale for all figures except 73, 75, and 78.



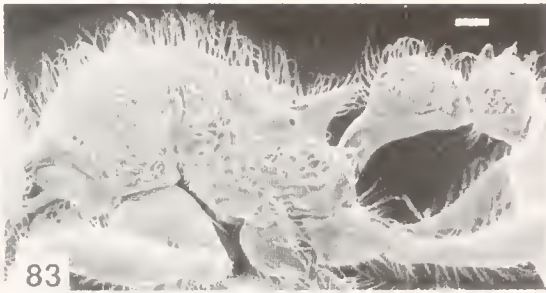
foreli

1.0 mm

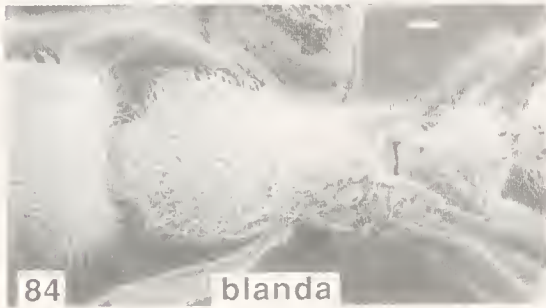


bruchi

Figs. 79-82. Figs. 79-81. *Rogeria foreli*. 79. Holotype profile. 80. Nontype mesosoma dorsum profile showing strongest metanotal groove (Cerro Azul, Pan.). 81. Lateral waist (Don Diego vic., Col.). Fig. 82. *Rogeria bruchi* holotype profile; dorsal mandibles and clypeus. All to same scale.

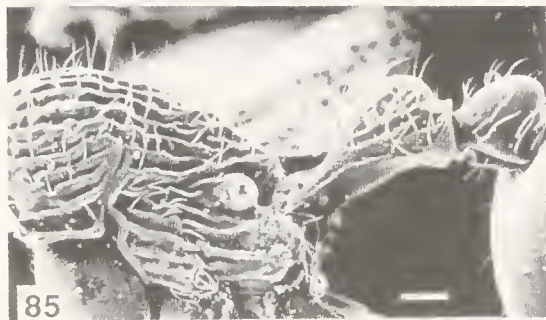


83

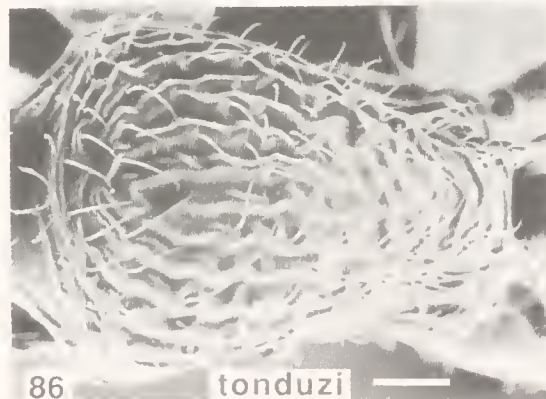


84

blanda

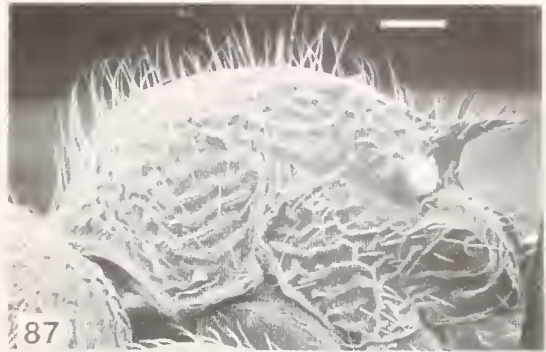


85



86

tonduzi

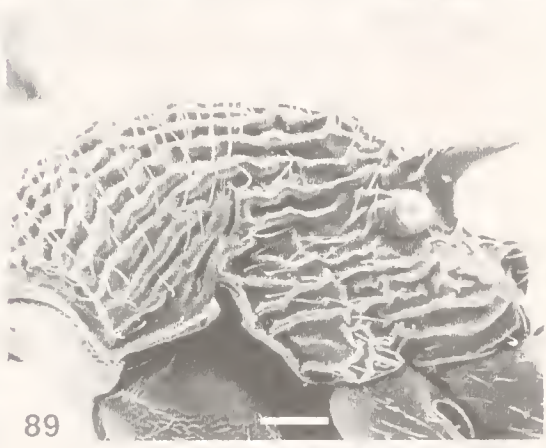


87

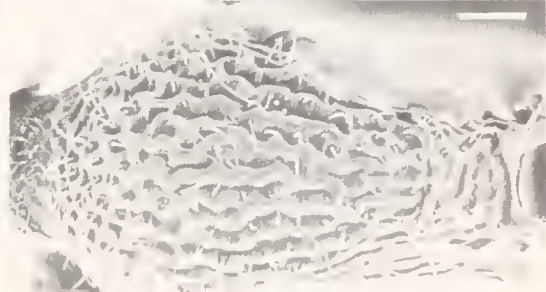


88

germaini



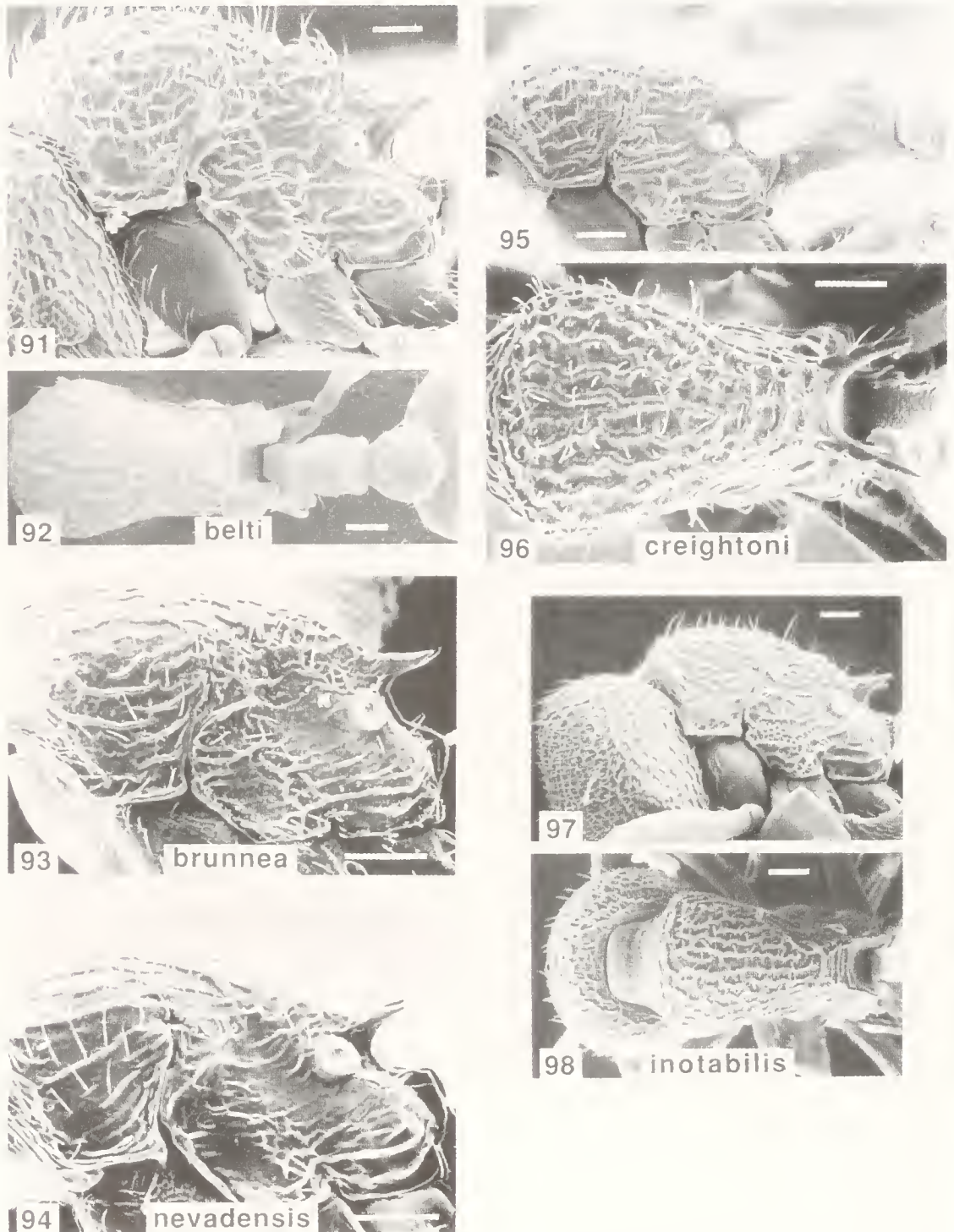
89



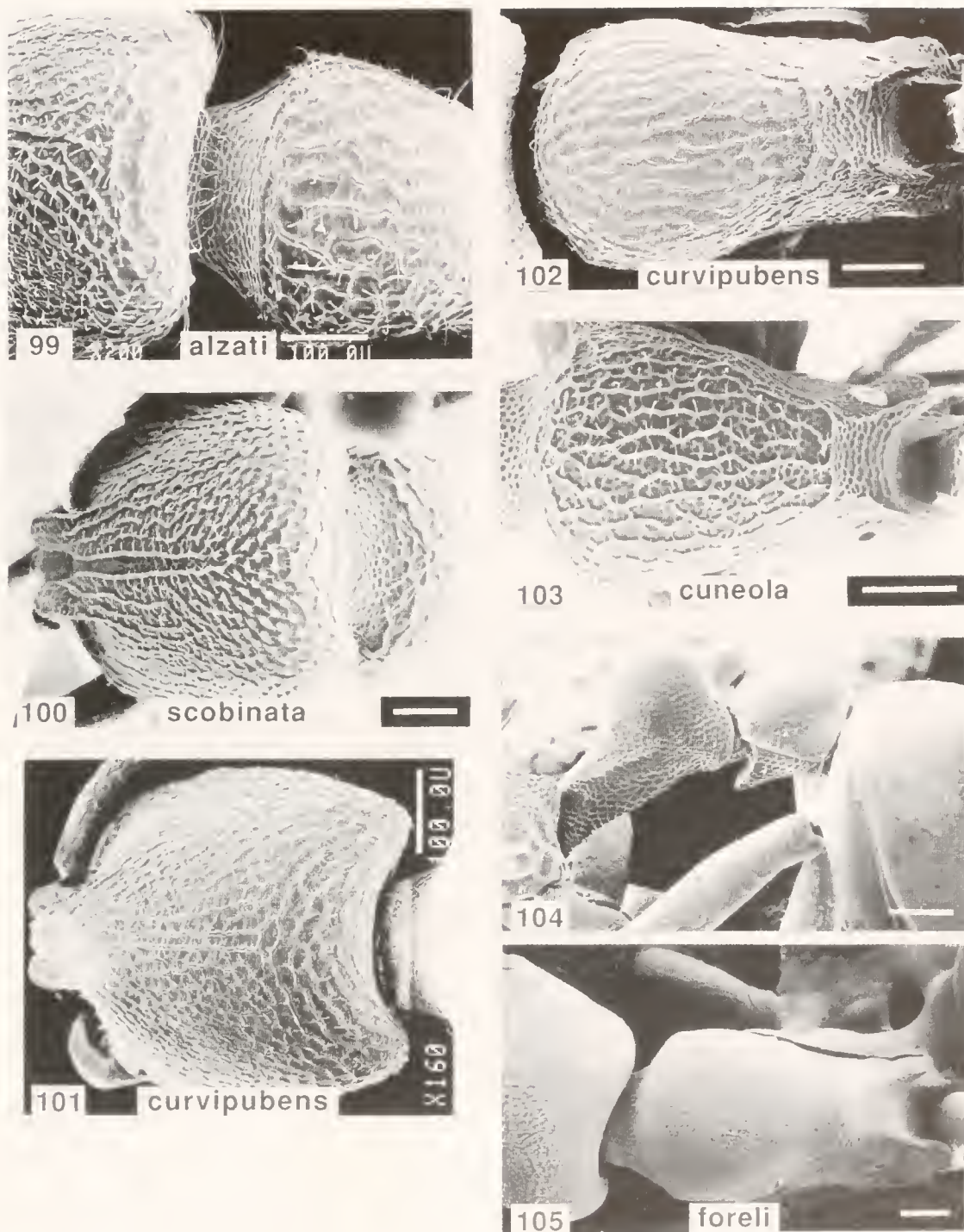
90

lirata

Figs. 83-90. Figs. 83-84. *Rogeria blanda* (L. Sandoval, Peru). 83. Lateral mesosoma, waist. 84. Dorsal head, mesosoma, petiole. Figs. 85-86. *Rogeria tonduzi* (La Selva Station, C. R.). 85. Lateral mesosoma and waist. 86. Dorsal mesosoma. Figs. 87-88. *Rogeria germaini* (Alto Paraná Prov., Para.). 87. Lateral mesosoma. 88. Dorsal mesosoma, posterior head. Figs. 89-90. *Rogeria lirata* paratype. 89. Lateral mesosoma. 90. Dorsal mesosoma. Scale lines = 0.10mm.



Figs. 91-98. Figs. 91-92. *Rogeria belti* (nr. El Bosque, Mex.). 91. Lateral head (part), mesosoma. 92. Dorsal mesosoma and waist of a smaller worker. Fig. 93. *Rogeria brunnea* lateral mesosoma (Blanco's Woods, Soledad, Cuba). Fig. 94. *Rogeria nevadensis* paratype lateral mesosoma. Figs. 95-96. *Rogeria creightoni* (Belmopan, Belize). 95. Lateral mesosoma, petiole. 96. Dorsal mesosoma. Figs. 97-98. *Rogeria innotabilis* paratype. 97. Lateral head, mesosoma. 98. Posterior head, dorsal mesosoma. Scale lines = 0.10mm.



Figs. 99-105. Fig. 99. *Rogeria alzatei* paratype posterodorsal head, dorsal pronotum. Fig. 100. *Rogeria scobinata* paratype posterodorsal head. Figs. 101-102. *Rogeria curvipubens* (R. Don Diego vic., Col.). 101. Posterodorsal head. 102. Dorsal mesosoma. Fig. 103. *Rogeria cuneola* paratype dorsal mesosoma. Figs. 104-105. *Rogeria foreli* (Parque Tayrona, Col.). 104. Lateral waist showing prominent anterior lip of postpetiolar sternum of some specimens. 105. Posterior head, dorsal mesosoma. Scale lines = 0.10mm.

The Genera of Bethylinae (Hymenoptera: Bethylidae)

ANDREW POLASZEK AND KARL V. KROMBEIN

(AP) Department of Entomology, Wageningen Agricultural University, The Netherlands
International Institute of Entomology, c/o The Natural History Museum, London, UK
(KVK) Department of Entomology, Smithsonian Institution, Washington, D. C. USA.

Abstract. —The taxonomic status of the genera comprising the bethylid subfamily Bethylinae is reassessed using computerised phylogenetic analysis. From this analysis seven genera are considered valid, and the following are synonymised: *Trissomalus* Kieffer 1905 with *Odontepyrus* Kieffer 1904; and *Anoxus* Thomson 1862 with *Bethylus* Latreille 1802. Several species are transferred generically, and several new combinations are presented. The distribution and biology of the Bethylinae are summarised.

INTRODUCTION

The aculeate family Bethylidae (Chrysidoidea) is a moderately large family of about 1,900 described species with probably at least as many undescribed. Bethylids are mainly gregarious ectoparasitoids, the Bethylinae mostly developing on larval Lepidoptera, the remainder mostly on Coleoptera, although the hosts are known for only a small proportion of the family. Bethylids are frequently encountered as parasitoids of crop pests, especially in tropical areas, and several species have been used in attempted biological control (Gordh & Evans 1976; Hempel 1934). Successful identification of Bethylidae is therefore important for many economic entomologists, but has been extremely difficult because the most recent revision was published eighty years ago (Kieffer 1914) and contains many errors. Even at the generic level identification can be very difficult, particularly for the Palaeotropical species. For the Nearctic and Neotropical species this problem has largely been alleviated by the work of Evans (1964, 1978).

During our independent studies on African and Asian Bethylinae we have each discovered related undescribed species that do not fit Kieffer's (1914) concepts of the bethylid genera, but which we do not regard as meriting description in new

genera. Kieffer's and subsequent authors' concepts of the bethylid genera needed modification to accommodate the degree of morphological variation which we had discovered. Computerised phylogenetic analysis was selected as the most objective method of assessing character states within the bethylid genera, while providing a more stable classification of the subfamily. The following study was carried out primarily to set new limits to some of these genera, and to facilitate their identification.

Here we address the internal phylogeny of the Bethylinae. In comparison to the other bethylid subfamilies, the Bethylinae have been little affected at the generic level since Kieffer's (1914) revision. Only one genus, *Neochlystospenella* Kurian (1955), was assigned to the Bethylinae since Kieffer's work. *Neochlystospenella* was synonymised with *Tapinoma* (Formicidae) by Brown (1987), but mistakenly retained by Gordh & Moczar (1990) in the Bethylidae. Gordh & Moczar (1990) also mistakenly transferred *Odontepyrus* Kieffer to Epyrinae, thus assigning a total of eight genera to the Bethylinae (Table 1). When attempting to identify Bethylinae genera using Kieffer's (1914) key, the primary source of confusion is his treatment of the genera *Goniozus* Förster, *Parasierola* Cameron and *Perisierola* Kieffer. The latter two genera have since correctly been synonymised with *Goniozus* (Evans

1978), but from our studies it is clear that Kieffer intended something different from what he inadvertently achieved when he keyed and diagnosed these genera in his revision. *Goniozus* (*sensu* Evans 1978) contains species that either possess, or do not possess, a closed discoidal cell (areola, areolet) (Fig. 1). Kieffer assigned those species with a discoidal cell to *Perisierola*, and those without one to *Goniozus*. Kieffer (1907, 1911, 1914), Brues (1907a, 1907b) and Muesebeck (1940) all mistakenly selected *Parasierola* Cameron (1883) to accommodate species with both a closed discoidal cell and with one or more longitudinal carinae on the propodeum, this latter character being absent from Kieffer's concepts of the other two genera. Furthermore, Kieffer (1914) transposed his concepts of *Parasierola* and *Perisierola* when going from his key to genera (1914:238) to his generic diagnoses (1914:533, 542). Thus began 80 years of confusion surrounding these bethyline genera.

METHODS

Selection of taxa

To clarify the status of the genera of Bethylinae we analysed 11 taxa of Bethylinae for 22 morphological characters using the parsimony programme 'Hennig86' (Farris 1988). To polarise characters the genus *Lytopsenella* Kieffer was selected as the outgroup. *Lytopsenella* possesses all the characters common to all the remaining bethyline genera in their hypothetical plesiomorphic conditions (see character selection). Characters that are prone to reduction (e.g., number of antennal segments, maxillary and labial palp segments, and wing venation) are found at their maxima within *Lytopsenella*. *Lytopsenella* has previously been chosen as a basal group, not just for Bethylinae but for Bethylinidae as a whole (Evans 1964; Sorg 1988).

Representatives of each of the currently valid bethylid genera were included in the analysis. In cases of existing doubt or controversy surrounding the limits of some genera, type species of both current genera and formerly recognised genera were examined. Particular attention was paid to previous authors' concepts of *Goniozus*, *Odontepyrus*, *Parasierola*, *Perisierola* and *Trissomalus*. Three species of *Goniozus* (in the broad sense, i. e. that of Evans 1978) were selected to cover the range of known variation in propodeal and wing

venation characters which are important for deducing the phylogeny of the subfamily. Current interpretations of the genera *Anoxus* and *Bethylus* differ from each other only in whether the eyes are setose or not. This is a character that we have observed to vary intragenerically, so only one representative species of *Bethylus* was included in the analysis. The taxa selected are given in the data matrix below (Table 2) in the generic combinations which have resulted from this study. Former generic combinations can be found in the treatments of *Bethylus* and *Odontepyrus* (see below).

Selection of Characters

We consider the following to represent the ground plan characters of the subfamily Bethylinae. This character list is based partly on the work of Evans (1964) and of Sorg (1988) but largely on our own independent assessments.

Ground plan characters within Bethylinae

Antennae 13-segmented; clypeus with a well-developed keel, and frontal streak present; maxillary palps 6-segmented; labial palps 3-segmented; notauli and parapsidal lines present; scutellum flat, with two small grooves at its proximal corners (Fig. 2); propodeum without carinae (but see below); fore femora expanded; prostigma absent; discoidal cell (areolet) present, submarginal and marginal cells present; subdiscoidal cell absent (=discoidal cell of Evans 1964); sternum of petiole with a complete keel, sexual dimorphism limited to genital characters and head shape.

Characters Analysed

The following characters include all of those which have been used previously for the discrimination of genera within the Bethylinae (except eye setation, see above) as well as some which have not been used previously. We generally agree with Sorg (1988) concerning both the selection and polarization of characters. However, we disagree with Sorg's polarization of the scutellar foveae (character 6, below; Figs. 3, 4). Sorg considers that the occurrence of scutellar foveae in the Embolemidae (Sorg 1988: p 30) suggests plesiomorphy. The probability is that, at least in the Bethylinae, they are represented in their

Table 1: Genera of Bethylinae

Kieffer (1914)	Gordh & Moczar (1990)	This paper
(Bethylini)	(Bethylinae)	(Bethylinae)
<i>Anoxus</i>	<i>Anoxus</i>	<i>Bethylus</i>
<i>Bethylus</i>	<i>Bethylus</i>	<i>Bethylus</i>
<i>Clystopsenella</i>	not mentioned	Scolebythidae (Evans, 1963)
<i>Digoniozus</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Eupsenella</i>	<i>Eupsenella</i>	<i>Eupsenella</i>
<i>Goniozus</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Kathepyris</i>	Pristocerinae	Pristocerinae (Evans 1964)
<i>Lytopsenella</i>	<i>Lytopsenella</i>	<i>Lytopsenella</i>
	<i>Neoclystopsenella</i> (incertae sedis)	Formicidae (Brown 1987)
<i>Odontepyris</i> (Bethylini)	<i>Odontepyris</i> (Epyrinae)	<i>Odontepyris</i> (Bethylinae)
<i>Parasierola</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Perisierola</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Progoniozus</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Prosierola</i>	<i>Prosierola</i>	<i>Prosierola</i>
<i>Sierola</i>	<i>Sierola</i>	<i>Sierola</i>
<i>Trissomalus</i>	<i>Trissomalus</i>	<i>Odontepyris</i>

plesiomorphic condition in *Lytopsenella*.

Assumed primitive (plesiomorphic) characters are coded '0' with '1', '2' representing assumed derived (apomorphic) states.

- Number of antennal segments:** The plesiomorphic condition in the Bethylinae is possession of 13-segmented antennae. In *Bethylus* (including *Anoxus*) a reduction to 12-segmented antennae has occurred. 0= antennae 13-segmented; 1= antennae 12-segmented.
- Number of labial palp segments:** The plesiomorphic condition is possession of 3-segmented labial palps. In *Bethylus* and *Sierola* the labial palps are 2-segmented. 0= labial palps 3-segmented; 1= labial palps 2-segmented.
- Number of maxillary palp segments:** The plesiomorphic condition is possession of 6-segmented maxillary palps, found in both *Eupsenella* and *Lytopsenella*. In the remaining taxa the number is reduced to five, except *Sierola* which has 4-segmented maxillary palps. 0= maxillary palps 6-segmented; 1= maxillary palps 5-segmented; 2= maxillary palps 4-segmented.
- Presence of an unsculptured streak frontally:** In many bethyline taxa a narrow impunctate, sometimes shiny, streak extends from the proximal end of the clypeal carina to the frontal ocellus (Fig. 12, see also Sorg 1988: 121, Fig. 33d, for its presence in Epyrinae: *Chilepyris*). In *Bethylus* (including *Anoxus*), *Goniozus* and *Sierola* the sculpturing of the head is reduced (i. e. smooth rather than strongly rugose) and this streak is absent. 0= frontal streak present; 1= absent.
- Presence of notauli:** The notauli, a pair of longitudinal furrows on the mesoscutum, occur throughout the Hymenoptera, and are often reduced. In the Bethylinae they are present only in the basal taxa, *Eupsenella* (Figs. 2, 3) and *Lytopsenella*. In all remaining Bethylinae the notauli are absent. The notauli should not be confused with the parapsidal lines, which are an additional pair of shallow grooves lateral to the position of the notauli (Menke 1993) (Fig. 2). 0= notauli present; 1= absent.
- Presence of scutellar grooves or pits:** In the basal taxa *Eupsenella* and *Lytopsenella* the scutellum has a pair of grooves at its anterior corners (Figs. 2, 3, 5). In several bethyline taxa

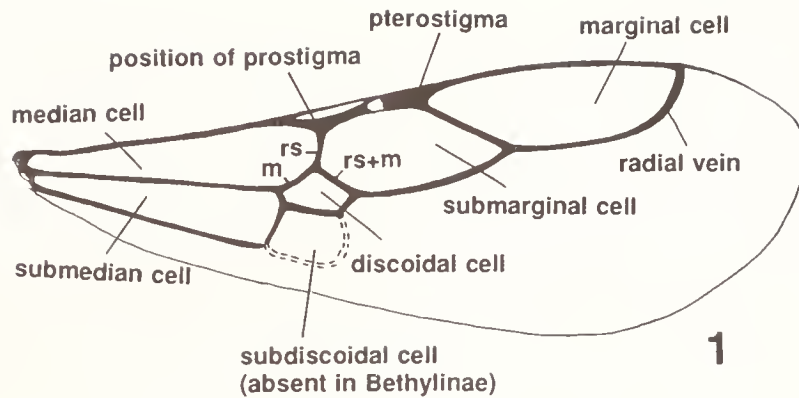


Fig. 1. Bethylinidae: terminology of wing venation

- these have apparently become enlarged to form pits, often connected by a broad transverse groove (Figs. 4, 6, 7). 0= scutellar pits or foveae present as grooves; 1= scutellar foveae enlarged.
7. **Expansion of mesopleuron:** Kieffer (1905) characterised his genus *Odontepyris* by the possession of dentate processes on the mesopleura (Figs. 6, 14). Although an apomorphic character in one lineage, it shows varying degrees of development in related taxa. 0= mesopleuron not expanded to form a dentate process; 1= mesopleuron moderately expanded; 2= mesopleura with dentate processes.
 8. **Presence of posterior transverse propodeal carina** (Figs. 2, 6, 7, 9, 10): 0= posterior transverse propodeal carina present; 1= posterior transverse propodeal carina absent.
 9. **Presence of median longitudinal propodeal carina** (Figs. 2, 5, 6, 8, 9): 0= median longitudinal propodeal carina present; 1= median longitudinal propodeal carina absent.
 10. **Presence of discal longitudinal propodeal carinae** (Figs. 2, 5, 6, 7, 8, 9, 10): 0= discal longitudinal propodeal carinae present; 1= discal longitudinal propodeal carinae absent.
 11. **Presence of median propodeal pits or foveae** (Figs. 4, 7, 10): The presence of these structures is characteristic of the genus *Prosierola*. 0= median propodeal pits absent; 1= median propodeal pits present.
 12. **Development of a smooth, triangular area on the dorsal propodeum:** In several bethyline taxa, particularly *Goniozus* and *Prosierola*, the proximal dorsum of the propodeum is characterised by a smooth, unsculptured triangular area which shows modifications in several taxa (Figs. 7, 10, 11). It is absent in the basal groups. The development of this character in some bethyline lineages should not be confused with the "propodeal triangle" in Apidae and Sphecidae (Brothers 1976). 0= smooth, triangular area absent from dorsal propodeum (Figs. 2, 5, 6, 8, 9); 1= smooth, triangular area present on dorsal propodeum (Figs. 7, 10, 11).
 13. **Petiole ventrally keeled:** To our knowledge, this character has not been used previously in defining the genera of Bethylinae, but is important for separating *Goniozus* from superficially similar taxa in *Odontepyris* (see key to genera, below). In most Bethylinae, a complete longitudinal keel is present on the ventral petiole (Fig. 13). This keel is reduced in several taxa (e. g. Fig. 15). 0= petiole with a complete ventral keel; 1= petiolar keel reduced; 2= petiolar keel absent.
 14. **Expansion of the fore femora:** Expansion of the fore femora for fossorial use is often encountered among the Bethylinidae, and also occurs in related chrysidoid taxa and other aculeates. Other modifications of the fore femora are frequent in the Aculeata. 0= fore femora strongly expanded; 1= fore femora less strongly expanded, half as wide as long.
 15. **Development of the prostigma:** The expansion of the junction of the subcostal and basal veins into a secondary pterostigma is characteristic of the genus *Goniozus* (Figs. 20, 25), but also occurs elsewhere within the subfam-

Table 2. Character matrix:

	Characters																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Lytopsenella</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eupsenella</i> sp.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
<i>Sierola</i> sp.	0	1	2	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1
<i>Bethylus cephalotes</i>	1	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	1
<i>Odontepyrus flavinervis</i>	0	0	1	0	1	1	2	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0
<i>Odontepyrus transvaalensis</i>	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0
<i>Odontepyrus xanthoneurus</i>	0	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	1	1	0
<i>Prosierola</i> sp.	0	0	1	0	1	1	1	1	0	1	1	1	0	0	0	1	1	0	0	1	1	0
<i>Goniozus</i> sp.	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0
<i>Goniozus gallicus</i>	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0
<i>Goniozus indicus</i>	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0

- ily. Its presence outside *Goniozus* has previously led to the generic misplacement of certain species. 0= prostigma absent; 1= prostigma present.
16. **Length of rs+m:** In the basal taxa, fore wing vein rs+m forms the upper distal part of the discoidal cell (Fig. 1). In all *Goniozus* species it is present and well-developed, despite the fact that in *Goniozus (sensu stricto)* the discoidal cell is open. The genus *Odontepyrus* is here characterised partly by the reduction of this vein (Figs. 22-24). The absence of this vein in *Bethylus* is clearly convergent with its reduction in *Odontepyrus* (see below). 0= rs+m long; as long as, or longer than, rs (Figs. 16-18, 20, 25); 1= rs+m shorter than rs, or absent (Figs. 19, 22-24).
17. **Length of rs:** The length of rs relative to m (Fig. 1) characterises the *Prosierola* / *Odontepyrus* clade, in which rs has become elongated. 0= rs equal to or shorter than m (Figs. 16-20, 25); 1= rs clearly longer than m (Figs. 21-24).
18. **Length of marginal (radial) cell:** In *Eupsenella*, one of the basal taxa, the marginal cell is characteristically shortened (Fig. 17). In the remaining taxa which have a closed marginal cell (*Lytopsenella*, *Sierola*), the marginal cell is of normal dimensions. For those taxa in which the marginal cell is open, it is necessary to calculate the size of a hypothetical closed marginal cell by the length of the radial vein ($2r - rs$ of Sorg 1988; $r + Rs$ of Evans 1964). 0= marginal cell long (Fig. 16); 1= marginal cell shortened (Fig. 17).
19. **Presence of discoidal cell (areolet):** Within all Bethylinae the discoidal cell appears to be homologous, being plesiomorphically present. In *Goniozus* it is either clearly present or absent, whereas in *Odontepyrus* various intermediate degrees of reduction of the discoidal cell are apparent (c. f. Figs. 22, 23, 24). 0= discoidal cell present (Figs. 16, 17, 18, 21, 22, 23, 25); 1= discoidal cell absent (Figs. 19, 20, 24).
20. **Presence of submarginal cell.** In the Bethylinae, the submarginal cell is present and complete only in *Eupsenella* and *Lytopsenella*. It is absent in all remaining taxa. 0= submarginal cell present (Figs. 1, 16, 17); 1= submarginal cell absent (Figs. 18-25).
21. **Presence of closed marginal cell:** In the basal taxa, and in *Sierola*, the marginal cell is closed, the plesiomorphic condition for Bethylinae. 0= marginal cell closed (Figs. 1, 16-18); 1= marginal cell open (Figs. 19-25).
22. **Angle of radial vein:** The radial vein (Fig. 1; = vein $2r - rs$ of Sorg 1988; vein $r + Rs$ of Evans 1964) is distinctly angled in *Bethylus* and *Sierola* (Figs. 18, 19), genera respectively with an open and a closed marginal cell. The angle of the radial vein is thus independent of the closure of the marginal cell. 0= radial vein without a sharp angle; 1= radial vein sharply angled.

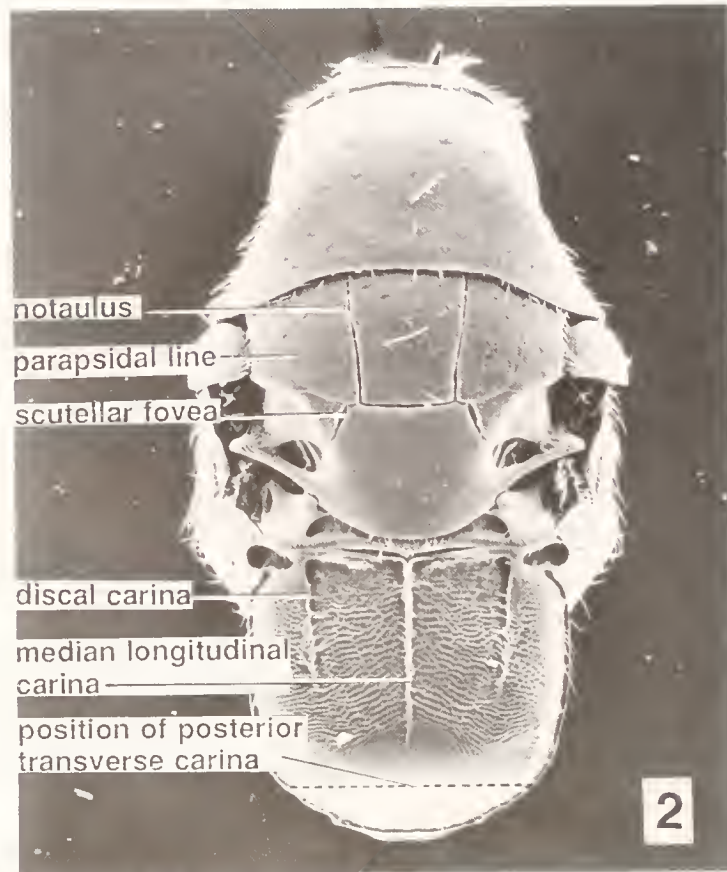


Fig. 2. Bethyline: terminology of mesosoma.

The character matrix was analysed using the 'implicit enumeration' option of Hennig86, the procedure which computes the maximum possible number of cladograms, or 'trees'. Multistate characters (3: number of maxillary palps; 5: presence of notauli; 7: expansion of the mesopleuron; 13: reduction of the petiolar keel) were treated both as unordered (non-additive) and ordered (additive).

RESULTS

A single cladogram (tree) resulted from the analysis, having the following characteristics: length 35 steps, consistency index 71 and retention index 80 (Fig. 26). Ordering the data had no effect on the topology of the tree, only increasing its length by one step, and reducing the consistency index by two.

Characters Supporting Monophyly of Bethyline Genera / Clades

1. (node A, Fig. 26): ((*Prosierola* + *Odontepyris*) + ((*Sierola* + *Bethylus*) + *Goniozus*)).
Monophyly of this clade is supported by the following synapomorphies: 3: reduction of number of maxillary palp segments from six to five; 5: loss of notauli; 20: loss of submarginal cell; 21: marginal cell open (reversed in *Sierola*).
2. (node B, Fig. 26): (*Prosierola* + *Odontepyris*)
Monophyly of this clade is supported by the following synapomorphies: 6: expansion of the scutellar pits; 7: expansion of the mesopleura; 8: presence of a posterior transverse propodeal carina; 10: presence of discal carinae; 16: rs+m shorter than rs; 17: rs longer than m.
3. (node C, Fig. 26): *Odontepyris*



Figs. 3-4. 3, *Eupsenella* sp.: detail of mesosoma. 4, *Prosierola* sp.: scutellum and propodeum.

Monophyly of *Odontepyris* is supported by the following synapomorphy: 9: presence of a median propodeal carina.

4. (node D, Fig. 26): *Prosierola*

Monophyly of *Prosierola* is supported mostly by convergent characters, except for the autapomorphic character (11) presence of propodeal pits.

5. (node E, Fig. 26): ((*Sierola* + *Bethylus*) + *Goniozus*)

Monophyly of this clade is supported by a single synapomorphy: 4: loss of the frontal streak.

6. (node F, Fig. 26): *Goniozus*

Monophyly of *Goniozus* is supported by a single synapomorphy: 13: reduction of the petiolar keel. Character 12, presence of a smooth triangular area on the propodeum is a synapomorphy for *Goniozus* which occurs as a homoplasy in *Prosierola*.

7. (node G, Fig. 26): (*Sierola* + *Bethylus*)

Monophyly of this clade is supported by the following synapomorphies: 2: reduction of the number of labial palp segments from three to two; 22: radial vein sharply angled.

8. (node H, Fig. 26): *Sierola*

Monophyly of *Sierola* is supported by 3: maxillary palps 4-segmented, as well as by the closed marginal cell (21) which is here a reversal.

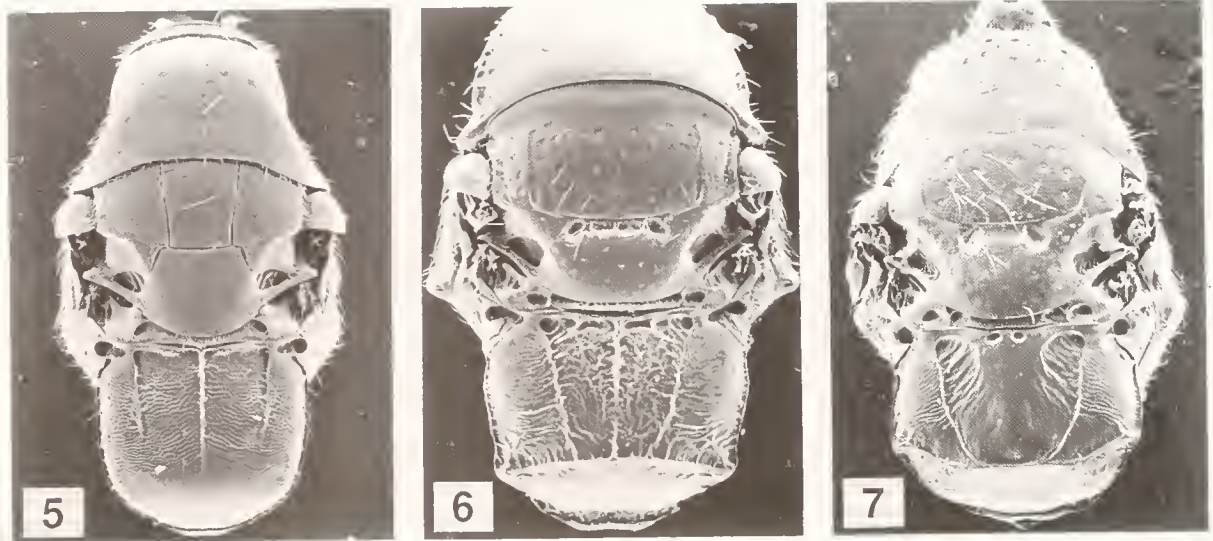
9. (node I, Fig. 26): *Bethylus*

Monophyly of *Bethylus* is supported by the following synapomorphies: 1: reduction of the number of antennal segments from 13 to 12; 13: petiolar keel absent.

DISCUSSION

The analysis supports monophyly of our modified concept of *Odontepyris*, including *Trissomalus* Kieffer, and *Parasierola* Cameron *sensu* Kieffer (1914), not Cameron (1883). The currently accepted definitions of most of the remaining genera are also supported by the analysis.

Trissomalus (Kieffer 1905) was characterised in a key, but not formally diagnosed until Kieffer's (1914) generic revision. *Odontepyris* (Kieffer 1904) was characterised mainly by the possession of dentate processes on the enlarged mesopleura



Figs. 5-7. 5. *Eupsenella* sp.: mesosoma. 6. *Odontepyris* sp.: mesosoma. 7. *Prosierola* sp.: mesosoma.

(Fig. 14). We have examined many described and undescribed species belonging to the *Odontepyris* / *Trissomalus* group, and conclude that the degree of variation in the development of the mesopleural processes, coupled with a successive reduction in the size of the discoidal cell (Figs. 22-24) suggests the group should be treated as a single genus, for which *Odontepyris* Kieffer is the oldest available name. The alternative would be to treat as new genera all intermediate species or species-groups.

Examination of *Anoxus* specimens shows that the genus differs from *Bethylus* only in the extent of setation of the eyes, other characters are identical in the two genera. Furthermore in some *Bethylus* species some setation can be found on the eyes (e. g. *B. amoenus* Fouts). Since we know that the degree of eye setation is a character that clearly varies interspecifically within other bethyline genera, we do not see how retaining *Anoxus* as a distinct genus can be justified, and it is therefore synonymised below.

GENERIC SYNONYMY

ODONTEPYRIS Kieffer

Odontepyris Kieffer 1904: 378. Type species *Odontepyris flavinervis* Kieffer 1904 by original designation. Holotype female: SUMATRA: Pangherang-Pisang x. 90 e iii. 91 (E. Modigliani) (MCSN) [examined].

Trissomalus Kieffer 1905: 105. Type species *Goniozus transvaalensis* Du Buysson, 1888: 354 by subsequent designation. Holotype female: [SOUTH AFRICA:] Transvaal, Hamman's Kraal 1893 (E. Simon) (MNHN) [examined] syn. n.

Diagnosis.—Antennae 13-segmented. Palpal formula 5:3. Frontal streak present. Notauli absent. Scutellar foveae well developed. Mesopleuron expanded, sometimes developed into a dentate prominence (Fig. 14). Median, discal and posterior transverse carinae present on propodeum, the longitudinal carinae occasionally reduced. Petiole with a complete ventral keel. Prostigma present or absent. *rs* + *m* reduced, *rs* elongate. Discoidal cell present, reduced or absent. Marginal and submarginal cells absent. Radial vein smoothly curved.

Included species.—*Odontepyris argyriae* Kurian; *O. batrae* Kurian; *O. cameroni* (Kieffer) (**comb. n.** from *Trissomalus*, holotype examined); *O. cirphi* Kurian; *O. erucarum* (Szelenyi) (**comb. n.** from *Parasierola*); *O. flavinervis* (Kieffer) (holotype examined); *O. fuscicrus* (Kieffer) (**comb. n.** from *Trissomalus*, holotype examined); *O. hypsipylae* (Kurian) (**comb. n.** from *Goniozus*); *O. indicus* Kurian (**comb. n.** from *Trissomalus*); *O. moldavicus* (Nagy) (**comb. n.** from *Prosierola*); *O. peringueyi* (Kieffer) (**comb. n.** from *Trissomalus*); *O. quadrifoveatus* (Muesebeck) (**comb. n.** from *Parasierola*, holotype examined); *O. ruficeps* Kieffer;

KEY TO GENERA OF BETHYLINAE

- 1 Closed submarginal cell present (Figs. 1, 16, 17) 2
 — Closed submarginal cell absent (Figs. 18-25) 3
 2 Marginal cell elongate, larger than submarginal (Figs. 1, 16) *Lytopsenella*
 — Marginal cell short, smaller than submarginal (Fig. 17) *Eupsenella*
 3 Marginal cell closed (Figs. 1, 16-18) *Sierola*
 — Marginal cell open (Figs. 19-25) 4
 4 Antennae 12-segmented. Wing venation as in Fig. 19; radial vein at apex turned abruptly upward, but not reaching wing margin. Fore wing with rs+m always absent *Bethylus*
 — Antennae 13-segmented. Wing venation different; radial vein shorter and evenly curved towards wing apex (Figs. 20-25). Fore wing with rs+m present or absent 5
 5 Propodeum without well-developed lateral carinae (fig 11). Scutellum without large foveae, with small grooves (as in Fig. 3). Petiole ventrally with a reduced, forked keel (Fig. 15) *Goniozus*
 — Propodeum with well-developed lateral carinae (Figs. 9, 10). Scutellum with large foveae (Figs. 6, 7). Petiole ventrally with a complete keel (Fig. 13) 6
 6 Median longitudinal propodeal carina present (Fig. 9). Propodeum without median foveae *Odontepyris*
 — Median longitudinal propodeal carina absent (Fig. 10). Propodeum with median foveae (Fig. 10) *Prosierola*

O. transvaalensis (De Buysson) (comb. n. from *Goniozus*, holotype examined); *O. waterhousei* (Kieffer) (comb. n. from *Parasierola*, holotype examined); *O. xanthoneurus* (Kieffer) (comb. n. from *Parasierola*, holotype examined).

Comments.—Tryapitsin (1978) and Terayama (1990) mistakenly included the Neotropical bethylid genus *Prosierola* in their respective keys to Russian and Japanese bethylid genera. In each case the error was due to misidentification of an *Odontepyris* species.

BETHYLUS Latreille

Bethylus Latreille, 1802: 315. Type species *Omalus fuscicornis* Jurine 1807: 301 by subsequent designation (International Commission on Zoological Nomenclature, opinion 153). Holotype ?female [not examined, ?lost].

Anoxus Thomson 1862: 451. Type species *Anoxus boops* Thomson 1862: 452. Monotypic. Lectotype female (Naturhistoriska Riksmuseet, Stockholm) [not examined] syn. n.

For full synonymy see Gordh & Moczar 1990.

Diagnosis.—Antennae 12-segmented. Palpal formula 5:2. Frontal streak absent. Eyes with or without long hairs. Notauli absent. Scutellar foveae narrow, groove-like. Mesopleuron not expanded. Propodeum without carinae. Petiole with the ventral keel absent. Prostigma and discoidal cells absent. Marginal and submarginal cells absent. Radial vein usually sharply angled.

Species transferred from *Anoxus*

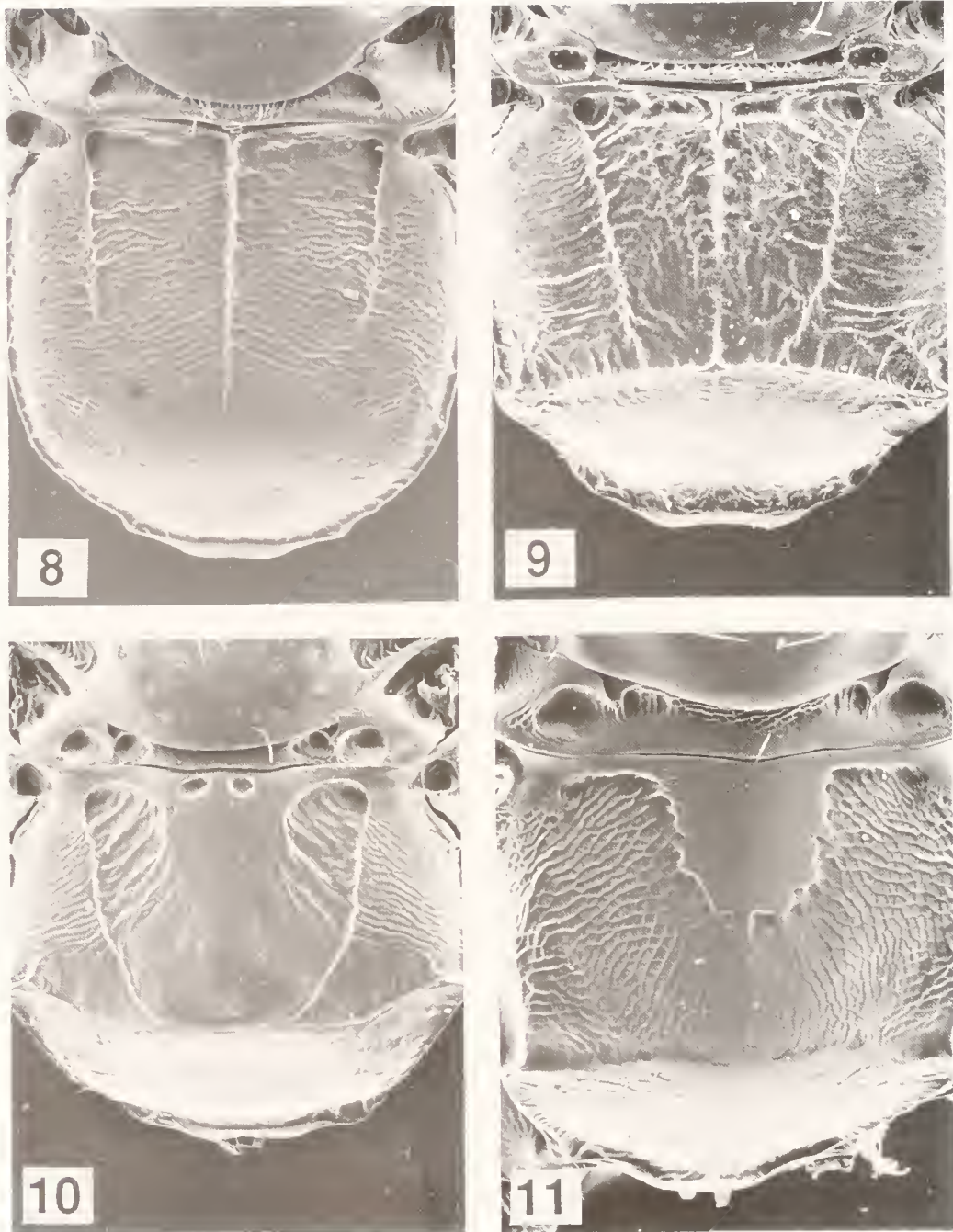
B. boops (Thomson) comb. n.; *B. coniceps* (Kieffer) comb. n.;
B. pilosus (Kieffer) comb. n.

Comments.—It might appear questionable to synonymise *Anoxus* with *Bethylus* without having examined the type species of either genus. However, there has not been any controversy surrounding these genera since Kieffer's (1914) generic revision, and we have examined sufficient material conforming to the original descriptions and Kieffer's interpretations of *Anoxus* and *Bethylus*.

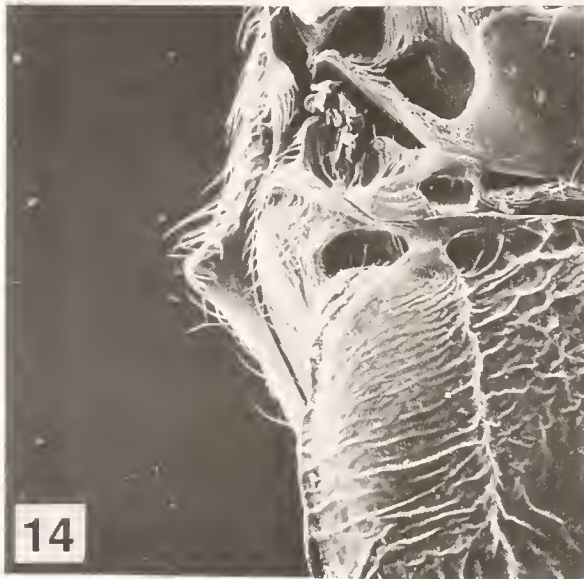
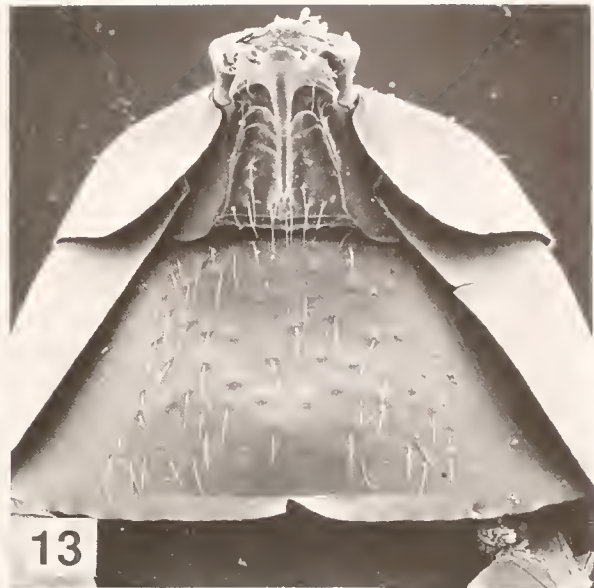
DISTRIBUTION OF BETHYLINAE

The most primitive bethylid, *Lytopsenella*, is known only from two extant species, both from Chile. Three fossil species are known from Baltic amber (Evans 1964). *Eupsenella* is known so far only from Australia.

Odontepyris is predominantly Palaetropical, but its distribution spans southeastern Europe to South Africa and northern Queensland. The small genus *Prosierola* is primarily Neotropical although one species ranges into the extreme southern United States; a fossil species from Baltic Amber is certainly incorrectly assigned to *Prosierola* (Brues 1933). *Goniozus*, with about 150 described species,



Figs. 8-11. 8, *Eupsenella* sp.: propodeum. 9, *Odontepyris* sp.: propodeum. 10, *Prosterola* sp.: propodeum. 11, *Gomozus* sp.: propodeum.

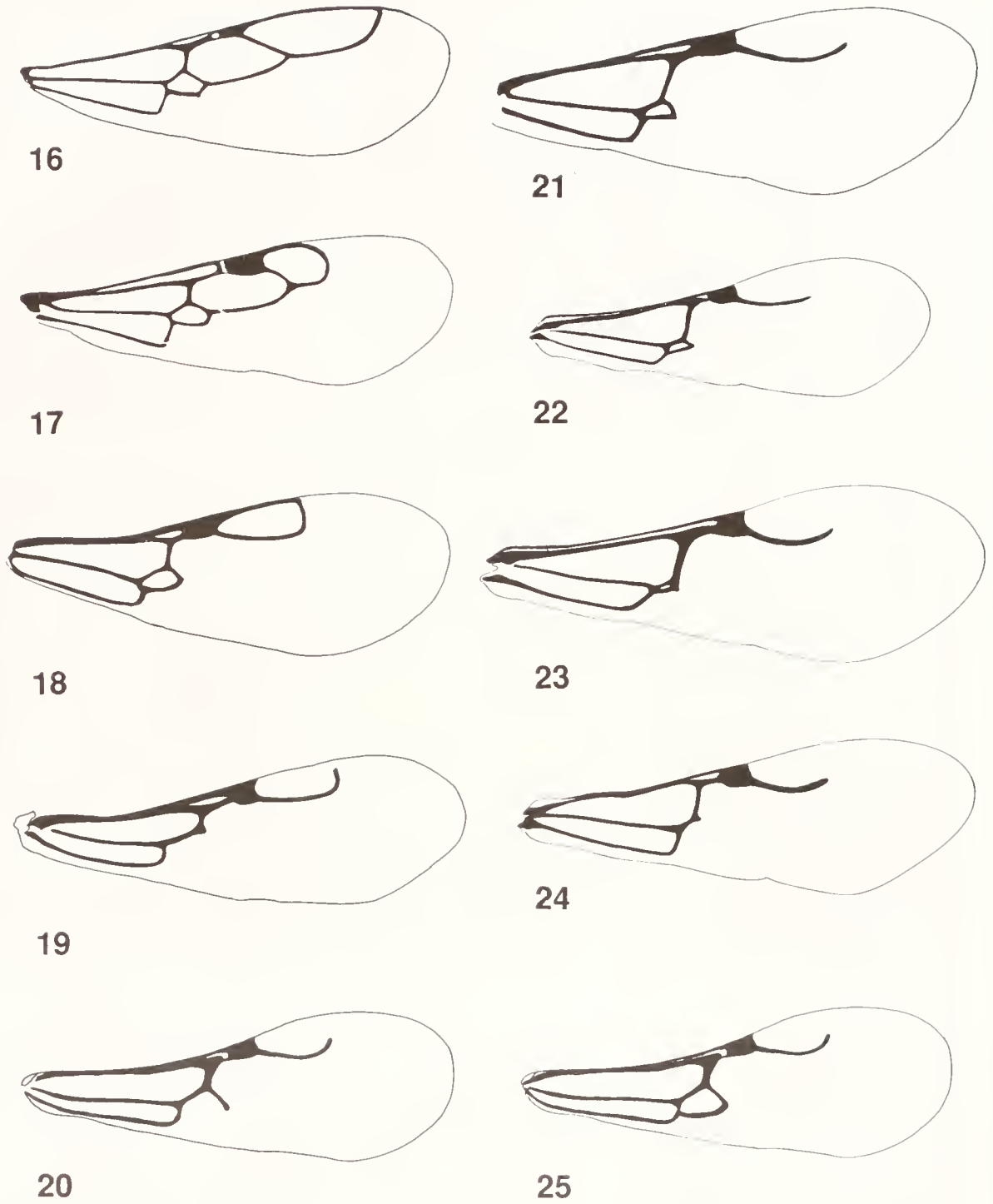


Figs. 12-15. 12, *Odontepyris* sp.: head. 13, *Odontepyris* sp.: ventral petiole and sternite 2. 14, *Odontepyris* sp.: side of mesopleuron showing dentate process. 15, *Goniozus* sp.: ventral petiole and sternite 2.

is cosmopolitan although only one species is known from the Pacific Islands. Approximately three dozen species each were described from the Oriental, Nearctic and Neotropical regions, and about a dozen each from the Palaeartic, Ethiopian and Australian regions. A number of species have been introduced into other countries as biological control agents. A few fossil species have been

described from Baltic and Dominican amber.

Sierola contains almost 200 described species, mostly from Hawaii, with three endemic species in Australia. The genus underwent tremendous speciation in Hawaii, and a secondary small speciation in the Marquesas Islands. Evans (1978) suggested that the single Californian species might be introduced, and this is possibly also true of the



Figs. 16-25. Fore wings of various Bethyloidea: 16, *Lytopsenella* sp. 17, *Eupsenella* sp.; 18, *Sierola* sp. 19, *Bethylus* sp. 20, *Goniozus* (*sensu stricto*) 21, *Prosierola* sp. 22-24, *Odontepyris* spp. 25, *Goniozus* ("*Parasierola*") sp.

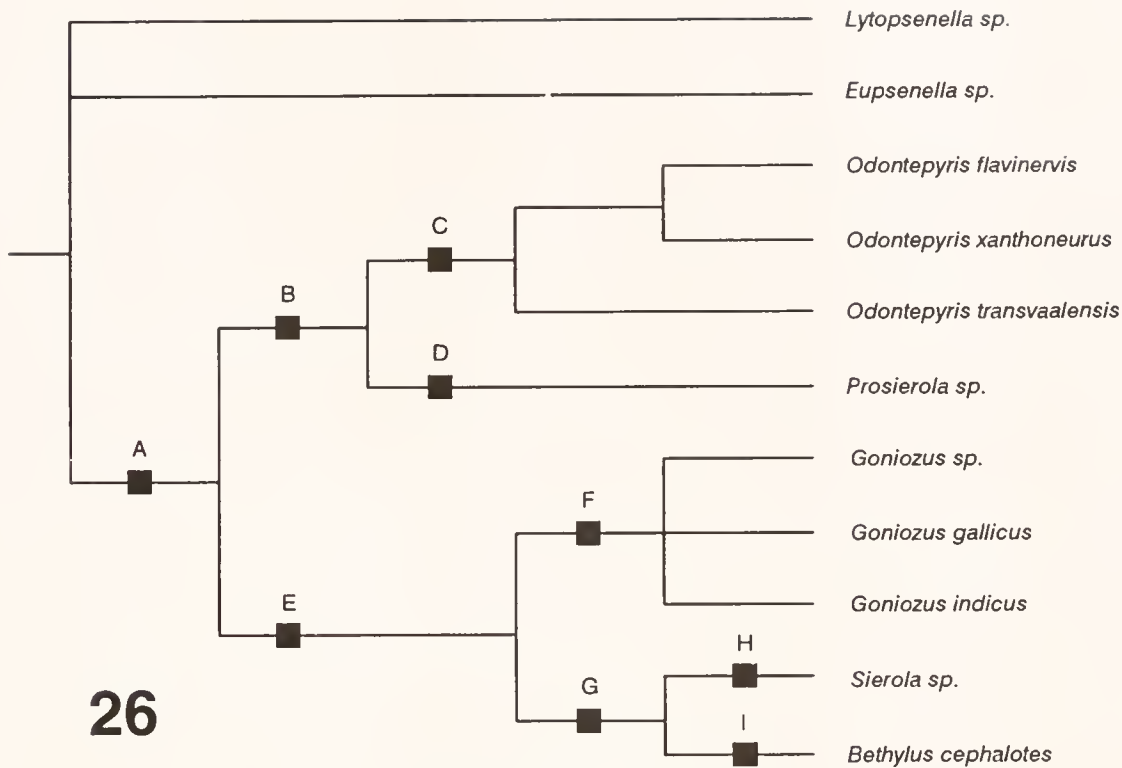


Fig. 26. Cladogram of the Bethylinae.

single Chinese species. A fossil species has been described from Baltic amber (Sorg 1988).

Bethylus, containing some 30 described species, was previously considered as Holarctic, and predominantly Palaearctic, only two species being definitely known from the Nearctic. Recently, the first author examined several specimens of *Bethylus* from South Africa. *Homalus ?amplipennis* Motschulsky was erroneously placed by Gordh & Moczar (1990) in *Bethylus*; Krombein (1987) transferred it to *Holepyris*.

BIOLOGY OF BETHYLINAE

Bethylinae are characterized in part by parasitizing lepidopterous larvae, whereas members of the other subfamilies attack primarily coleopterous larvae. A few exceptions to these host preferences are documented in Bethylinae, Epyrinae and Pristocerinae, but the few known hosts of Mesitiinae are case-bearing coleopterous larvae.

The preferred hosts within the Bethylinae are mostly microlepidopterous as listed by Evans (1978) and Gordh & Moczar (1990). However,

there are a few anomalous or questionable host records. It should be noted that, under experimental conditions, females of the epyrine *Sclerodermus immigrans* Bridwell (1920) will successfully parasitize a variety of insect larvae other than their normal coleopterous host. These include other Hawaiian beetles, bees, wasps, ants, and even braconid and chalcidoid parasites of the normal host larva. Bridwell also reared *S. immigrans* from normal workers, dealate adults, and nymphs of the termite *Neotermes castaneus* (Burmeister), although not from the soldiers. Perhaps some of the questionable records below may reflect this capability in other bethylids.

Evans (1964) reported that a specimen of *Lytopsenella herbsti* (Kieffer) was labelled as attacking an adult cantharid beetle. This record is dubious, inasmuch as hosts of all other bethylids are larvae. The only other records of bethylines attacking a host stage other than the larva are those of Nagy (1976). He reported *Odontepyris moldavicus* (Nagy) (as *Prosierola moldavica*) as reared from "pupae of a noctuid moth" and *Goniozus plugarui* Nagy attacking a lepidopterous pupa. These

records of bethylids reared from pupae are dubious, and the most probable explanation is that "pupal parasites" were reared from larvae which had spun cocoons but had not yet pupated.

Evans (1962) reported that *Bethylus amoemus* Fouts was reared from an olethreutid moth and a nitidulid beetle. The latter record was later omitted from Evans' (1978) list of host records, and to us seems doubtful. A species tentatively identified as *Goniozus gestroi* (Kieffer) was reported by Richards (1955) as being reared from larvae of the anobiid beetle, *Lasioderma*. The rearing was not questioned, only the specific identity of the *Goniozus*, and we therefore accept this record as authentic. *Goniozus morindae* Kurian (1952), described from a single male, was reared from the gall of a cecidomyiid fly, *Asphondylia morindae* Mani in flowers of *Morinda tinctoria*. The record is anomalous, and is the first for a dipteran as a host of a bethylid. The most recent authentic record of a hymenopterous host for a bethyline is that of Melo and Evans (1992) who reported *Goniozus microstigni* Evans as being reared from a brood cell of the sphecid wasp *Microstigmus xylicola* Melo, a predator of nymphal Thysanoptera. The nests were in abandoned beetle galleries in beams of an exposed roof, and a dozen *G. microstigni* females were collected while walking near and entering nests of *M. xylicola* and *M. similis* Melo.

So far as is known, all Bethylinae are gregarious parasitoids, laying a clutch of eggs on each host larva. The host is stung, sometimes repeatedly, behind the gula. Paralysis of the host larva may be temporary or permanent, depending upon the species of wasp. The number of eggs per clutch varies according to the size of the host, as well as interspecifically (Gordh & Evans 1976), ranging from one or two to as many as 40. Placement of the eggs depends upon the species, eggs being deposited either intersegmentally or longitudinally, and either dorsally, ventrally or laterally. Eggs hatch about two days after oviposition, and the larvae complete feeding in 2 to 5 days. Each larva spins a cocoon on the substrate near the host remains. The pupal period varies from 8-14 days, depending upon the species and ambient temperature. Males emerge a day or two before females are ready to eclose; they have been observed chewing into a cocoon containing a female and mating with her while she is still teneral. The progeny from a clutch usually consists of a single male and a number of

females, and sibling mating is common (Hardy 1992). Maternal care of the larvae has been observed in *Bethylus* and *Prosierola*, and the mother may subsequently mate again with one of her male offspring. Maternal care has also been observed in *Goniozus* (Hardy & Blackburn 1991). Adults of both sexes feed on honey in culture, and females have been observed feeding on haemolymph exuding from the paralysed host.

ACKNOWLEDGMENTS

This work was carried out while the first author was in receipt of a grant from the Directorate General for International Cooperation of the Netherlands Government (DGIS). We thank the following for the loan of material: J. Casevitz-Weulersse and M. LaChaise (Museum National d'Histoire Naturelle, Paris MNHN), E. De Coninck (Musée Royal de l'Afrique Centrale, Tervuren, Belgium), V. Raineri (Museo Civico di Storia Naturale, Genoa, Italy MCSN) and M. Terayama (Biological Laboratory, Toho Institute of Education, Tokyo). J. M. Carpenter (American Museum of Natural History, New York), H. E. Evans (Dept of Entomology, Colorado State University), I. C. W. Hardy (Dept of Population Biology, University of Leiden), A. Menke (Systematic Entomology Lab., USDA) and M. Mickevich (Maryland Center for Systematic Entomology, University of Maryland) are thanked for their comments on the manuscript, and R. W. Hodges (Systematic Entomology Laboratory, USDA) for assistance with Lepidoptera systematics.

LITERATURE CITED

- Brothers, D. J. 1976. Modifications of the metapostnotum and origin of the 'propodeal triangle' in Hymenoptera Aculeata. *Systematic Entomology* 1: 177-182.
- Brown, W. L. 1987. *Neoclystopenella* (Bethylidae) a synonym of *Tapinoma* (Formicidae). *Psyche* 94: 337.
- Brues, C. T. 1907. Notes and descriptions of North American parasitic Hymenoptera IV. *Bulletin of the Wisconsin Natural History Society* 5: 96-111.
- Brues, C. T. 1933. The parasitic Hymenoptera of the Baltic Amber. Part 1. *Bernstein-Forschungen* 3 (1932): 4-172.
- Cameron, P. 1883. Descriptions of new genera and species of Hymenoptera. *Transactions of the Entomological Society of London* 1883: 187-197.
- Du Buysson, R. 1898. Voyage de M. E. Simon dans l'Afrique australe (janvier-avril 1893). *Annales de la Société Entomologique de France* 66: 351-363.
- Evans, H. E. 1962. The genus *Bethylus* in North America. *Breviora* 16: 1-12.
- Evans, H. E. 1964. A synopsis of the American Bethylidae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology, Harvard University* 133:67-151.
- Evans, H. E. 1978. The Bethylidae of America north of Mexico. *Memoirs of the American Entomological Institute* 27: 1-332.

- Farris, J. S. 1988. *Hennig86 Reference. Version 1. 5. User's Manual* 17 pp.
- Gordh, G. and H. E. Evans. 1976. A new species of *Goniozus* imported into California from Ethiopia for the biological control of pink bollworm and some notes on the taxonomic status of *Parasierola* and *Goniozus* (Hymenoptera: Bethyloidea). *Proceedings of the Entomological Society of Washington* 78: 479-489.
- Gordh, G. and L. Moczar. 1990. A catalog of the World Bethyloidea (Hymenoptera: Aculeata). *Memoirs of the American Entomological Institute* 46: 1-364.
- Hardy, I. C. W. 1992. Non-binomial sex allocation and brood sex ratio variances in the parasitoid Hymenoptera. *Oikos* 65: 143-158.
- Hardy, I. C. W. and T. M. Blackburn. 1991. Brood guarding in a bethylid wasp. *Ecological Entomology* 16: 55-62.
- Hempel, A. 1934. A *Prorops nasuta* Waterston no Brasil. *Archivos do Instituto Biologico Sao Paulo* 5: 197-212.
- Jurine, L. 1807. *Nouvelle méthode de classer les Hyménoptères et les Diptères*. J. J. Paschaud, Geneva. 1-319.
- Kieffer, J. J. 1904. Description de nouveaux Dryininae et Bethylinae du Musée Civique de Gènes. *Annali Museo Civico di Storia Naturale di Genova* 41: 351-412.
- Kieffer, J. J. 1905. Description de nouveaux proctotrypidés exotiques. *Annales de la Société Scientifique de Bruxelles* 29: 95-142.
- Kieffer, J. J. 1907 (1906). Beschreibung neuer in Naturhistorischen Museum zu Hamburg aufbewahrter Proctotrypiden und Evaniiden. *Berliner Entomologische Zeitschrift* 51: 258-278.
- Kieffer, J. J. 1911. Nouveaux Bethylides et Dryinides exotiques du British Museum du Londres. *Annales de la Société Scientifique de Bruxelles* 35: 200-233.
- Kieffer, J. J. 1914. Hymenoptera, Proctotrupoidea, Bethyloidea. *Das Tierreich* 41: 1-595.
- Krombein, K. V. 1987. Synonymic notes on the Bethyloidea described by V. de Motschulsky (Hymenoptera: Aculeata). *Proceedings of the Entomological Society of Washington* 89: 356-358.
- Kurian, C. 1952. Descriptions of four new and record of one known Bethyloidea (Parasitic Hymenoptera) from India. *Agra University Journal of Research* 1: 63-72.
- Kurian, C. 1955. Bethyloidea (Hymenoptera) from India. *Agra University Journal of Research* 4: 67-155.
- Latreille, P. A. 1802. *Histoire Naturelle des Crustacés et Insectes*. Tome 3, 1-467.
- Melo, G. A. R. and H. E. Evans. 1993. Two new *Microstigmus* species (Hymenoptera, Sphecidae), with the description of their parasite, *Goniozus microstigmis* sp. n. *Proceedings of the Entomological Society of Washington* 95: 258-263.
- Menke, A. S. 1993. Notauli and parapsidal lines: just what are they? *Sphecos* 24: 9-12.
- Muesebeck, C. F. W. 1940. Two new hymenopterous parasites of sugarcane borers in India. *Proceedings of the Entomological Society of Washington* 42: 120-122.
- Nagy, C. G. 1976. Bethyloidea (Hymenoptera) parasitizing orchard caterpillars. *Revue Roumaine de Biologie, Série de Biologie Animale* 21: 103-108.
- Richards, O. W. 1955. On the Bethyloidea (Hymen.) of Israel. *Bulletin of the Research Council of Israel* 4: 357-359.
- Sorg, M. 1988. Zur phylogenie und systematik der Bethyloidea (Insecta: Hymenoptera: Chrysidoidea). *Geologisches Institut der Universitaet zu Koeln Sonderveroeffentlichungen* 63: 1-146.
- Terayama, M. 1990. Keys to the Japanese Bethyloidea (Hymenoptera, Aculeata) I. Subfamilies and Genera. *Bulletin of the Toho Gakuen* 5: 19-43.
- Thomson, C. G. 1862. Sveriges Proctotruper (Fortsattning). *Svenska Vetenskapsakademien. Stockholm. Oefversigt af K. Academinens. Forhandlingar*. 18: 451-453.
- Tryapitsyn, V. A. 1978. [Identification of the insects of the European part of the USSR. Volume 3. Hymenoptera. Bethyloidea, Bethyloidea.] *Opredelitel' Faune SSSR* 120: 3-16 (in Russian).

Variation in the Haemolymph Protein Composition of Confined *Apis Mellifera* and Partial Restoration of Vitellogenin Titre by Juvenile Hormone Analogue Treatment

M. M. G. BITONDI, Z. L. P. SIMÕES, A. M. DO NASCIMENTO AND S. L. GARCIA

Dept. Biology, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto Universidade de São Paulo, C.E.P. 14040-901
Ribeirão Preto, S.P., Brasil (AMN and SLG are undergraduate fellows of the Convênio CNPq/USP)

Abstract.—Haemolymph proteins, especially vitellogenin (Vg), were investigated in confined *Apis mellifera* workers, that were fed different diets and treated with juvenile hormone (JH) I, III or with pyriproxifen (PPN). Vg and total protein concentrations were drastically decreased in the haemolymph of workers removed from the colony and confined for different periods of time. SDS-PAGE analysis demonstrated that confinement also caused induction and repression of the synthesis of certain haemolymph proteins. All of these changes occurred even when the confined workers were fed a protein-rich diet. In workers with Vg deficiency induced by confinement PPN, but not JHI or JHIII, induced a partial increase in Vg concentration.

INTRODUCTION

The vitellogenin (Vg) of *Apis mellifera*, the precursor of vitellin—the major protein of yolk—is a glycolipoprotein produced in the fat body (Harnish and White 1982; Trenczek and Engels 1986; Shapiro *et al.* 1988; Wheeler and Kawooya 1990). In most insects, Vg synthesis may be controlled by the diet, which obviously provides the materials and energy needed for this process (Bianchi and Pereira 1987; Bownes 1989; Bownes and Reid 1990). However, other factors in addition to diet are also involved. Many studies have been conducted on the role of neurosecretory cells (Elliott and Gillott 1978) and neurohormones (Keeley and Mckercher 1985; Keeley *et al.* 1988; Girardie *et al.* 1992), and of juvenile hormones and ecdysteroids in the regulation of Vg synthesis (Adams *et al.* 1985; Borowsky *et al.* 1985; Hagedorn 1985; Schwartz *et al.* 1985; Wojchowsky and Kunkel 1987; Adams and Filipi 1988; Keeley *et al.* 1988; Ma *et al.* 1988; Röseler and Röseler 1988; Wyatt 1988; Bownes 1989; Bownes and Reid 1990; Davis *et al.* 1990; Hatakeyama and Oishi 1990; Yin *et al.* 1990; Agui *et al.* 1985, 1991; Don-Wheeler and Engelman 1991; Socha *et al.* 1991).

In *Apis mellifera*, a highly eusocial insect, the

control exerted by the queen over the workers represents an additional factor influencing Vg synthesis. A queen pheromone inhibits oocyte development in the workers. As a result Vg is not incorporated into the oocytes, although Vg is detected in the workers haemolymph. However, in queenless colonies the Vg titre of workers increases, reaching a level similar to that observed in the queens, followed by oocyte growth and oviposition (Engels 1974; Engels and Fahrenhorst 1974).

How Vg synthesis is regulated in *A. mellifera* still remains an interesting question, and aspects of this regulation have been studied in queens, workers and drones. In queens Vg synthesis does not depend on functional *corpora allata* and is not mediated by JH (Engels and Ramamurty 1976; Kaatz 1985). Similarly, JH topical application does not increase Vg synthesis in drones (Trenczek *et al.* 1989). But in workers, Rutz *et al.* (1976) and Fluri *et al.* (1977) observed that low JH doses applied on 6 day old workers stimulate Vg synthesis whereas high doses have an inhibitory effect. Furthermore, Rutz *et al.* (1976) observed a correlation *in vivo* between low JH titre and Vg synthesis. Within the first few days after worker emergence, characterized by low JH titres in haemolymph there is an increase in Vg synthesis. After this period Vg

synthesis decreases while JH titre increases. This increase in JH titre was confirmed by Huang *et al.* (1991) and the temporal changes in Vg titre observed by Rutz *et al.* (1976) were similar to those related by Engels *et al.* (1990).

The investigation of factors that affect *A. mellifera* Vg synthesis can help to understand how this protein is regulated. In the present work, the effect of some factors such as changes in social environment (confinement of workers with or without a queen) and diet (protein-rich or not) and JH or PPN (pyriproxyfen, 2-[1-methyl-2(4-phenoxyphenoxy) ethoxyl] pyridine, a JH analogue, were investigated not only on worker Vg synthesis but also on other haemolymph proteins.

MATERIALS AND METHODS

Apis mellifera

We used "wild type" Africanized *Apis mellifera* bees (hybrids of European *A. m. ligustica*, *A. m. carnica*, *A. m. mellifera* and the African bee *A. m. scutellata*) from the Experimental Apiary of the Department of Genetics, Faculty of Medicine of Ribeirão Preto, University of São Paulo.

Combs containing workers ready to emerge were removed from colonies and placed in an incubator whose temperature (34°C) and R.H. (80%) were similar to those in the colony. The workers that emerged within 15-20 hours were collected. About 100 newly emerged workers were marked on the thorax and put back into a small colony, formed by a queen, approximately 3000 workers (hive and forager bees), brood (eggs, larvae and pupae) and, sometimes, a few drones. Presence of nectar and pollen into the combs were also checked.

Confinement

The remaining workers were separated into groups of 150-200 and immediately submitted to confinement in 8 x 11 x 13 cm wooden cages with a sliding glass door and a screened bottom. The workers in these cages were placed in an incubator at 34°C and 80% R.H. and confined for 6 days (short confinement) or 15-16 days (long confinement). The confined bees received water and food *ad libitum*. The diet consisted of 50% sugar in water (syrup), a mixture of pollen from the comb (bee-

bread) and candy (powdered sugar and honey), or only candy.

In three experiments, three naturally mated queens aged 60-90 days were removed from the respective colonies and confined with groups of 150-200 newly emerged workers. These groups formed by workers and a queen were confined for 15-16 days, and fed on the mixture of beebread and candy. Water was also supplied.

Treatment of confined workers with JHIII, JHI and PPN

Some groups of 150-200 workers confined for 6 days were treated with JHIII, JHI or PPN applied topically to the abdominal cuticle. Each worker received 1 µl of a hormone solution in acetone at a concentration of 1 µg/µl, administered in two equal doses, the first immediately after emergence, before the introduction into the cages, and the other on the third day after rapid anesthesia with gaseous nitrogen. Two worker groups were treated with JHIII, two groups with JHI and nine groups with PPN.

Three control groups were prepared in parallel: the first consisted of marked workers reintroduced into the colony (control a), the second formed by confined workers treated with two 1 µl doses of acetone on the first and third days, respectively (control b). This group was also submitted to a rapid anesthesia with gaseous nitrogen at third day, immediately before acetone treatment. The third group consisted of untreated confined workers (control c). All worker groups, except control a, were allowed to feed *ad libitum* on the mixture of beebread and candy. Water was also supplied.

Haemolymph

For collecting haemolymph the workers were anesthetized with gaseous nitrogen and immobilized on dissection plates. Haemolymph was extracted through a small superficial incision in the dorsal cuticle between the 2nd and 3rd tergites.

Haemolymph was withdrawn from 6 day old and 15-16 day old confined workers that were fed on different diets, treated or not with hormones or acetone and maintained with or without a queen (Table 1). Haemolymph was also extracted from colony reared workers (6 or 15-16 day old) and from newly emerged workers before confining or

returning them to the colony.

Haemolymph pools were prepared from groups of at least 80 workers obtained from the same confinement cage. Similar pools were prepared with the haemolymph of at least 20 workers of the same age maintained in the colony and of 12 newly emerged workers. Phenylthiourea was added to the pools. Haemolymph pools were centrifuged at 3080 g for 10 min at 0°C and the supernatant was stored at -20°C.

Rocket immunoelectrophoresis

Immunoelectrophoresis was used for the quantitative determination of the vitellogenin fraction in haemolymph. Monospecific vitellogenin antiserum produced in rabbits (Simões 1980) was added at a 1% concentration to 1% agarose gels prepared with 0.06 M Tris-HCl buffer, pH 8.6. Immunoelectrophoresis was carried out at 10°C for 16 hours, at 0.08 V/cm gel. The same buffer used in the gel was used in the electrode compartments at a concentration of 0.3 M. The gels were stained with Coomassie Blue R-250. The height of the peaks detected (reported as mm) was proportional to the amount of antigen. The values obtained for confined workers were compared to those for workers of the same age maintained in colonies. The Vg peaks detected in colony reared workers (control c) was considered to be 100%.

Total protein

Protein concentration in the haemolymph pools was determined using bovine serum albumin as a standard (Bradford 1976).

SDS-PAGE

Soluble haemolymph proteins were separated by SDS-PAGE according to the method of Laemmli (1970) except that SDS was not used in the separating and stacking buffers. A 5-12% acrylamide gradient was used on a 0.7-mm thick gel. Electrophoresis was run at 12mA constant current at 10°C until bromophenol blue tracking dye reached the bottom of the slab.

Haemolymph samples (5 µl) from confined and newly emerged workers (diluted 1: 2, v/v, in sample buffer) and from workers maintained in the colonies (diluted 1: 20 or 1: 40, v/v) were applied to the acrylamide gel.

RESULTS

Confinement blocks the increase of haemolymph Vg

The confinement of workers for a period of 6 days after emergence prevented the increase of Vg titre in haemolymph that normally occurs in workers in colonies. This occurred even when beebread, the natural source of bee protein was supplied to the confined bees. In some of the haemolymph pools an extremely low Vg titre was detected (Fig. 1, wells 5 and 6), but, on average, Vg titres in these pools corresponded to $6.0 \pm 2.1\%$ (Table II) of that present in workers maintained in the colonies under natural conditions (Fig. 1, wells 1 and 2).

A small increase in Vg titre was observed in 15-16 day confined workers (Fig. 1, wells 3 and 4). This only occurred when the workers were fed beebread and candy. Even with this diet, the Vg concentration was much lower than in workers of the same age maintained in the colonies (Fig. 1, wells 1 and 2).

Confinement changes the protein pattern of haemolymph obtained by SDS-PAGE

The pattern of soluble haemolymph proteins from six day confined workers (Fig. 2, lane 4) differed from that observed in workers maintained in colonies during the same period of time (Fig. 2, lane 3). In the confined bees, in addition to the fact that the Vg band (as determined by Trenczek *et al.* 1989) was very weak, the *a* and *c* polypeptides were not observed, whereas the *b* polypeptide formed a strong band. This polypeptide corresponded to a weak band in the workers living in colonies. These were the most obvious differences, however differences between low molecular weight polypeptides, were also observed.

In Fig. 2, lanes 1, 2 correspond to the haemolymph protein pattern of newly emerged workers, collected immediately before the bees were confined or returned to the colony. This pattern changed as the bees maintained in the colony aged (Fig. 2, lane 3). However, the changes depended on the social environment as shown by the protein pattern of confined workers (Fig. 2, lane 4).

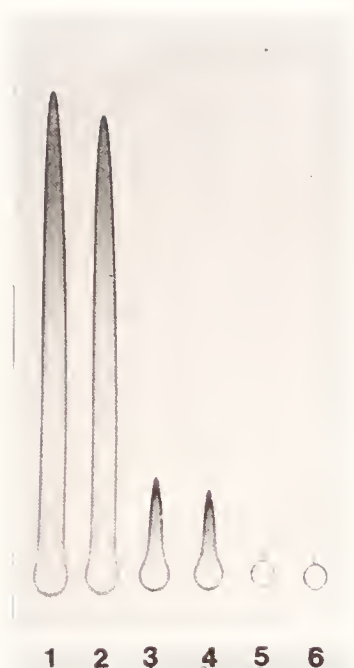


Fig. 1. Rocket immunoelectrophoresis of worker haemolymph. 150 μ l queen egg antiserum in 15 ml agarose gel. Antigen: 2 μ l of a haemolymph pool per well. Staining: Coomassie Brilliant Blue R-250. Adult workers (6 days) maintained naturally in the colony (1, 2), confined for 15-16 days (3, 4) and fed beebread and candy and confined for 6-days (5, 6) and fed the same diet.

The haemolymph pattern of workers confined for 15-16 days and fed candy and pollen (Fig. 3, lanes 5 and 6) did not differ from that obtained after a short confinement (Fig. 2, lane 4). However, a discrete increase was observed in the Vg band of workers confined for 15-16 days. The value of diet protein content for protein synthesis is clearly shown in Fig. 3, lanes 3, 4, corresponding to the protein pattern of a haemolymph pool from workers maintained on a carbohydrate (syrup) diet for 15-16 days. In the same figure, the protein pattern of haemolymph from confined workers can also be compared with that of newly emerged ones (lanes 7, 8) and with that of workers maintained in the colony for 15 days (lanes 1, 2).

There is no Vg in workers confined for 15-16 days with a queen

Workers confined for 15-16 days in the absence of a queen had Vg in their haemolymph

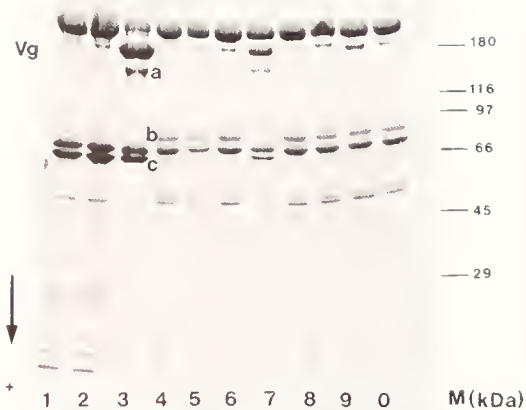


Fig. 2. SDS-PAGE (5.0-12%). Coomassie Blue staining. Patterns of worker haemolymph proteins. (1, 2) Newly emerged workers. Haemolymph diluted 1: 2 (v/v) in sample buffer; (3, 7) 6-day old workers maintained naturally in the colony. Haemolymph diluted (3) 1: 20 (v/v) and (7) 1: 40 (v/v) in sample buffer. Workers confined for 6 days after emergence and treated with PPN (10), JHI (5,9), JHIII (6), or acetone (8, 11), or untreated (4). Haemolymph diluted 1: 2 (v/v) in sample buffer. (M) - molecular weights in kDa according to marker proteins. Note: Columns should be numbered 1-11.

when fed on the beebread and candy mixture, as can be seen by immunoelectrophoresis Fig. 1, wells 3 and 4. However if a queen is confined together with a group of 150-200 workers during this same time interval, from emergence until 15-16 days, the workers will not have Vg in the haemolymph. Thus, the queen effect on Vg synthesis could be observed even in a different environment condition, i.e. that established by confinement. The haemolymph protein SDS-PAGE pattern of these workers was similar to that of bees confined in the absence of a queen, except for a weak Vg band present in the latter (results not shown).

PPN induces Vg titre increase in workers confined for 6 days

Workers confined for six days after emer-

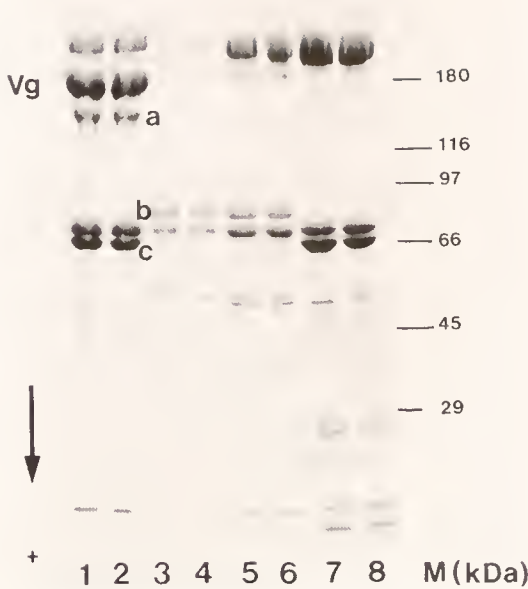


Fig. 3. SDS-PAGE (5.0-12%), Coomassie Blue staining. Patterns of worker haemolymph proteins. (1, 2) 15-day old workers maintained naturally in the colony. Haemolymph diluted 1: 20 (v/v) in sample buffer; (3, 4) workers confined for 15-16 days after emergence and fed syrup or (5, 6) bee-bread and candy; haemolymph diluted 1: 2 (v/v) in sample buffer; (7, 8) Newly emerged workers. Haemolymph diluted 1: 2 (v/v) in sample buffer. (M) - molecular weights in kDa according to marker proteins.

gence, fed beebread and candy and treated with PPN consistently showed a significant increase ($p < 0.001$) in haemolymph Vg concentration (Fig. 4, wells 3, 4, and Fig. 5, wells 3, 4) when compared to confined workers treated with acetone (Fig. 4 wells 1, 2, 7, 8; Fig. 5 well 1) or untreated (Fig. 4, wells 9, 10). This increase corresponded to approximately 17% of the Vg levels in the haemolymph of workers naturally maintained in the colonies (Fig. 4 wells 11, 12; Fig. 5, well 5). To calculate Vg percentage, we used a total of 9 haemolymph pools derived from 9 experiments, each consisting of 150-200 workers treated with PPN. In this case, Vg concentration in control a (workers maintained in the colonies) was considered to be 100% (Table II). Table II also shows that the percentage of Vg detected in acetone-treated workers (control b, $7.4 \pm 3.2\%$) did not differ ($0.5 > p > 0.4$) from that detected in the untreated control c ($6.0 \pm 2.1\%$).

The Vg titre detected in workers treated with PPN was similar to that detected in workers confined for 15-16 days and feeding on pollen and candy (Fig. 1, wells 3 and 4). This Vg concentration, however, was never detected in controls c (workers confined for six days and feeding on pollen and candy) or b (workers confined for six days, feeding on pollen and candy and treated

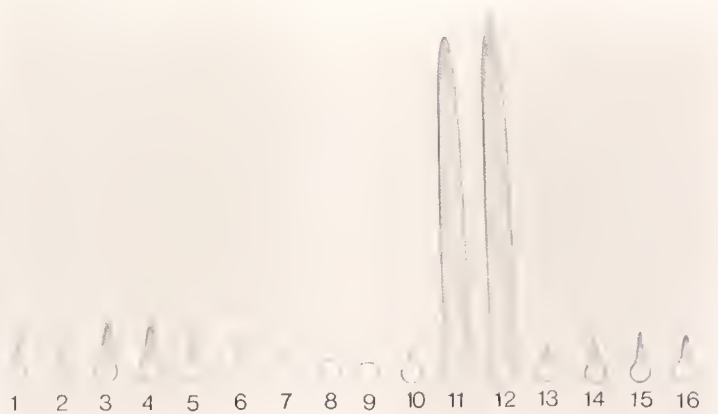


Fig. 4. Rocket immunoelectrophoresis of worker haemolymph. 150 μ l queen egg antiserum in 15 ml agarose gel. Antigen: 2 μ l of a haemolymph pool per well. Staining: Coomassie Brilliant Blue R-250. Adult workers confined for 6 days after emergence and treated with JHIII (13, 14), JHI (5, 6, 15, 16), PPN (3, 4), or acetone (control b, 1, 2, 7, 8), or untreated (control c, 9, 10). These confined workers were fed beebread and candy. Wells 11 and 12 correspond to the Vg of adult 6-day old workers maintained naturally in colonies.



Fig. 5. Rocket immunoelectrophoresis of worker haemolymph 150 μ l queen egg antiserum in 15 ml agarose gel. Antigen: 2 μ l of a haemolymph pool per well. Staining: Coomassie Brilliant Blue R-250. Adult workers confined for 6 days after emergence, fed beebread and candy and treated with acetone (control b, well 1), JHI (well 2), or PPN (wells 3 and 4). Well 5 corresponds to the Vg of adult 6-day old workers maintained naturally in colonies.

with acetone). Thus, under conditions of prolonged confinement, there is an increase in Vg concentration in haemolymph during the second week of confinement, but this increase never occurs during the first week of confinement unless the workers are treated with PPN.

PPN does not change the SDS-PAGE protein pattern

The protein pattern (Fig. 2) from workers confined for six days and treated with PPN (lane 10) was similar to that observed in the acetone-treated (lanes 8, 11) and untreated controls (lane 4), except by an increase in Vg band.

PPN does not significantly change the total protein concentration in the haemolymph

There was no significant difference in haemolymph protein content between PPN-treated workers and their controls: acetone treated (control b, $p > 0.35$) and untreated (control c, $p > 0.15$). (Table III).

Comparison between untreated groups (control c) and the groups maintained in the colonies (control a) demonstrated a drastic decrease in haemolymph protein concentration in the first group, maintained under confinement conditions, even when beebread and candy was supplied.

JHI and JHIII did not induce Vg titre increase in workers confined for 6 days

Treatment with JHI (Fig. 4, wells 5, 6, 15, 16 and Fig. 5, well 2) or JHIII (Fig. 4, wells 13, 14) under the same experimental conditions as those with PPN did not increase Vg concentration in haemolymph. The Vg peaks detected in the workers treated with JHI or JHIII did not differ statistically ($p > 0.15$ and $p > 0.5$, respectively) from the acetone-treated control b (Fig. 4, wells 1, 2, 7, 8 and Fig. 5, well 1) as showed in Table IV). However, the Vg peaks obtained from workers treated with JHI, a hormone not synthesized by *Apis mellifera* (Robinson et al. 1987), were found to be slightly higher than the peaks obtained for workers treated with acetone or with JHIII, the natural hormone of these bees. This result should be considered with caution since it is based only on the data obtained for two haemolymph pools from workers treated with JHI or JHIII. But we do not exclude the possibility of this homologue (JHI) being more effective on *Apis mellifera* than JHIII.

JHI and JHIII did not change the SDS-PAGE protein pattern

The haemolymph protein pattern of workers confined for six days and treated with JHI (Fig. 2, lanes 5, 9) or JHIII (Fig. 2, lane 6) was similar to that observed in the controls treated with acetone (Fig. 2, lanes 8, 11) or untreated (Fig. 2, lane 4).

DISCUSSION

Effect of confinement, queen presence and diet on haemolymph protein composition

Our results show that the normal Vg titre in workers mainly depends on social environment established in the colony. When workers were removed from the colony, and maintained during 6 days in an appropriate environment (where mortality was practically zero) and on a protein-rich diet, profound physiological changes occurred, that inhibited Vg titre and probably Vg synthesis. The initiation of Vg synthesis in these workers can be observed if confinement is lengthened for 15-16 days. But the haemolymph Vg peak detected by immunoelectrophoresis in these workers (after 15-16 days of confinement) is smaller than that observed in colony reared workers. The onset of Vg in the haemolymph of 15-16 days confined workers is dependent on administration of a protein-rich diet: Vg is not detected in these confined workers fed a diet without protein such as syrup, or a low protein content diet, such as candy made with honey. Besides if a queen is confined with the workers for 15-16 days no Vg is produced although a protein rich diet (beebread and pollen) had been available.

The influence of factors related to the social environment, on Vg synthesis has been studied in social Hymenoptera, especially the interaction among individuals of different castes in the colonies. Reproductively active queens characteristically inhibit Vg synthesis and egg-laying in other females capable of reproduction. This fact has been well documented in *A. mellifera* (Engels et al. 1990), *Melipona* (Engels and Imperatriz-Fonseca 1990), and *Camponotus festinatus* (Martinez and Wheeler 1991) among other social insects. We verify that *A. mellifera* queens can inhibit Vg synthesis in workers even under conditions of confinement, i.e., far from the normal colony environment. Engels et al. (1990) maintained groups of 25 workers for three weeks confined from emergence on a piece of comb, in the presence and absence of a queen. They detected that both worker groups had Vg in the haemolymph, but the Vg titre of workers confined in the absence of a queen was higher than that of workers confined in the presence of a queen. In our experiments, we found that workers confined without a queen for 15-16 days

produced Vg when fed beebread and candy. However, when the workers were confined with a queen during this same period of time, no Vg was detected in the haemolymph. Perhaps, the experimental conditions employed by Engels *et al.* 1990, with a piece of comb (with brood?) within the confinement cage, provided a more favorable environment (maybe more similar to that of a normal colony) that permitted Vg synthesis even in the presence of a queen. For comparison, other conditions employed in both experiments should also be taken into account, such as the age of the queens used, the size of the worker population and the time of confinement.

Confinement affects not only Vg synthesis, which is also controlled by the queen and by the food available, but also the synthesis of other haemolymph proteins, as determined by SDS-PAGE. The polypeptide *a* showed marked reduction, the polypeptide *c* was not detected, whereas another, *b*, showed markedly increased titer (Figs. 2 and 3). This indicates that confinement can simultaneously provoke contrasting gene expressions. This was observed in confined workers fed proteic or non-proteic diets. Workers maintained on a syrup diet had a lower protein content, but similar protein pattern in the haemolymph (Fig. 3) when compared to workers maintained on a proteic diet. Thus the social interactions and not the protein supply are responsible for the contrasting gene expressions mentioned above.

Action of PPN, JHIII and JHI on haemolymph protein composition changed by confinement

A significant ($p < 0.001$) increase in Vg titre occurred in workers with confinement-induced Vg deficiency, after treatment with PPN. However the observed induction was partial. Apparently other factors are also involved in the regulation of normal Vg synthesis. The action of these factors may be prevented or impaired by the confinement conditions employed.

PPN seems to be specific for Vg synthesis, since the haemolymph SDS-PAGE pattern of the other proteins in confined workers apparently did not change when treated with this JH analogue. However as the small increase in Vg titre induced by PPN was not reflected in total protein measurement we can not exclude the possibility that PPN also partially inhibits other haemolymph

protein(s).

Contrary to what is observed with PPN, the natural JHIII (Robinson *et al.* 1987) and its homologue JHI did not significantly increase Vg concentration in haemolymph. JHIII and JHI also did not seem to modify the haemolymph protein pattern induced by confinement. We should consider that PPN may have caused an increase in Vg titre in haemolymph by being a more potent analogue. PPN is considered to be one of the most effective juvenile hormone analogues known for locusts (De Kort and Koopmanschap 1991), with a strong juvenilizing effect on these insects. PPN has a strong morphogenetic effect when topically applied to *A. mellifera* larvae. Larvae treated with 1 µg undergo metamorphosis, but the pupae show drastic changes in pigmentation, especially in the eyes and thorax, and can also die before emergence (Bitondi *et al.*, unpublished data). Similarly to what occurs in *Locusta*, the effect of PPN on *A. mellifera* larvae and pupae is more drastic when compared to the effects induced by JHIII or JHI.

Kaatz (1985) proposed a model of regulation of Vg synthesis in *A. mellifera* queens. According to this model, Vg synthesis may be influenced by JH but also by ecdysteroids and by a haemolymph factor. These factors mentioned by Kaatz (1985) may be involved in the regulation of normal Vg synthesis in workers. However, the simple adaptation to workers of the model proposed for queens should be considered with caution since some data obtained in studies on Vg synthesis regulation in queens indicate that this regulation may differ between the two castes (Engels *et al.* 1990).

In summary the absence of one or more types of social interaction induced by confinement caused a reduction of total protein content in haemolymph, induction and repression of protein synthesis and impairment of Vg synthesis in *A. mellifera* workers. Only haemolymph Vg titer can be partially recovered by PPN treatment of confined workers.

ACKNOWLEDGMENTS

This work was supported by grants from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) Proc. 91/2587-8.

We thank Dr. H. Oouchi, Sumitomo Chemical Co., Ltd, Osaka, Japan, for providing the pyriproxyfen, and P.R. Epifânio and L. R. Aguiar for the technical assistance. We thank also Dr. David De Jong for correcting the English.

LITERATURE CITED

- Adams, T. S. and P. A. Filipi. 1988. Interaction between juvenile hormone, 20-hydroxyecdysone, the *corpus cardiacum* - *allatum* complex, and the ovaries in regulating vitellogenin levels in the housefly, *Musca domestica*. *Journal of Insect Physiology* 34: 11-19.
- Adams, T. S., H. H. Hagedorn and G. D. Wheelock. 1985. Haemolymph ecdysteroid in the housefly, *Musca domestica*, during oögenesis and its relationship with vitellogenin levels. *Journal of Insect Physiology* 31: 91-97.
- Agui, N., S. Izumi and S. Tomino. 1985. The role of ecdysteroids and juvenoids in vitellogenin levels and follicle development in the housefly, *Musca domestica*. *Applied Entomology and Zoology* 20: 179-188.
- Agui, N., T. Shimada, S. Izumi and S. Tomino. 1991. Hormonal control of vitellogenin mRNA levels in the male and female housefly, *Musca domestica*. *Journal of Insect Physiology* 37: 383-390.
- Bianchi, A. G. de and S. D. Pereira. 1987. Time of synthesis of *Musca domestica* vitellogenin during the first gonotrophic cycle. *Comparative Biochemistry, and Physiology* 86B(4): 697-700.
- Borovsky, D., B. R. Thomas, D. A. Carlson, L. R. Whisenton and M. S. Fuchs. 1985. Juvenile hormone and 20-hydroxyecdysone as primary and secondary stimuli of vitellogenesis in *Aedes aegypti*. *Archives of Insect Biochemistry and Physiology* 2: 75-90.
- Bownes, M.. 1989. The roles of juvenile hormone, ecdysone and the ovary in the control of *Drosophila* vitellogenesis. *Journal of Insect Physiology* 35(5): 409-413.
- Bownes, M. and G. Reid. 1990. The role of the ovary and nutritional signals in the regulation of fat body yolk protein gene expression in *Drosophila melanogaster*. *Journal of Insect Physiology* 36(7): 471-479.
- Bradford, M.. 1976. A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein dye binding. *Analytical Biochemistry* 72: 248-254.
- Davis, R. E., T. J. Kelly, E. P. Masler, H. W. Fescemyer, B. S. Thyagaraja and A. B. Borkovec. 1990. Hormonal control of vitellogenesis in the gypsy moth, *Lymantria dispar* (L.): suppression of haemolymph vitellogenin by the juvenile hormone analogue, methoprene. *Journal of Insect Physiology* 36(4): 231-238.
- De Kort, C. A. D. and A. B. Koopmanschap. 1991. A juvenile hormone analogue affects the protein pattern of the haemolymph in last-instar larvae of *Locusta migratoria*. *Journal of Insect Physiology* 37(2): 87-93.

- Don-Wheeler, G. and F. Engelmann. 1991. The female - and male - produced vitellogenins of *Leucophaea maderae*. *Journal of Insect Physiology* 37(12): 869-882.
- Elliot, R. H. and C. Gillot. 1978. The neuro-endocrine control of protein metabolism in the migratory grasshopper, *Melanoplus sanguinipes*. *Journal of Insect Physiology* 24: 119-126.
- Engels, W. 1974. Occurrence and significance of vitellogenins in female castes of social Hymenoptera. *American Zoologists* 14: 1229-1237.
- Engels, W. and H. Fahrenhorst. 1974. Alters - und kasten - spezifische Veränderungen der Haemolymph - Protein - Spektren bei *Apis mellifica*. *Wilhelm Roux' Archiv* 174: 285-296.
- Engels, W. and V. L. Imperatriz-Fonseca. 1990. Caste development, reproductive strategies, and control of fertility in honey bees and stingless bees. In: Engels, W. (ed.) *Social Insects. An evolutionary approach to castes and reproduction*. Springer-Verlag, Berlin, pp167-230.
- Engels, W., H. Kaatz, A. Zillikens, Z. L. Paulino-Simões, A. Trube, R. Braun and F. Dittrich. 1990. Honey bee reproduction: vitellogenin and caste-specific regulation of fertility. In: M. Hoshi and O. Yamashita (eds.) *Advances in invertebrate reproduction* 5, 495-502. Elsevier, Amsterdam.
- Engels, W. and P. S. Ramamurty. 1976. Effects of carbon dioxide on vitellogenin metabolism in unmated queen honeybees. *Journal of Apiculture Research* 15: 3-10.
- Fluri, P., H. Wille; L. Gerig and M. Lüscher. 1977. Juvenile hormone, vitellogenin and haemocyte composition in winter worker honey bees (*Apis mellifera*). *Experientia* 33: 1240-1241.
- Girardie, J., O. Richard and A. Girardie. 1992. Time-dependent variations in the activity of a novel ovary maturing neurohormone from the nervous corpora cardiaca during oögenesis in the locust, *Locusta migratoria migratorioides*. *Journal of Insect Physiology* 38: 215-221.
- Hagedorn, H. H.. 1985. The role of ecdysteroids in reproduction. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*. (Edited by G. A. Kerkut and L. I. Gilbert), vol. 8, pp 205-262. Pergamon Press, Oxford.
- Harnish, D. G. and B. N. White. 1982. Insect vitellins: identification, purification, and characterization from eight orders. *Journal of Experimental Zoology* 320: 1-10.
- Hatakeyama, M. e K. Oishi. 1990. Induction of vitellogenin synthesis and maturation of transplanted previtellogenic eggs by juvenile hormone III in males of the sawfly, *Athalia rosae*. *Journal of Insect Physiology* 36: 791-797.
- Huang, Z. Y., G. E. Robinson, S. S. Tobe, K. J. Yagi, C. Strambi, A. Strambi and B. Stay. 1991. Hormonal regulation of behavioral development in the honey bee is based on changes in the rate of juvenile hormone biosynthesis. *Journal of Insect Physiology* 37(10): 733-741.
- Kaatz, H.H.. 1985. Initiation und Regulation der Vitellogenin-Synthese bei der Bienenkönigin (*Apis mellifera* L.). Inaugural-Dissertation, Universität Tübingen, pp. 146-159.
- Keeley, L. L. and S. C. McKercher. 1985. Endocrine regulations of ovarian maturation in the cockroach *Blaberus discoidalis*. *Comparative Biochemistry and Physiology* 80A: 115-121.
- Keeley, L. L., S. M. Sowa, T. K. Hayes and J. Y. Bradfield. 1988. Neuroendocrine and juvenile hormone effects on fat body protein synthesis during the reproductive cycle in female *Blaberus discoidalis* cockroaches. *General Comparative Endocrinology* 72: 364-373.
- Laemmli, U. K. 1970. Cleavage of structural proteins during the assembly of the head of bacteriophage T₄. *Nature* 227: 680-685.
- Ma, M., J. -Z. Zhang and H. Gong. 1988. Permissive action of juvenile hormone on vitellogenin production by the mosquito *Aedes aegypti*. *Journal of Insect Physiology* 34: 593-596.
- Martinez, T. and D. Wheeler. 1991. Effect of the queen, brood and worker caste on haemolymph vitellogenin titre in *Camponotus festinatus* workers. *Journal of Insect Physiology* 37(5): 347-352.
- Robinson, G. E., Strambi, A., Strambi, C., Paulino-Simões, Z.L., Tozeto, S.O., Barbosa, J. M. N. 1987. Juvenile hormone titers in Africanized and European honey bees in Brazil. *Gen. Comp. Endocrinol.* 66: 457-459.
- Röseler, P. F. and I. Röseler. 1988. Influence of juvenile hormone on fat body metabolism in ovarioectomized queens of the bumblebee, *Bombus terrestris*. *Insect Biochemistry* 18(6): 557-563.
- Rutz, W., L. Gerig,, H. Wille and M. Lüscher. 1976. The function of juvenile hormone in adult worker honeybees, *Apis mellifera*. *Journal of Insect Physiology* 22: 1485-1491.
- Schwartz, M. B., T. J. Kelly, R. B. Imberski and E. C. Rubenstein. 1985. The effects of nutrition and methoprene treatment on ovarian ecdysteroid synthesis in *Drosophila melanogaster*. *Journal of Insect Physiology* 31: 947-957.
- Shapiro, J. P., J. H. Law and M. A. Wells. 1988. Lipid transport in insects. *Annual Review of Entomology* 33: 297-318.
- Simões, Z. L. P. 1980. Estudo da vitelogenina e da vitelina em *Apis mellifera* L. (Hymenoptera : Apoidea). Tese de doutoramento, Universidade de São Paulo. pp.: 1-108.
- Socha, R., J. Sula, D. Kodrik and I. Gelbic. 1991. Hormonal control of vitellogenin synthesis in *Pyrrhocoris apterus* (L.) (Heteroptera). *Journal of Insect Physiology* 37(): 805-816.
- Trenczek, T. and W. Engels. 1986. Occurrence of vitellogenin in drone honeybees. *International Journal of Invertebrate Reproduction and Development* 10: 307-311.
- Trenczek, T., A. Zillikens and W. Engels. 1989. Developmental patterns of vitellogenin haemolymph titre and rate of synthesis in adult drone honey bees (*Apis mellifera*). *Journal of Insect Physiology* 35: 475-481.
- Wheeler, D. E. and J. K. Kawooya. 1990. Purification and characterization of honey bee vitellogenin. *Archives of Insect Biochemistry and Physiology* 14: 253-267.
- Wojchowski, D. M. and J. G. Kunkel. 1987. Purification of two distinct oocyte vitellins and identification of their corresponding vitellogenins in fat body and hemolymph of *Blaberus discoidalis*. *Insect Biochemistry* 17: 189-198.
- Wyatt, G. R.. 1988. Vitellogenin synthesis and the analysis of juvenile hormone action in locust fat body. *Canadian Journal of Zoology* 66: 2600-2610.
- Yin, C. -M., B. -X. Zou, S. -X. Yi and J. G. Jr. Stoffolano. 1990. Ecdysteroid activity during oögenesis in the black blowfly, *Phormia regina* (Meigen). *Journal of Insect Physiology* 36: 375-382.

Table I. Haemolymph pools prepared from workers confined for 6 or 15-16 days in the presence or absence of a queen, fed on different diets and submitted or not to hormonal treatment.

No. of pools analysed	Confinement (days from emergence)	Diet	Hormonal or acetone treatment	Queen
1	6	Syrup	-	absent
1	6	Candy	-	absent
5	6	breebread and candy	-	absent
2	6	breebread and candy	JHIII	absent
2	6	breebread and candy	JHI	absent
9	6	breebread and candy	PPN	absent
6	6	breebread and candy	Acetone	absent
2	15-16	Syrup	-	absent
1	15-16	Candy	-	absent
3	15-16	breebread and candy	-	absent
3	15-16	breebread and candy	-	present

Table II - Vitellogenin (Vg) in haemolymph pools from confined workers treated with PPN or acetone (control b), from untreated confined workers (control c) and from workers maintained in colonies (control a).

Experiment No.	PPN treated		Acetone treated (control b)		Untreated (control c)		Maintained in the colonies (control a)	
	Peak Height (mm)	Vg# (%)	Peak Height (mm)	Vg# (%)	Peak Height (mm)	Vg# (%)	Peak Height (mm)	Vg# (%)
1	5.0	16.13	3.5	11.29	1.5	4.39	31.0	100
2	5.5	17.74	*	*	*	*	*	*
3	4.0	12.90	*	*	*	*	*	*
4	6.5	20.97	*	*	*	*	*	*
5	6.5	15.12	2.0	4.65	3.0	6.98	43.0	100
6	7.0	17.95	1.0	2.56	3.0	7.69	39.0	100
7	8.5	21.80	3.5	8.97	3.0	7.69	+	+
8	4.5	14.52	2.5	8.06	1.0	3.22	31.0	100
9	6.5	14.61	4.0	8.99	z	z	44.5	100
MEAN ± SD		16.9±3.0		7.4±3.2		6.0±2.1		100

Percent Vg in relation to workers maintained in the colony (control a = 100% Vg);

* Since experiments 1-4 were performed simultaneously, the same controls (a, b and c) were used in each;

z There was no control c for experiment 9;

+ Experiments 6 and 7 were performed during subsequent weeks. The same control a was used

Table III. Protein titre* ($\mu\text{g}/\mu\text{l}$ haemolymph in BSA equivalents) of 6-day old workers confined from emergence and treated with PPN or acetone (control b), untreated (control c) and maintained in the colony (control a).

Experiment No.	PPN treated $\mu\text{g}/\mu\text{l}$	Acetone treated (control b) $\mu\text{g}/\mu\text{l}$	Untreated (control c) $\mu\text{g}/\mu\text{l}$	Maintained in the colonies (control a) $\mu\text{g}/\mu\text{l}$
1	6.76	7.22	5.04	53.15
2	7.03	—	—	—
3	6.81	—	—	—
4	8.38	—	—	—
5	—	—	—	33.88
6	7.0	6.62	5.64	31.05
7	7.98	6.89	7.93	—
MEAN \pm SD	7.3 \pm 0.7	6.9 \pm 0.3	6.2 \pm 1.5	39.4 \pm 12.0

(*Protein concentrations were only measured in 6 of the 9 experimental groups treated with PPN, in 3 of the 6 groups treated with acetone, in 3 of the 5 untreated groups, and in 3 of the 5 groups maintained in the colonies.

Table IV. Vitellogenin (Vg) percent in haemolymph pools from confined workers treated with JHIII, JHI or acetone (control b) and from workers maintained in the colonies (control a).

Experiment No.	JHI treated		JHIII treated		Acetone treated		Maintained in the colonies	
	Peak Height (mm)	Vg (%)	Peak Height (mm)	Vg (%)	Peak Height (mm)	Vg (%)	Peak Height (mm)	Vg (%)
1	4.5	10.00			4.0	8.89	*	*
2	4.0	8.89	3.5	7.78	1.5	3.33	45	100
3			2.0	4.60	2.0	4.60	43.5	100
MEAN \pm SD		9.4 \pm 0.8		6.2 \pm 2.2		5.6 \pm 2.9		

* Since experiments 1 and 2 were performed on subsequent days, the same control a was used.

A Review of the Agile Species Group of *Pison* (Hymenoptera: Sphecidae: Trypoxylini)

ALEXANDER V. ANTROPOV

Zoological Museum of the Moscow State University, Herzen Street 6, Moscow K-9, 103009 Russia

Abstract.—The agile species group of *Pison* is redescribed, the 12 included species are reviewed, and a key is provided for identification. The agile group is restricted to the Oriental and eastern Palearctic Regions, although one species, *koreense*, is adventive in North America. Five species are new: *agiloides* from Sri Lanka; *chrysoptilum* from Borneo; *ningyuenfuense* from southwestern China; *vechti* from Malaya and Indonesia; and *pulawskii* from India. Other species of the group are: *agile* (Smith) from southern India and Sri Lanka; *erythropus* Kohl from western India; *koreense* (Radoszkowski) from eastern Asia and North America; *rothneyi* Cameron from southeast Asia; *browni* (Ashmead) from the Philippines; *differens* Turner from Assam, India; and *hissaricum* Gussakovskij from Uzbekistan and Tajikistan. Lectotypes are designated for *agile*, *differens* and *rufipes* (Smith) and a neotype is designated for *koreense*. *Pison koreense* is removed from synonymy with *agile*.

INTRODUCTION

The genus *Pison*, which contains nearly 200 described species (Bohart and Menke 1976; Menke 1988), is well represented in all faunal regions except North America where only an adventive species, *koreense*, is known.

In this paper I review the agile species group which contains 12 species, five of which are new. Members of this assemblage have been placed in the subgenera *Pisonoides* and *Krombeiniellum*, but Menke (1988) used species groups rather than subgenera for infrageneric groups. The agile group is restricted to the eastern Palearctic and the Oriental Regions, except for the east Asian species *koreense* which was introduced into North America presumably after World War II (Krombein 1958a).

Morphological terminology used here follows Bohart and Menke (1976) and Menke (1988). The following abbreviations are used in the text: OOD = ocello-ocular distance; OD = ocellus diameter; POD = distance between posterior ocelli.

The following museum and institutions lent specimens for this study (abbreviations are used in the text):

- AUZM Universiteit van Amsterdam, Zoologisch Museum, Amsterdam, The Netherlands (W. Hogenes).
BMNH The Natural History Museum, London, England (C. R. Vardy, L. Ficken).

- CAS California Academy of Sciences, San Francisco, California (W. J. Pulawski).
NMNH Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (C. van Achterberg).
OUM Hope Entomological Collections, University Museum, Oxford, England (C. O'Toole).
USNM U.S. National Museum, Washington, DC, USA (K. V. Krombein, A. S. Menke).
ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (V. I. Tobias).
ZMK Zoological Museum, Copenhagen, Denmark (O. Lomholdt).

The specimens from the collection of the Zoological Museum of the Moscow State University (ZMUM) were also used in the review.

THE AGILE GROUP

This group is characterized as follows: compound eyes densely setose, antenna clavate, occipital carina complete or nearly so, anterior pronotal pit small, subomolus present, episternal sulcus straight, forewing with only two submarginal cells (true second submarginal cell lost through diminution), hindcoxa without dorsolateral carina, metapleural flange usually lamelliform, propodeum without lateral carina or crenulate ridge, male sternum VIII narrow, gonostyle simple, volsella small, penis valve compressed

laterally and without teeth or notched ventrally.

Menke (1988) regarded the setose eyes, the clavate antenna, the two submarginal cells, the presence of a subomaulus, the straight episternal sulcus, the lamelliform metapleural flange and claw shape as apomorphies of the *agile* group. Its species apparently represent a monophyletic assemblage. Morphologically they are very similar and differ mainly in leg color, tergal bands, punctuation, vestiture and proportions of tergum I. Male genitalia are also similar. One of the new species, *pulawskii*, stands apart from the others in the group because its metapleural flange is narrow. I regard it as a plesiomorphic state. Two other species have unique autapomorphies: in *browni* the propodeal dorsum is delimited laterally by a shallow, broad sulcus and tergum I has a distinct preapical depression; in *agiloides* submarginal cell II is open distally.

Description.—Inner orbits of eyes moderately emarginate, parallel (eyes equidistant at vertex and clypeus) or slightly converging below (rarely above); eyes covered densely with short, erect setae (Fig. 3); clypeus convex, in female rounded (Figs. 4a, 5a), in male angulate or prominent apically (Figs. 4b, 5b); frons convex; antennae clavate, comparatively short, with distal flagellomeres wider than long; labrum subquadrate, truncate or slightly emarginate apically; occipital carina a complete (or almost complete) circle, narrowly separated from hypostomal carina; male mandible simple, that of female with inner tooth slightly distad of midpoint; pronotum with small round pit anteriorly, without lamellae; scutum and mesopleuron moderately, uniformly punctate; episternal sulcus almost straight, not curved forward ventrad; subomaulus recurved ventrad; omaulus and acetabular carina absent; mesopleural sulcus paralleled anteriorly by a row of foveolae; metapleuron smooth; metapleural flange usually broadly lamelliform posteriorly (Figs. 6-8); tegula entirely punctate; forewing media diverging after cu-a; forewing with two submarginal cells (Figs. 10-13), 2nd

(really 3rd) usually not petiolate; recurrent veins received by 1st and 2nd submarginal cells or 2nd recurrent vein interstitial between 1st and 2nd submarginal cells; hind coxa dorsum with low inner carina, without outer carina; legs finely sculptured, without stout spines on tibiae and tarsomeres; all tarsomeres IV with small plantulae; tarsal claw thick to just before apex; propodeum rounded, without lateral carinae or lines of foveae and crenulate ridges, punctate with smooth interspaces; propodeal dorsum not delimited (*browni* with shallow lateral sulcus), with medium furrow containing short to complete ridge; abdomen compact; tergum I simple or with preapical transverse depression (Figs. 15-19); apical bands of terga often translucent and with silvery or golden pubescence; male sternum VIII long, narrow, rounded or weakly notched apically; genitalia compact, compressed laterally; volsellae small, rounded and weakly setose; gonostyle triangular, simple, with long, coarse lateral setae curved beneath; penis valve compressed laterally, considerably widened apically, without teeth or notches ventrally.

Included Species.—*agile* (Smith), *agiloides* sp. n., *browni* (Ashmead), *chrysoptilum* sp. n., *differens* Turner, *erythropus* Kohl, *hissaricum* Gussakovskij, *koreense* (Radoszkowski), *ningyuenfuense* sp. n., *pulawskii* sp. n., *rothneyi* (Cameron), *vechti* sp. n.

Biology.—Information is available for two species of the group, *koreense* and *erythropus*. The former was studied by Iwata (1964) in Japan and by Sheldon (1968) in North America. The Indian species, *erythropus*, was studied by Horne (1870). These wasps construct small, clay cells, placing them separately or in groups on variable surfaces, but not within linear cavities (borings in wood or empty stems of plants). The groups may include up to 21 cells which do not merge in a common mass but keep their independence. Prey consists of 6-31 paralyzed, small, usually immature spiders.

KEY TO SPECIES OF THE *AGILE* GROUP

- | | | |
|------|--|-------------------------|
| 1 | All femora completely reddish | 2 |
| — | Mid- and hindfemora brown, forefemora mainly brown | 6 |
| 2(1) | Metapleural flange narrow (Fig. 9); India | <i>pulawskii</i> sp. n. |
| — | Metapleural flange broadly lamelliform posteriorly (Figs. 6-8) | 3 |

- 3(2) Pronotum, scutum, scutellum, metanotum and propodeal dorsum and hindface with suberect golden setae; Borneo *chrysoptilum* sp. n.
 — Thorax and propodeum with only silvery pubescence 4
- 4(3) All legs including tarsi and base of trochanters yellowish-red; western India *erythropus* Kohl
 — Trochanters, hintibiae apically and tarsi dark brown 5
- 5(4) Abdominal tergum I densely punctate (punctures separated by a diameter or less), dull due to dense microsculpture; translucent apical bands of terga I-III whitish, at middle hardly broader than hindtarsal diameter; Uzbekistan, Tajikistan *hissaricum* Gussakovskij
 — Abdominal tergum I finely, sparsely punctate (punctures more than a diameter apart), surface smooth, weakly shiny in spite of microstriae; translucent apical bands of terga golden, broad, those of II-III at middle almost equal to diameter of hindtibia; Malaysia, Indonesia *vechti* sp. n.
- 6(1) Abdominal tergum I polished, sculpture nearly same as following terga 7
 — Abdominal tergum I dull or weakly shiny in contrast to following terga 8
- 7(6) Tibiae reddish; scutal punctures fine, dense, less than a diameter apart; translucent apical bands of abdominal terga golden, apical bands of terga I-III at middle at least twice as broad as diameter of hindtarsomere I; submarginal cell II open distally (Fig. 14); Sri Lanka *agiloides* sp. n.
 — Mid- and hindtibiae brown, foretibia partly reddish; scutal punctures coarse, more than a diameter apart; translucent apical bands of abdominal terga mainly whitish, those on I-III equal to or hardly broader than diameter of hindtarsomere I (Fig. 15); submarginal cell II closed; southern India and Sri Lanka *agile* (Smith)
- 8(6) Lamelliform part of metapleural flange mainly dark; translucent apical bands of abdominal terga not broader than diameter of hindtarsomere I 9
 — Lamelliform part of metapleural flange reddish at least posteriorly; translucent apical bands of abdominal terga (at least of terga II-III) obviously broader than diameter of hindtarsomere I 10
- 9(8) Abdominal tergum I dull, very densely, finely sculptured, transversely depressed preapically (Fig. 17); apical bands of abdominal terga II-III dark brown, that of tergum I narrower than hindtarsal diameter; propodeal dorsum delimited by shallow depression at least laterally; Philippines *browni* (Ashmead)
 — Abdominal tergum I shiny dorsally, coarsely, sparsely punctate, faintly transversely depressed preapically; apical bands of abdominal terga II-III yellowish, band on tergum I almost as broad as hindtarsal diameter and half as wide as band on tergum II; propodeal dorsum not delimited by depressions; southeastern China *ningyuenfuense* sp. n.
- 10(8) Translucent apical bands of abdominal terga I-II bright golden, of equal width; propodeum as long as wide (seen from above), with hind surface mostly punctate apically; ocelli (especially in male) small (OOD>OD); India: Assam *differens* Turner
 — Translucent apical bands of abdominal tergum I very narrow or absent; propodeum wider than long (seen from above), hind surface transversely carinate apically; ocelli larger (OOD<OD=POD) 11
- 11(10) Abdomen comparatively short, terga II-III twice as wide as long (dorsal view); translucent apical bands of female tergum I often absent, narrow on terga II-III (hardly broader than diameter of hindtarsomere I), bright golden; tergum I dull due to dense microsculpture; metapleural flange with narrower, densely pubescent lamella (Fig. 11); Russian Far East, Korea, eastern China, Japan, United States *koreense* (Radoszkowski)
 — Abdomen comparatively longer, terga II-III 1.5 times as wide as long; translucent apical band of tergum I present, those on terga II-III whitish-yellow; tergum I weakly shiny, with sparse microsculpture; metapleural flange with broader, spoon-shaped, sparsely pubescent lamella (Fig. 8); southeast Asia, Malaysia, Indonesia *rothneyi* Cameron

Pison agile (Smith)
 Figs. 3, 4, 6, 10, 15

Parapison agilis Smith 1869:300. Lectotype: female, "Ceylon" (now Sri Lanka) (BMNH), present designation.

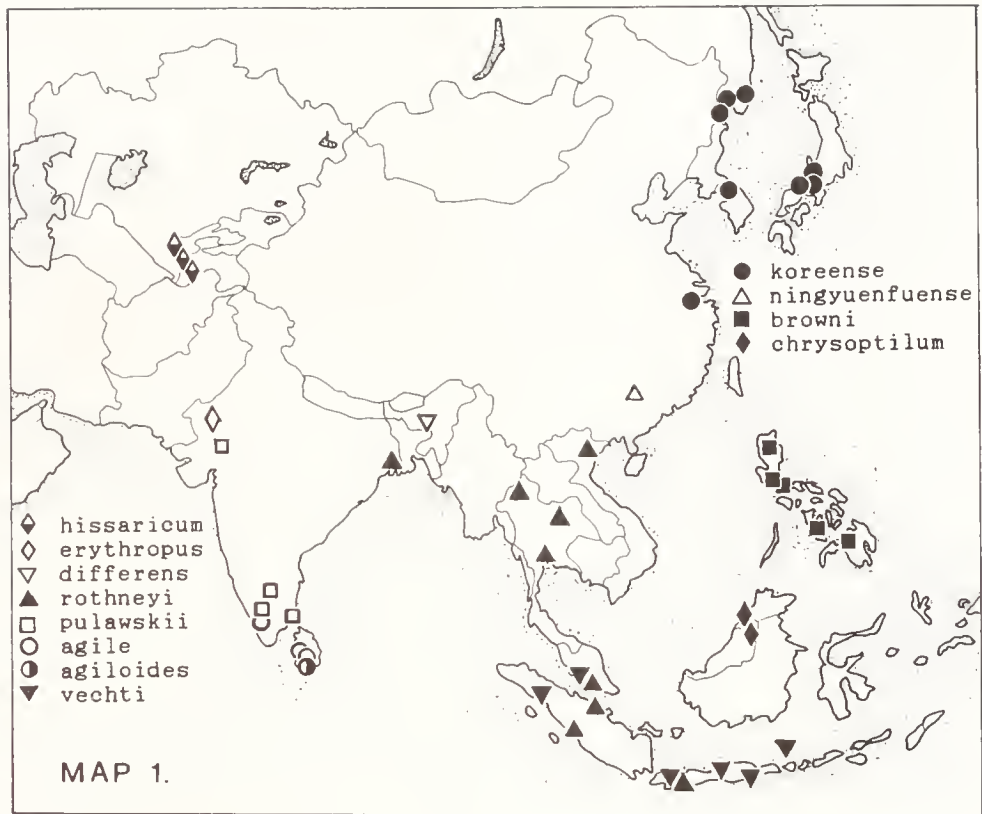
P. (Parapison) agile: Kohl 1885:186 (listed).

P. (Pisonoides) agilis: Turner 1916:616 (new combination, re-described).

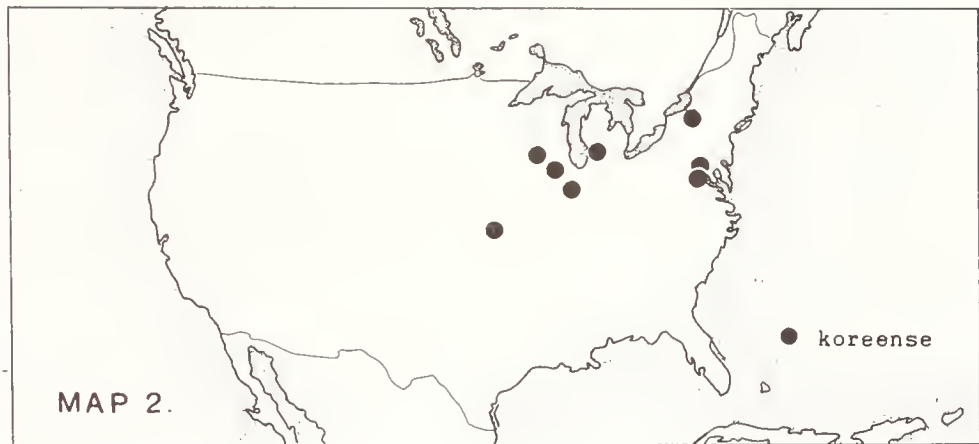
P. (Pison) agile: Bohart and Menke 1976:333 (listed).

P. agile: Menke 1988:38 (member of *agile* group, re-described).

Lectotype Selection.—The natural History Museum has two females with Smith's handwritten type labels. The first female has the museum white round label (1) with "Type" printed inside a red

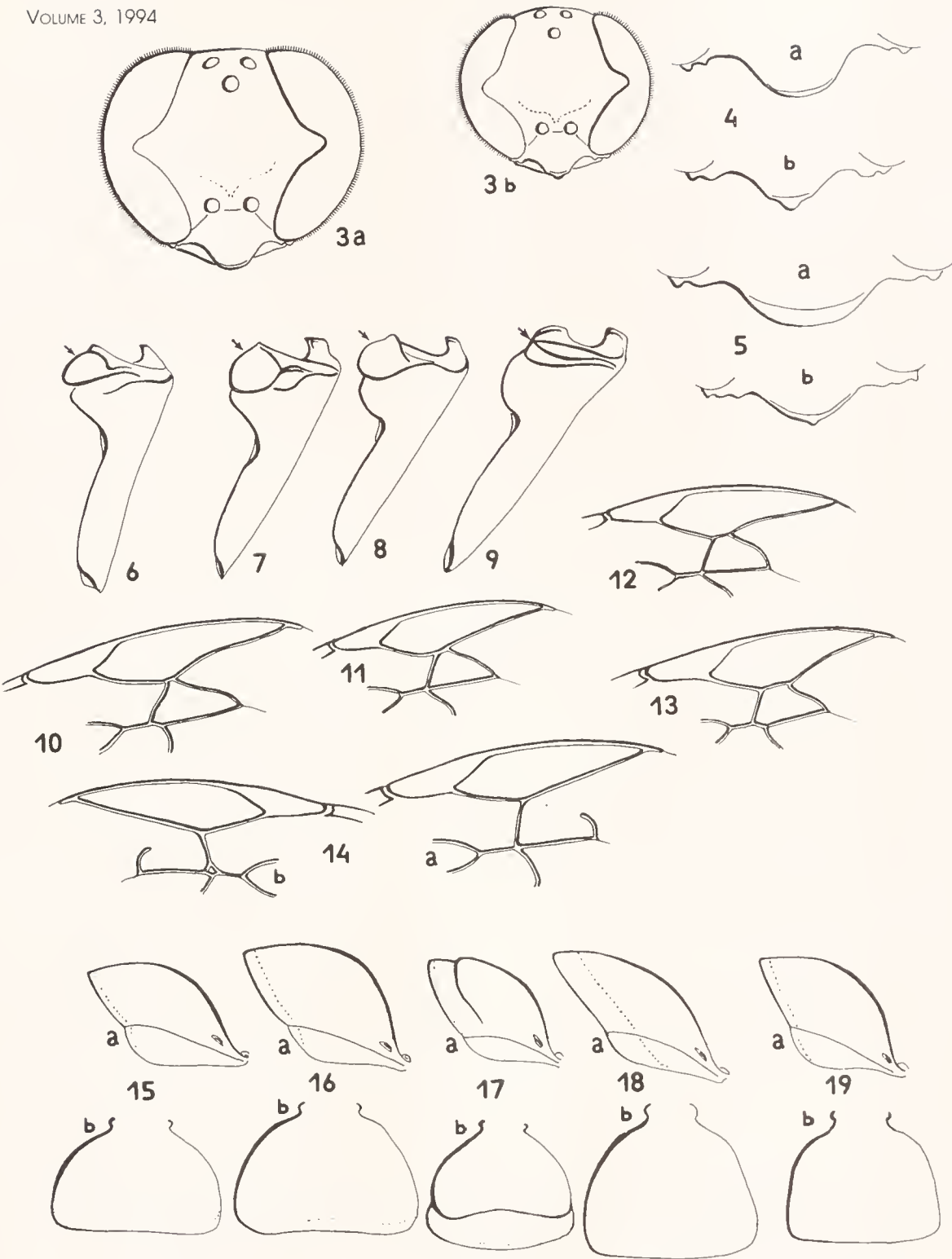


1



2

Fig. 1. Geographic distribution of the *Pison agile* species group in the Old World.
 Fig. 2. Geographic distribution of *P. koreense* in the New World.



Figs. 3-19. Morphological features of *Pison* species. 3, head in frontal view of *P. agile* (a, female; b, male). 4-5, clypeus in frontal view (a, female; b, male): 4, *P. agile*; 5, *P. pulawskii*. 6-9, right metapleuron in lateral view (arrow shows metapleural flange): 6, *P. agile*; 7, *P. koreense*; 8, *P. rothneyi*; 9, *P. pulawskii*. 10-13, submarginal cell area of right forewing: 10, *P. agile*; 11, *P. browni*; 12, *P. vechti*; 13, *P. pulawskii*. 14, submarginal cell area of forewing of *P. agiloides* (a, right; b, left). 15-19, abdominal tergite I (a, lateral view; b, dorsal view): 15, *P. agile*; 16, *P. koreense*; 17, *P. browni*; 18, *P. vechti*; 19, *P. pulawskii*.

oval, a pale-blue round label (2) with "India" handwritten on the upper side and "56/150" handwritten in two lines on the under side, a white rectangular label (3) with "agilis Sm. Type" handwritten in two lines, and the museum white rectangular label (4) with "B.M. TYPE. HYM." printed in two lines and "21.538" handwritten below. Another female has a pale-blue round label (1) with "Ceylon" handwritten on the upper side and "61/36" on the under side, a pale-blue rectangular label (2) with "P. agilis Smith. Type" handwritten in two lines. Only "Ceylon" was mentioned as the type locality in the original description so the "India" type may not be a true type. The Natural History Museum also has more than a dozen *agile* females from "Ceylon" and three of them have the same pale-blue round labels found on the second "type." I believe them to be the members of the type series and I have selected the specimen with Smith's type label as lectotype and the three other females as paralectotypes. I am discounting the Indian specimen as a type.

Discussion.—*Pison agile* is a member of a subgroup of species with mainly dark legs. Together with *agiloides* sp. n., it differs from other such species in having comparatively fine microsculpture of abdominal tergum I in which the interspaces are polished. The remaining terga are similarly polished. *Pison agile* differs from *agiloides* in having completely brown mid and hind legs, sparser and coarser scutal punctures and narrower whitish translucent apical tergal bands.

Range.—Known only from southern India and Sri Lanka.

Material Examined.—2 males, 18 females. INDIA: Anamalai Hills, Cinchona (BMNH, NMNH). SRI LANKA: North Western Prov., Kurunegala Dist., Kurunegala; Central Prov., Kandy Dist., Kandy, Udawattakele (BMNH, USNM, ZMUM).

Pison browni (Ashmead)

Figs. 11, 17

Pisonoides browni Ashmead 1905:961. Holotype: male, Philippines, "Manila" (USNM no. 8332), examined.

P. (Pisonoides) browni: Turner 1916:617 (new combination, listed).

P. (Krombeiniellum) browni: Bohart and Menke 1976:337 (new combination, listed).

P. (Krombeiniellum) browni: Tsuneki 1983:81 (redescribed)

P. browni: Menke 1988:38 (member of *agile* group).

Discussion.—This is the darkest species in the *agile* group, differing from other members by the narrow, brown apical bands on terga II-III, by the strong, transverse preapical depression of tergum I and the shallow depressions that delimit the propodeal dorsum. The last character is unique in the group.

Range.—Philippines.

Material Examined.—1 male, 2 females. LUZON: Manila (USNM), Laguna (CAS). Tsuneki (1983) recorded the species from Bontoc, Luzon; Mambucal, Negros; Cagayan de Oro, Mindanao.

Pison differens Turner

P. (Pisonoides) differens Turner 1916:617. Lectotype: female, India, "Shillong, Assam" (BMNH No. 21.540), present designation.

P. (Krombeiniellum) differens: Bohart and Menke 1976:337 (new combination, listed).

P. differens: Menke 1988:38 (member of *agile* group).

Lectotype Selection.—Turner described this species from three females without selecting a holotype. They have two identical rectangular labels: (1) "Shillong. 5.03" handwritten in two lines and (2) "Assam. R. Turner. 1905-125" printed in three lines ("Shillong, Assam, 5000 ft. (Turner), May" was mentioned in the original description). One female has in addition Turner's label "*Pison (Pisonoides) differens*. Turn. Type." handwritten in four lines and two museum labels, a round one with "Type. H.T." printed in two lines inside a red ring and a white rectangular one with "B.M. TYPE. HYM." printed in two lines and "21.540" handwritten below. I have selected the last female as lectotype and the two others as paralectotypes.

Discussion.—*Pison differens* is similar to *rothneyi* in color of the body and of the translucent apical tergal bands. The female differs from *rothneyi* by its comparatively small lateral ocelli and elongate propodeum with its hindface punctate (transversely carinate in *rothneyi*). The male also has very small ocelli but the propodeum is not elongate. In both sexes the propodeal dorsum is polished, finely sparsely punctate. The scutum is finely densely punctate in females. I think that *differens* may be a local form of *rothneyi* but more material will be required to resolve this.

Range.—Known only from Assam State, India.

Material Examined.—1 male, 3 females. INDIA: Assam State, Shillong, IV.1903, V.1903 (BMNH).

Pison erythropus Kohl

Parapison rufipes Smith 1869:299. Lectotype: female, "India" (BMNH No. 21.539), present designation. Nec *Pisonitus rufipes* Shuckard 1838:79 (now in *Pison*).

Parapison rufipes Horne, in Horne and Smith 1870:165 (biology).

P. rufipes Smith, in Horne and Smith 1870:188 (redescribed).

Pison (Parapison) erythropus Kohl 1885:183 (new name for *Parapison rufipes* Smith 1869, nec *Pisonitus rufipes* Shuckard 1838).

P. (Parapison) erythropus Kohl 1885:186 (listed).

P. erythropus: Bingham 1897:221 (listed).

P. Pisonoides erythropus: Turner 1916:616 (listed).

P. (Pison) erythropus: Bohart and Menke 1976:335 (new combination, listed).

P. erythropus: Menke 1988:38 (member of *agile* group).

Lectotype Selection.—The Natural History Museum has three females of this species bearing round labels with "India" handwritten on the upper side and "98.69" on the under side. One of them also has a rectangular label with "rufipes Sm. Type" handwritten in two lines. I believe them to be the members of the type series and I have selected the last female as lectotype and the other two females as paralectotypes.

Discussion.—*Pison erythropus* belongs to the subgroup whose members have brightly colored legs. This species is easily recognized by its entirely reddish-orange legs (including tarsi and basal parts of the trochanters).

Biology.—The nests observed by Horne (1870) in northwestern India as *Parapison rufipes* (Sm.) included "a mass of loosely arranged cells of earth attached to some hanging objects, such as a creeper, tendril, or pendent straw, or even a curled dry leaf." Horne mentioned that the cells were "very globular" and that their walls consisted of comparatively large "pellets...loosely attached to one another." He also "counted eighteen ("smallest spiders" in Horne) in two chambers." Nothing was reported about the number of cells per nest, the species or even family of the prey nor was the cocoon described.

Range.—Known with certainty only from western India.

Material Examined.—2 males, 9 females. INDIA (BMNH, ZMUM); Maharashtra District, Western Ghats, Lonavale (NMNH).

Pison hissaricum Gussakovskij

P. (Parapison) hissaricum Gussakovskij 1937:622. Holotype: female, Tajikistan, "Stalinbad" (now Dushanbe) (ZIN), examined

P. (Pison) hissaricum: Bohart and Menke 1976:336 (new combination, listed).

P. hissaricum: Menke 1988:38 (member of *agile* group).

Discussion.—*Pison hissaricum* also belongs to the subgroup whose members have brightly colored legs. This species can be recognized by the following combination of features: legs except trochanters, tarsi and tibiae reddish apically; tergum I dull due to dense microsculpture of interspaces, punctures of tergum I dense; and whitish translucent apical bands of terga I-III narrow.

Range.—Known from Uzbekistan and Tajikistan.

Material Examined.—8 males, 10 females. UZBEKISTAN: Aman-Kutan (ZMUM). TAJIKISTAN: Dushanbe; Varzob Valley, Kondara (ZIN, ZMUM).

Pison koreense (Radoszkowski)

Figs. 7, 16

Paraceramus koreensis Radoszkowski 1887:433. Holotype: female, "Koree" (Krakow, Poland. Lost). Neotype: female, Russia, Primorskiy Krai (ZMUM), present designation.

Ceramius koreensis: Morawitz in Dalla Torre 1894:3 (new combination, listed in Vespidae).

Pison (Parapison) koreense: Kohl in Dalla Torre 1897:712 (new combination, listed in Crabroninae).

Pison (Pisonoides) koreensis: Turner 1916:617 (new combination, listed).

P. (Pisonoides) koreensis: Yasumatsu 1935:229 (listed).

P. (Parapison) koreense: Gussakovskij 1937:622 (listed).

P. (Pisonoides) koreensis: Yasumatsu 1939:83 (listed).

P. (Paraceramus) koreense Krombein 1958a:166 (first record from United States).

P. (Paraceramus) koreense: Krombein 1958b:189 (listed).

Krombeiniellum koreense: Richards 1962:118 (new name for *Paraceramus* Radoszkowski 1887, nec Saussure 1854).

P. (Pisonoides) koreensis: Iwata 1964:1 (biology).

P. (Krombeiniellum) koreense: Krombein 1967:394 (new combination, listed).

P. (Krombeiniellum) koreense: Menke 1968a:7 (listed).

P. (Krombeiniellum) koreense: Menke 1968b:1102 (redescribed).

P. koreense: Sheldon 1968:107 (biology, larval morphology).

P. (Krombeiniellum) koreense: Hawkins 1974:279 (biology).

P. (Krombeiniellum) koreense: Bohart and Menke 1976:337 (listed).

P. (Krombeiniellum) agile: Krombein, et al 1979:1641 (synonymized).

P. koreense: Kazenas 1980:92 (listed).

P. agile: Menke 1988:38 (listed).

Neotype Selection.—At my request, A. P. Rasnitsyn recently searched for the type of *koreense* in Radoszkowski's collection in Krakow, Poland but could not find it. I presume it was lost and I have selected a specimen from the southern part of Primorskiy Kray (32 km SE Ussurijsk, 25.VIII.1986; eastern Russia not far from Korea) as the neotype.

Discussion.—*Pison koreense* is the best known member of the *agile* group because its biology has been studied both in its native habitat in Japan (Iwata 1964) and in the United States (Sheldon 1968) where it was introduced apparently after World War II (Krombein 1958a).

Krombein (1979) synonymized *koreense* with *agile* and Menke (1988) accepted this synonymy. After comparing the syntypes of *agile* with material from Sri Lanka, Japan, Russian Far East and the United States, I have concluded that *koreense* is a distinct species. It differs from *agile* in having a dull tergum I that contrasts with a shiny tergum II (tergum I shiny in *agile*). *Pison koreense* also differs from *agile* in having bright golden translucent apical bands on terga II-III (whitish in *agile*), largely yellowish tibiae (brown in *agile*) and a transversely carinate propodeal hind surface (mostly punctate in *agile*). The metapleural flange of *koreense* is broad and reddish (Fig. 7); it is narrow and dark in *agile* (Fig. 6). *Pison koreense* differs from *differens* and *rothneyi* in having a more compact abdomen and a weakly developed translucent apical band on tergum I.

Biology.—The wasps were studied in detail in Japan by Iwata (1964) and in North America by Sheldon (1968) who also provided a detailed description of the immature stages of *koreense*. Both Iwata and Sheldon observed that *koreense* constructed small (6.0-10.2 X 4.0-6.0 mm), fragile, cylindrical mud cells with finely cemented walls. The cells are placed separately or in groups of up to 21 independent cells. The cells are attached in various protected places: inside a photographic tank (Krombein 1958a); in a culvert, in small depressions and cracks and under a bridge (Sheldon 1968); in the nooks of a mud wall under eaves (Iwata 1964); and even within the old empty cells of *Trypoxylon (Trypargilum) politum* (Say) (Sheldon 1968; Hawkins 1974). Construction of cells on

plants, as in *erythropus*, is unknown. The cells were provisioned with six immature spiders of the genus *Araneus* (Araneidae) (Iwata 1964) or by 20-31 small spiders of the genus *Dictyna* (Dictynidae), including males and females of *D. bellans* Chamberlin and *D. sublata* Hentz (Sheldon 1968). *P. koreense* cocoons are cylindrical (6.0-9.1 X 2.0-3.6 mm) and, according to Sheldon, were surrounded by "delicate silken threads attaching cocoon to inside of cell." Sheldon also mentioned a large number of adult *Melittobia chalybii* Ashmead (Eulophidae) which were reared from *koreense* cocoon "from a nest constructed in an unsealed cell of *Trypoxylon politum*."

I also observed nesting and hunting activities of *koreense* during 1983-1986 in the Primorskiy Kray in the Far East of Russia. The females made their small clay cells between logs in the wall of an old rural shed, placing them in groups of up to 20 independent cells. Five to seven specimens of immature spider of the genus *Araneus* were put into each cell. When hunting the female of *koreense* looked for the prey on their webs and attacked them from the dorsum, embracing the carapace and applying a single sting to the venter of the spider. After paralyzing the spider, the female turned the prey venter up, clutched the base of its chelicerae with her mandibles and flew with it to her cell. I observed egg-laying only once and it was the last operation before sealing the cell. Sheldon (1968) also mentioned that the egg was attached to the abdomen of the last spider in the cell.

Thus, populations of *koreense* in Russian Far East, Japan and the United States have similar biological features except prey. Spiders of the family Dictynidae were preferred in North America and Araneidae in eastern Asia.

Range.—Russian Far East, Korea, Japan, eastern China, United States: Illinois, Kansas, Maryland, Michigan, New York, Virginia, Wisconsin.

Material Examined.—28 males, 18 females. RUSSIA, Primorskiy Kray: Sichote-Alin, Vangou; 32 km SE Ussurijsk; Partizansk; 70 km ENE Partizansk (CAS, USNM, ZMUM). CHINA, Zhejiang: Hangchow (USNM). JAPAN, Fukui, Mt. Haku: Ichinose; Chugu; Mie (USNM, ZMUM). USA: Kansas, Lawrence; Virginia, McLean (USNM).

Pison rothneyi Cameron

Fig. 8

P. (Parapison) rothneyi Cameron 1897a:81. Holotype: female, India, West Bengal State, "Barrackpore" (now Barakpur) (OUM), examined.

P. (Parapison) crassicornis Cameron 1897a:25. Holotype: male (female in original description), India, West Bengal State, "Barrackpore" (now Barakpur) (OUM), examined. Synonymy by Turner (1916:617).

P. (Pisonoides) rothneyi: Turner 1916:617 (new combination, listed).

P. (Krombeiniellum) erythropus: Tsuneki 1974:637 (new combination, misidentified).

P. (Pison) rothneyi: Bohart and Menke 1976:336 (listed).

P. rothneyi: Menke 1988:38 (member of *agile* group).

Discussion.—This species is similar to *differens* and also *koreense*, differing from the first by the narrower translucent whitish-yellow apical bands of the terga, by the comparatively larger ocelli and by the shorter propodeum whose dorsum is distinctly punctate and the hind surface transversely carinate apically. Also, *rothneyi* has a more coarsely sculptured scutum and deeper impressed parapsidal lines. *Pison rothneyi* differs from *koreense* by the comparatively longer abdominal terga with well developed whitish-yellow translucent bands on all terga, including tergum I. *Pison rothneyi* also has a broader, spoon-shaped reddish-orange metapleural flange (Fig. 8) and its tergum I is shiny (semidull in *differens* and *koreense*). Tsuneki (1974) misidentified specimens of *rothneyi* as *erythropus*. The dark femora and tarsi of his specimens confirm this.

Range.—This is the most widely distributed Oriental member of the *agile* group. It is recorded from eastern India, Thailand, Viet Nam, Malaysia and Indonesia.

Material Examined.—1 male, 13 females. INDIA, West Bengal: Barrackpore (OUM). THAILAND, Chiang Mai Province: Fang Horticultural Exp. Station; Doi Inthanon N. P.: Huai Sai Luang (ZMK). Malaysia: Teluk Merban (ZMK); Kuala Lumpur (BMNH). VIET NAM: Tonkin, Poste de Dong-Dang (ZMUM). INDONESIA, Sumatra: Pakanbaru, Solok; Java: Bogor, Semarang (NMNH).

Pison agiloides Antropov, new species

Fig. 14

Description of Holotype Female.—Black except the following reddish: palpi, mandible largely,

labrum, tibiae except apically, femora apically, pronotal lobe posteriorly, tegula and metapleural flange; translucent apical bands of abdominal terga I-V and sterna II-V, and terga I-V laterally yellowish-white.

Clypeus, frons beneath, pronotum anteriorly, scutellum, metanotum and propodeum with dense erect silvery pubescence, longest setae on propodeum laterally and posteriorly; pronotal collar, scutum, mesopleuron and abdomen with suberect, dense, short pubescence, longest setae on apical band of tergum I.

Labrum slightly emarginate apically, inner orbits almost parallel, OOD < OD.

Frons densely punctate, interspace smooth, shiny; scutum densely, finely punctate, punctures separated by less than a diameter; scutellum, mesopleuron, metanotum and propodeum more sparsely punctate, punctures 1-3 diameters apart, interspaces polished; propodeal dorsum not enclosed by sulcus or carina; metapleural flange broad, spoon-shaped, translucent, with long silvery setae.

Right forewing (Fig. 14a) with two, left forewing (Fig. 14b) with three submarginal cells, outer submarginal cell of forewings open distally; recurrent vein II ending on tiny submarginal cell II (left forewing) and interstitial on right forewing.

Abdomen simple; terga shiny, densely punctate, diameter of punctures decreasing from basal to apical terga; tergum I with microsculpture, other terga more polished between punctures; sternum I similar to frons, other sterna densely, finely punctate, shiny; translucent apical bands of abdominal segments 1.5 to twice as broad as diameter of first hind tarsomere.

Male.—Unknown.

Discussion.—The new species differs from *agile* in having the dense, fine punctation of the scutum and abdomen, the longer propodeum, the comparatively short setae of the thorax and abdomen, the broad translucent apical bands of the abdominal segments and the reddish tibiae and metapleural flange. The last features are shared with *rothneyi*, but the latter has completely reddish tibiae, tergum I is shiny and the propodeum is elongate. *Pison differens* also has fine, dense scutal punctures, but it differs from *agiloides* by its larger OOD, by its dark-brown tibiae and by the weakly shiny surface of tergum I.

The open second submarginal cell of the unique

specimen of *agiloides* may prove to be individual when more material is available. The presence of the true second submarginal cell in the left forewing is likely to be atypical also, but it illustrates that the loss of this cell is achieved via diminution of its size in the *agile* group (see also Menke 1988).

Etymology.—The ending of the species name emphasizes the likeness of this species and *agile*.

Range.—Sri Lanka.

Type.—Holotype female: SRI LANKA, Sabaragamuwa Province, Ratnapura District, Belihuloya Resthouse, 9.IV.1978, M. D. Hubbard, T. Wijesinhe (USNM).

***Pison ningyuenfuense* Antropov, new species**

Description of Holotype Female.—Black except the following reddish: palpi, mandible largely, labrum, foretibia anteriorly, midtibia basally, hindtibia basally and posteriorly and all spurs; apical rim of clypeus, tarsi ventrally and tegula reddish-brown; metapleural flange brown; translucent apical bands of abdominal terga I-V whitish.

Pubescence silvery; clypeus, frons, vertex, pronotum, scutum posteriorly, scutellum, metanotum and propodeum with erect setae, longest on pronotum laterally and on propodeum; gena, mesopleuron and abdomen with suberect, dense, short setae, those on gena and lateral angles of abdominal tergum I longest; scutum with extremely short, erect setae as on femora.

Pronotum and scutum finely and densely punctate, shiny, punctures less than a diameter apart; mesopleuron, scutellum and metanotum more sparsely punctate (punctures 1-2 diameters apart); propodeum coarsely punctate (punctures at least twice as large as those on scutum); abdominal tergum I moderately coarsely, sparsely punctate (punctures similar in size to those on propodeum), interspaces weakly shiny due to dense microsculpture; sternum I similarly punctate but shiny; following abdominal segments densely, finely punctate (like scutellum), shiny.

Translucent apical bands of abdominal terga II-V as broad as diameter of first hind tarsomere, bands of tergum I and sterna II-V less than diameter of first hind tarsomere; apex of tergum I shallowly but distinctly depressed (depressed part as broad at middle as maximal diameter of hind tibia); terga II-IV laterally with rounded tubercles.

Recurrent vein I ending on submarginal cell I, recurrent vein II ending on submarginal cell II near its base (nearly interstitial).

Length 7.6 mm.

Male.—Unknown.

Discussion.—*Pison ningyuenfuense* differs from the most similar *browni* by having an undefined propodeal dorsum (no limiting sulcus or carina), by the comparatively shallowly depressed apical part of abdominal tergum I, which is more coarsely punctate, with interspaces only weakly shiny, and by the whitish translucent apical bands of terga I-V.

Etymology.—The species name is derived from the native name of the holotype locality.

Range.—Known only from the type locality in southeastern China.

Type.—Holotype female: CHINA, Hunan Province, Ningyuenfu, July 24-26-28, alt. 600-10,800, D. C. Graham (USNM).

***Pison vechti* Antropov, new species**

Figs. 12, 18

Description of Holotype Female.—Black except the following bright reddish-orange: palpi, mandible largely, fore and mid tibiae and fore femur completely, mid and hind femora except dorsum and hind tibia except posteriorly, tegula and metapleural flange posteriorly, apical band on abdominal tergum I and medial spots on terga II-III before translucent apical bands; pronotal lobe posteriorly and spical tarsomeres beneath yellowish; translucent apical bands of terga I-V and sterna II-VI bright golden.

Pubescence of head and thorax silvery, mainly golden on abdominal terga (especially on translucent bands laterally); frons, vertex, gena, pronotum, scutum, scutellum, mesopleuron and metanotum with dense, short, erect setae (not longer than mid ocellus diameter); propodeum posteriolaterally with longer dense, erect setae (almost twice as long as mid ocellus diameter); abdomen with suberect or almost appressed dense, short setae.

Labrum truncate apically; median lobe of clypeus obtusely angulate, with narrow, shiny apical margin; inner orbits almost parallel; $OOD < OD = POD$.

Clypeus, frons, pronotum and scutum densely, minutely punctate, weakly shiny (punctures

mostly less than a diameter apart); scutellum, mesopleuron and metanotum with sparse punctation (punctures 1.5-2.0 diameters apart), interspaces polished; metapleural flange broad, spoon-shaped, translucent posteriorly; propodeum posteriorly and laterally punctured like mesopleuron but obviously coarser; propodeal dorsum shiny, not enclosed by sulcus or carina, with sparse punctures (2-4 diameters apart) and with deep median furrow containing simple carina on basal half; abdominal tergum I punctate (punctures 1-3 diameters apart), densely microsculptured, weakly shiny, sternum I, tergum and sternum II densely, finely punctate (punctures of sternum I coarsest), shiny; other abdominal segments densely micropunctate, surface smooth, weakly shiny; translucent apical bands of abdominal terga II-IV as broad laterally and medially as hindtibial diameter (those of terga I and V and sterna II-IV 1.5 times diameter of first hindtarsomere (Fig. 18).

Recurrent vein I ending on submarginal cell I, recurrent vein II ending near base of submarginal cell II, the latter very narrow anteriorly, almost triangular (Fig. 12).

Length 7.6 mm.

Variation in Females (18 specimens).—Femora and tibiae all bright reddish-orange in two females from Buitenzorg, Java (28.VI.1932) and Tembajangan, Kangean Island all femora dark posteriorly in a female from Mulie, Java, and submarginal cell II completely triangular in another female from Buitenzorg (16.X.1941). Length 7.0-7.8 mm.

Male.—As in female except: median lobe of clypeus narrower, acutely prominent apically; punctation sparser on scutum (punctures 1-2 diameters apart) and mesopleuron (punctures 2-4 diameters apart). Length 5.4 mm.

Discussion.—*Pison vechti* is very similar to *hissaricum*, *erythropus* and *differens* in having widened metapleural flange and largely bright reddish-orange legs. It is easily separated from *hissaricum* and *erythropus* in having the broad, golded, translucent apical bands of the terga. Furthermore, it differs from *erythropus* in having dark-brown trochanters and tarsi and a densely punctate, weakly shiny scutum. *Pison vechti* differs from *differens* in having the larger lateral ocelli and a comparatively short propodeum. The color of the abdomen of *vechti* is similar to *rothmeyei*, but the

latter has mainly brown femora and tibiae. *Pison pulawskii* also has bright reddish-orange legs but differs from all mentioned species in having a narrow metapleural flange.

Etymology.—This species is dedicated to Jacobus van der Vecht.

Range.—Malaysian Peninsula and southeastern Asian islands (Malaysian and Indonesian).

Types.—Holotype female: INDONESIA, E. Java, Idjen, Plateau Blawan, 900 m, 28.V.1939, J. v. d. Vecht (NMNH). Paratypes (1 male, 19 females): MALAYSIA, Kuala Lumpur: 27.X.1929, H. Pendlebury (NMNH); Tanglui Road, 20.V.1928, T. T. Pagden (BMNH). INDONESIA, Sumatra: Fort de Kock, 920 m, 1926, E. Jacobson (AUZM); Sibolga, 142°N-98 48'E, V_VIII.1954, W. Vergeest (NMNH); Java: Buitenzorg, J. v. d. Vecht; Buitenzorg, 16.X.1941, II.1953, J. v. d. Vecht; Buitenzorg, Pebaton, 28.VI.1932, J. v. d. Vecht; Buitenzorg, Jnsl. v. Pln., 15.VI.1929, J. v. d. Vecht; Malang, IV.1933, Betrem; Bogor, 1955, Hamann; Mulie; W. Preanger, Z. Soekaboemi, IV.1933, J. v. d. Vecht; Ambarawa, Lundeking (NMNH); Malang, IV.1933, Betrem (ZMUM); Mt. Tijoeng, Djampang Tengah, I.1939, K. M. Walsh (BMNH); Kangean Isl.: Tembajangan, II.1936, M. E. Walsh (NMNH).

Pison chrysoptilum Antropov, new species

Description of Holotype Female.—Black except the following reddish-orange: palpi, mandible except apically, labrum, pronotal lobe posteriorly, tegula mainly, widened part of metapleural flange, all femora except posteriorly and tibiae except apically; translucent apical bands of abdominal terga I-V golden.

Pubescence silvery on clypeus, mesopleuron, propodeum laterally and abdominal sterna, golden on frons, vertex, gena, pronotum, scutum, scutellum, metanotum, propodeal corsum and hindface and abdominal terga. Clypeus, pronotal collar, propodeal dorsum and terga with suberect or decumbent dense setae (shortest on abdomen, longest on pronotum); other areas with erect setae, shortest on scutum and abdominal sterna, longest on metanotum and propodeum posterolaterally.

Median clypeal lobe rounded, with narrowly semitranslucent brown apical margin; inner orbits of eyes converging above; OD>POD>OOD.

Clypeus, frons, vertex, pronotum, scutum, scutellum and mesopleuron finely, densely punc-

tate (punctures 0.5-1.5 diameters apart), shiny; metapleural flange broad, spoon-shaped, widened part translucent; propodeum more coarsely, sparsely punctate laterally and dorsally (at least 2 diameters apart), hindface coarsely and densely punctate (0.5-1.0 diameters apart), with transverse ridges ventrally; propodeal dorsum not enclosed by sulcus or carina, with narrow median furrow containing simple carina; tergum I punctate (1-# diameters apart), shiny in spite of microstriation; sternum I with coarser punctures (as on propodeal hindface), shiny; other abdominal sclerites microscopically but distinctly, densely and uniformly punctate (approximately a diameter apart), shiny; translucent apical margins of terga I-IV twice as broad as diameter of first hind tarsomere (on tergum V and sternum III-V slightly less than diameter).

Recurrent vein I ending on submarginal cell I, recurrent vein II ending near base of submarginal cell II.

Length 8.2 mm.

Variation in Females (2 specimens).—Paratype female differs by its smaller size (6.2 mm) and almost parallel inner orbits of eye.

Male.—Unknown.

Discussion.—Unlike all other members of the *agile* group, *chrysoptilum* has golden pubescence on the frons, vertex, thorax and propodeum. It resembles *vechti* because of its brightly colored legs and golden translucent bands on the abdominal terga. *Pison chrysoptilum* and *vechti* may be two forms of one species, but more material will be necessary to resolve this.

Etymology.—This species name is derived from the Greek words *chrysos* (=gold) and *ptilon* (=down, fluff) emphasizing the color of the pubescence.

Range.—Northern Borneo (Sarawak, Brunei).

Types.—Holotype female: MALAYSIA, Sarawak: 4th div., Gn. Mulu, RGS Exp., 17.IX-23.X.1977, D. Hollis (BMNH). Paratype (1 female): BRUNEI: Ulu Temburong, Base camp hut, 300 m, 115 16'E, 4 26'N, 16.II-9.III.1982, M. C. Day (BMNH).

Pison pulawskii Antropov, new species

Figs. 5, 9, 13, 19

Description of Holotype Female.—Black except the following reddish-orange: palpi, mandible largely, labrum, fore legs distad of coxal apex, mid and hind legs except basal parts of coxae and

tarsomeres III-V; antennal articles beneath, apical margin of clypeus, tegula, mid and hind tarsomeres III-V reddish-brown.

Pubescence silvery only; clypeus, frons, vertex, pronotal collar, scutum, scutellum, metanotum, metapleuron and propodeum with erect setae, longest on propodeum posterolaterally and shortest on scutum (scarsely longer than on femora); gena, mesopleuron and abdomen with suberect or appressed short setae (longest on apical bands of terga and shortest on sternum).

Labrum truncate apically; clypeus comparatively broadly rounded (Fig. 5A); inner orbits of eyes almost parallel; OOD=OD=POD.

Frons densely punctate, shiny; scutum very densely, finely punctate, weakly shiny; mesopleuron uniformly, sparsely punctate (1.0-1.5 diameters apart), polished; metapleural flange not lamellate (Fig. 9); propodeal dorsum obliquely carinate basally and along median furrow, dorsum not enclosed by sulcus or carina, sparsely punctate (as on propodeal side) (1-3 diameters apart); tergum I uniformly, densely punctate (as on mesopleuron), shiny; tergum II more densely and finely punctate, shiny; remaining terga weakly shiny because of very dense microscopic punctures; sternum I dull, punctured as frons; sternum II shiny, punctate as mesopleuron; other sternum with dense micropunctures, weakly shiny; translucent apical bands of terga I-V and sternum II-IV whitish, as broad as diameter of hindtarsomere I (Fig. 19).

Recurrent vein I ending on submarginal cell I, recurrent vein II ending on submarginal cell II near its base (Fig. 13).

Length 7.0 mm.

Variation in Females (11 specimens).—Mid tarsi completely reddish-orange in three specimens from holotype locality and one from Kurumbagaram; hind tibiae and tarsi brownish posteriorly and antennal flagellum completely dark-brown in one specimen from Coimbatore. Length 6.0-7.0 mm.

Males (3 specimens).—As in females except: clypeus with acute median prominence apically (Fig. 5b); labrum slightly emarginate; mandibles without inner teeth. Length 4.8-5.2 mm.

Discussion.—The nonlamellate metapleural flange of *pulawskii* sets the species apart from other in the *agile* group. Other features of the species are the form of the clypeus, the mostly reddish-orange

legs and the narrow whitish translucent apical bands of the abdominal segments. Reddish legs occur in *erythropus* and whitish abdominal bands occur in *erythropus*, *agile* and *ningyuenfuense*, but these species have a lamellate metapleural flange.

Etymology.—This species is dedicated to Wojciech J. Pulawski.

Range.—Western and southern India.

Types.—Holotype female: INDIA, Rajasthan: Udaipur (24 35'N), 27.V.1989, W. J. Pulawski (CAS). Paratypes (3 males, 9 females): same place, date and collector as holotype (CAS); same place and collector as holotype, 21-25.V.1989 (CAS, ZMUM); Gujarat: Disa (=Deesa), 4-6.VI.1989, W. J. Pulawski (CAS); Karnataka: Bangalore, 915 m, 26.V.1980, 30.V.1980, K. D. Ghorpade (ZMK); Karikal Territory: Kurumbagaram, III.1947, P. S. Nathan (USNM).

ACKNOWLEDGMENTS

I express my gratitude to all colleagues who lent material for study. I am grateful to Dr. A. P. Rasnitsyn for his help in searches for the type specimen of *koreense* in Radoszkowski's collection. I am extremely grateful to Dr. A. S. Menke who read earlier versions of the manuscript and suggested many important improvements of the text and who helped me in the English. Finally, I thank Dr. K. V. Krombein and Dr. W. J. Pulawski who critically and attentively reviewed the entire manuscript and who provided many useful comments.

LITERATURE CITED

- Ashmead, W. H. 1905. Additions to the recorded Hymenopterous fauna of the Philippine Islands, with descriptions of new species. *Proceedings of the United States National Museum* 28(1413): 957-971.
- Bingham, C. T. 1987. *The fauna of British India. Hymenoptera*, vol. 1. Taylor and Francis, London. 179 pp.
- Bohart, R. M. and A. S. Menke. 1976. *Sphecid wasps of the World, a generic revision*. University of California Press, Los Angeles, London. iv + 695 pp.
- Cameron, P. 1897a. IV. Hymenoptera Orientalia, or contributions to a knowledge of the Hymenoptera of the Oriental zoological region. Part V. *Memoirs and Proceedings of the Manchester Literary & Philosophical Society* 41(2): 1-144.
- Dalla Torre, C. G. 1894. *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*. Vol. IX. G. Engelmann, Lipsiae. 181 pp.
- Dalla Torre, C. G. 1897. *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*. Vol. VIII. G. Engelmann, Lipsiae. 750 pp.
- Gussakovskij, V. V. 1937. Espèces paléarctiques des genres *Didineis* Wesm., *Pison* Latr. et *Psen* Latr. (Hymenoptera, Sphecoidea). *Travaux de l'Institut Zoologie de l'Académie des Sciences de l'URSS* 4(3-4): 599-695.
- Hawkins, W. A. 1974. A western record for an introduced *Pison* (Hymenoptera, Sphecidae). *Journal of the Kansas Entomological Society* 47(2): 279.
- Horne, C. and F. Smith. 1870. Notes on the habits of some hymenopterous insect from the north-west provinces of India. With an appendix, containing descriptions of some new species of Apidae and Vespidae collected by Mr. Horne. *Transactions of the Zoological Society of London* 7(3): 161-196.
- Iwata, K. 1964. Ethological notes on four Japanese species of *Pison* (Hymenoptera, Sphecidae). *Mushi* 38: 1-6.
- Kazenas, V. L. 1980. Materials to the fauna of digger wasps (Hymenoptera, Sphecidae) of the Far East of the USSR. *Taxonomy of insects of the Far East, Vladivostok*, pp. 80-94.
- Kohl, F. F. 1885. Die Gattungen und Arten der Lariden Auctororum. *Verhandlungen der k. k. zoologisch-botanischen Gesellschaft in Wien* 34: 171-268.
- Krombein, K. V. 1958a. *Pison* (*Paraceramus*) *koreense* (Rad.), a new adventive wasp in the eastern United States. *Entomological News* 69: 166-167.
- Krombein, K. V. 1958b. Superfamily Sphecoidea. In: Krombein, K. V., et al., *Hymenoptera of America North of Mexico - Synoptic Catalog*. Agriculture Monograph 2, First Supplement, U. S. Department of Agriculture, Washington, DC. pp. 186-204.
- Krombein, K. V. 1967. Superfamily Sphecoidea. In: Krombein, K. V., B. D. Burks et al., *Hymenoptera of America North of Mexico—Synoptic Catalog*. Agriculture Monograph 2, Second Supplement, U. S. Department of Agriculture, Washington, DC. pp. 386-421.
- Krombein, K. V., P. D. Hurd, D. R. Smith and B. D. Burks. 1979. *Catalog of Hymenoptera in American North of Mexico*. Vol. 2. Smithsonian Institution Press, Washington, DC. pp. 1199-2209.
- Menke, A. S. 1968a. New genera and species of wasps of the tribe Trypoxylonini from the neotropical region (Hymenoptera: Sphecidae: Larrinae). *Los Angeles County Museum Contributions in Science* 135: 1-9.
- Menke, A. S. 1968b. A review of the New World species of *Pison*. I. The subgenus *Krombeiniellum* (Hymenoptera: Sphecidae). *The Canadian Entomologist* 100(10): 1100-1107.
- Menke, A. S. 1988. *Pison* in the New World: a revision (Hymenoptera: Sphecidae: Trypoxylonini). *Contributions of the American Entomological Institute* 24(3): 1-171.
- Radoszkowski, O. 1887. Hymenopteres de Koree. *Horae Scottatis Entomologicae Rossicae* 21(3-4): 428-436.
- Richards, O. W. 1962. *A revisional study of the masarid wasps*. Wm. Clowes and Sons, London. 294 pp.
- Sheldon, J. K. 1968. The nesting behavior and larval morphology of *Pison koreense* (Radoszkowski). *Psyche* 75: 107-117.
- Shuckard, W. E. 1838. Descriptions of new exotic aculeate Hymenoptera. *Transactions of the Entomological Society of London* 2(1): 68-82.
- Smith, F. 1869. Descriptions of new species of the genus *Pison*, and a synonymic list of those previously described. *Transactions of the Entomological Society of London*. 9: 289-300.
- Tsuneki, K. 1974. A contribution to the Knowledge of Sphecidae occurring in Southeast Asia (Hym.). *Polskie*

- Pismo Entomologiczne* 44(3): 585-660.
- Tsuneki, K. 1983. Further studies on the Larrinae of the Philippine Islands, with remarks on the Indian species of the genus *Lyroda* (Hymenoptera, Sphecidae). *Special Publications of the Japan Hymenopterists Association* 24: 1-116.
- Turner, R. E. 1916. Notes on the wasps of the genus *Pison* and some allied genera. *Proceedings of the Zoological Society of London* 1916: 591-629.
- Yasumatsu, K. 1935. The genus *Pison* Spinola of the Japanese Empire (Hymenoptera, Trypoxylonidae). *Annotationes zoologicae Japonenses* 15(2): 227-238.
- Yasumatsu, K. 1939. Notes supplementaires sur le genre *Pison* Spinola du Japon (Hymenoptera, Trypoxylonidae). *Festschrift zum 60 Geburtstag von Professor Dr. Embrik Strand, Riga* 5: 81-84.
-

Colony Densities and Preferences for Nest Habitats of Some Social Wasps in Mato Grosso State, Brazil (Hymenoptera, Vespidae)

IVONE R. DINIZ AND KINITI KITAYAMA

Departamento de Zoologia, Instituto de Biologia
Universidade de Brasília, 70910-900 Brasília DF, BRAZIL

Abstract.—Studies of colony densities and preferences for nest habitats of some social wasps were conducted in cerrado vegetation in Southern Mato Grosso state in Central Brazil. Wasp colony densities were estimated in three habitats (campo úmido, cerrado *sensu-stricto* and gallery forest). Regarding the wasp nest habitats preferences, we found 100 colonies of 30 species in 15 genera nesting in six different habitats in Southern Mato Grosso. In Northern Mato Grosso, based on Richards (1978), we found 199 colonies of 51 species in 14 genera nesting in six different habitats. Considering both regions together, we came out with 299 colonies of 61 species in 16 genera nesting in nine different habitats.

INTRODUCTION

The effectiveness and efficacy of predation by social wasps on many insects (Gobbi *et al.* 1984, Gobbi and Machado 1985, Machado *et al.* 1987, Raw 1988) confers on them a fundamental importance as biological control agents. Nonetheless, the study of the nests of these insects has focused mainly on their architecture (Jeanne 1975, Kojima 1982) and on the numbers of individuals per colony (Richards 1978), with few reports on pairs of species nesting close together (Windsor 1972, Starr 1988).

Information on preferences for nest habitats (Richards 1978, Reed and Vinson 1979, Forsyth 1980) and on colony densities (Rau 1942, Kitayama *et al.* 1989) of neotropical social wasps is still very scarce. In central Brazil, 130 species of wasps have been collected (Richards 1978, Raw pers. comm. and our own collections), but studies on their ecology are very fragmentary.

The aim of this report is to add new information on colony densities and preference for nest habitats of social wasps in the cerrado *sensu-lato* of Central Brazil.

METHODS AND STUDY AREA

The study was conducted in cerrado vegetation during a five week survey (August, October through December 1988 and June 1989) at the Rio Manso Hydroelectric Power Station (HPS-Rio Manso) (14°52' S and 55°50' W), in the Chapada dos Guimarães county, southern Mato Grosso State in central Brazil.

Cerrado *sensu-lato* is a semideciduous xeromorphic vegetation dominant in Central Brazil, occupying about 20% of the whole country. It occurs in various structures from closed forest-like forms to pure grasslands (Eiten 1972). "Habitat" is used here to refer to a vegetation subtype within the cerrado *sensu-lato*.

The censuses of social wasp colonies (nests with resident adults) were conducted in campo úmido, vereda, campo sujo, cerrado *sensu-stricto*, gallery forest and surrounding dirt roads. Characterizing these habitats very briefly it could be said that campo úmido is a wet grassland without visible woody plants (Fig. 1); vereda is a broad marshy valley bottom grassland with buriti palm (*Mauritia vinifera*) galleries (Fig. 2); campo sujo is a cerrado grassland with a few, very scattered, low conspicuous shrubs or acaulescent palms (Fig. 3);



Fig. 1. Area of 100 m² of campo úmido where wasp nests were surveyed.

Fig. 2. Area of Vereda (Photo by Dr. Roberto Cavalcante).



Fig. 3. Area of campo sujo.

Fig. 4. Area of cerrado *sensu-stricto* (Photo by Dr. Roberto Cavalcante).



Fig. 5. Area of gallery forest (Photo by Dr. Roberto Cavalcante).

cerrado *sensu-stricto* includes forms with the total woody plant cover of about 30-40% and with a canopy generally less than seven meters (Fig. 4) and gallery forest is usually a narrow evergreen mesophytic forest following the streams (Fig. 5) (Eiten 1972).

Searches for nests were conducted in four different months, covering two seasons: dry season (June and August) and wet season (October and December) in six habitats. Each habitat received the same intensity of searching during each of these seasons.

From each nest, adult wasps were collected to guarantee identification of the species. All the nests and insects sampled are deposited in the Laboratório de Zoologia, Departamento de Zoologia in the Universidade de Brasília.

The data on Xavantina and Serra do Cachimbo (10°50'S and 51°47'W), in northern Mato Grosso state were compiled from Professor Richards' (1978) species descriptions of nest habitats using only the data where there was no doubt on the location of the nests). Richards' censuses were conducted in campo sujo, dirt roads and clearings, cerrado *sensu-stricto*, Cerradão (the medium tall arboreal form of cerrado with a closed or semi-open canopy with 30-40% tree crown cover, Eiten

1972), gallery forest and dry forest (deciduous and semi deciduous mesophytic forest, Eiten 1972).

For the study on colony density, known areas were sampled, in gallery forest (7500 m²) and in cerrado *sensu-stricto* (10000 m²). Nests were located among leaves, on branches, on the trunks of trees and in holes in tree-trunks and in the ground. Binoculars were used to locate nests in the canopy. In addition, five squares of 100 m² each were surveyed in campo úmido, where nests of wasps were sought among tufts of grasses and sedges (Fig. 1).

The survey for estimates of the density of colonies, within the study area, was done during the wet season. Three people spent approximately 360 hours searching for nests. In each habitat the time spent per square meter was about one person-minute.

For the estimates of density of adult wasps/ha, the number of adults within some of the nests were counted and also, for some species, data from Richards (1978) were compiled.

In each table the habitats, when it was possible, were arranged in order of increasing complexity of structure because this makes it easier to see general patterns in species preferences for habitats.

RESULTS AND DISCUSSION

1. Nesting Habitat Preference of Wasps

A total of 100 colonies, comprising 30 species in 15 genera of wasps were encountered in six different habitats in Chapada dos Guimarães (Table 1). Among them, 18 species nested in only one habitat, nine in two, and three (*Polybia (Myrapetra) ruficeps* Schrottky—a very common species of the region, *Chartergus chartarius* (Olivier) and *Chartegellus communis* Richards) in three habitats (Table 1). Of the species that nested in only one habitat, most were found in cerrado *sensu-stricto* (seven species), in gallery forest (five species) and in campo úmido (four species) (Table 1). Of the 30 species collected in this study, only *Polistes (Epicnemius) pacificus liliaciosus* de Saussure was not collected by Richards (Table 1 and 2). This subspecies has been collected only rarely in central Brazil and, until Richards' 1978 record, its distribution was thought to be restricted in Brazil to the North (Amazonas, Amapá and Pará states). *Polybia ruficeps* was the commonest species of wasp at Rio-Manso with 23 colonies, of which 70% were found in cerrado *sensu-stricto*. Three other species, *Epipona tatus* (Cuvier), *Synoeca surinama* (L) and *Chartergus chartarius*, with eight colonies each, were also common (Table 1).

Richards (1978) recorded 199 colonies comprising 51 species in 14 genera nesting in six habitats (Table 2). Most of the species he collected (25 of the 51), were found nesting only in one habitat (eight of them in dry forest), 12 species nested in two habitats, eight nested in three habitats, three nested in four, and one species *Polybia (Myrapetra) platycephala* Richards nested in five habitats. In Xavantina and Serra do Cachimbo, *Polybia (Myrapetra) occidentalis* (Olivier) with 24 colonies (12%), was the most abundant, followed by *Polybia ruficeps* (10%), *Polybia (Apopolybia) jurinei* de Saussure (8%), *Polybia (Trichothorax) ignobilis* (Haliday) (7%) and *Polybia (Formicicola) rejecta* (F) (5%) (Table 2).

The data collected by us and by Richards were combined and for the same type of habitat the data were lumped (Table 3 representing the sum of Tables 1 and 2). At the nine habitats 299 colonies, comprising 61 species and 16 genera, were collected. Twenty eight species (46%) nested in only one habitat, 13 species nested in two, 10 in three,

seven in four and three in five habitats (Table 3). The area surveyed was different in each habitat so the number of colonies found do not represent one absolute abundance but the relative habitat preference for nesting.

Of the total number of colonies recorded by Richards and us from Mato Grosso, the species with the largest number of colonies was *Polybia ruficeps* (14%), followed by *Polybia occidentalis* (9%), *Polybia jurinei* (6%), *Polybia (Myrapetra) erythrothorax* Richards (5%), *Polybia ignobilis* (5%), *Parachartergus fraternus* (Gribodo) (4%) and *Epipona tatus* (4%). The genus *Polybia* represents 60% of the colonies reported from the two regions of Mato Grosso State (Table 3), ranging from 67% in Xavantina and Serra do Cachimbo (Table 2) to 45% in Rio Manso (Table 1). Among all the colonies of the 19 species of *Polybia* collected, 58% were found in cerrado *sensu-stricto* (Table 3) ranging from 31% in Rio Manso and 55% in Xavantina and Serra do Cachimbo (Tables 1 and 2).

Richards (1978) suggested that the choice of habitat for nesting is very characteristic and less diverse than that used for foraging. His opinion is confirmed in our survey at Rio Manso. For example, both *Synoeca surinama* (L), which nests in gallery forest, and *Polybia (Trichothorax) sericea* (Olivier) in cerrado *sensu-stricto*, were collected when they hunted in gallery forest, cerrado *sensu-stricto*, campo sujo and campo úmido. Of the 30 species of wasps at Rio Manso, 21 (70%) were encountered foraging in more than one habitat (in preparation).

A water source is important for wasps to nest successfully, (Rau 1942, Forsyth 1980). The latter author concluded that the greater colony density of wasps in gallery forest was due mainly to the presence of water. Wet habitats at Rio Manso (gallery forest, eight/ha and campo úmido 60/ha) also had higher colony densities than did dry habitats (cerrado *sensu-stricto* five/ha). *Polistes (Epicnemius) subsericeus* de Saussure and *Mischocyttarus (Mischocyttarus) drewseni* de Saussure which nest in campo úmido, had higher colony density compared to other species in drier habitats, such as cerrado *sensu-stricto*. Availability of water all year round and nest protection by tufts of grasses and sedges, could be the cause of that high density.

Most animals have preferences for particular habitats (Partridge, 1978). In Mato Grosso ap-

Table 1. Wasps nesting habitats in Rio Manso Chapada dos Guimarães: Mato Grosso, Brazil.

Species	CU	VE	CS	OF	CE	GF	TT
<i>Apoica c.f. pallens</i>	0	0	0	0	1	1	2
<i>Brachygastra bilineolata</i>	0	0	0	0	1	0	1
<i>Chartegellus communis</i>	0	1	1	0	1	0	3
<i>Chartergus chartarius</i>	0	0	4	0	3	1	8
<i>Epipona tatua</i>	0	0	0	0	5	3	8
<i>Metapolybia cingulata</i>	0	0	0	0	1	0	1
<i>Mischocyttarus cerberus</i>	0	0	0	0	2	0	2
<i>Mischocyttarus drewseni</i>	2	0	0	0	0	0	2
<i>Mischocyttarus labiatus</i>	0	0	0	0	1	0	1
<i>Mischocyttarus matogrossoensis</i>	1	0	0	0	0	0	1
<i>Mischocyttarus methathoracicus</i>	0	0	0	0	1	0	1
<i>Parachartergus fraternus</i>	0	1	0	0	4	0	5
<i>Polistes canadensis</i>	1	0	0	0	0	0	1
<i>Polistes pacificus</i>	0	0	0	0	0	1	1
<i>Polistes subsericeus</i>	4	0	0	0	0	0	4
<i>Polybia emaciata</i>	0	0	0	0	0	1	1
<i>Polybia erythrothorax</i>	0	0	2	0	4	0	6
<i>Polybia jurinei</i>	0	0	0	0	2	0	2
<i>Polybia occidentalis</i>	0	0	0	1	2	0	3
<i>Polybia paulista</i>	0	0	0	0	0	2	2
<i>Polybia quadricincta</i>	0	0	0	2	0	0	2
<i>Polybia ruficeps</i>	0	0	0	5	16	2	23
<i>Polybia sericea</i>	0	0	0	1	2	0	3
<i>Polybia singularis</i>	0	0	0	0	1	2	3
<i>Protopolybia exigua</i>	0	0	0	1	1	0	2
<i>Pseudochartergus chartergoides</i>	0	0	0	0	0	1	1
<i>Pseudopolybia compressa</i>	0	0	0	0	0	1	1
<i>Pseudopolybia vespiceps</i>	0	0	0	0	1	0	1
<i>Stelopolybia lobipleura</i>	0	0	1	0	0	0	1
<i>Synoeca surinama</i>	0	0	0	2	0	6	8
Total of nests	08	02	08	12	49	21	100
Total of species	04	02	04	06	18	11	30

CU - Campo úmido

VE - Vereda

CS - Campo sujo

OF - Old field

CE - Cerrado *sensu-stricto*

GF - Gallery forest

TT- Total

Table 2. Wasp nesting habitats of Xavantina and Serra do Cachimbo: Mato Grosso, Brazil (Data from Richards, 1978)

Species	CS	DC	CE	CD	GF	DF	TT
<i>Apoica gellida</i>	0	0	0	2	0	1	3
<i>Apoica pallens</i>	0	0	0	0	1	2	3
<i>Brachygastra augustii</i>	0	3	1	3	0	0	7
<i>Brachygastra moebiana</i>	0	0	1	1	0	0	2
<i>Brachygastra scutellaris</i>	0	0	0	0	0	2	2
<i>Chartegellus communis</i>	0	0	1	1	0	0	2
<i>Chartergus chartarius</i>	0	0	1	1	0	0	2
<i>Chartergus metanotalis</i>	0	0	1	0	0	0	1
<i>Clypearia humeralis</i>	0	1	0	0	0	0	1
<i>Epipona tatua</i>	0	1	2	0	0	0	3
<i>Mischocyttarus flavicornis</i>	0	2	0	0	0	0	2
<i>Mischocyttarus latior</i>	0	0	1	0	0	0	1
<i>Mischocyttarus matogrossoensis</i>	1	0	0	0	0	0	1
<i>Mischocyttarus melanoxanthus</i>	0	1	0	0	0	0	1
<i>Mischocyttarus methathoracicus</i>	0	0	0	0	0	1	1
<i>Mischocyttarus omicron</i>	0	1	0	0	0	0	1
<i>Mischocyttarus surinamensis</i>	0	0	0	0	1	0	1
<i>Mischocyttarus undulatus</i>	0	0	0	0	2	0	2
<i>Parachartergus fraternus</i>	0	4	4	0	0	0	8
<i>Polistes billardieri</i>	1	0	0	0	0	0	1
<i>Polistes cinerascens</i>	0	0	1	0	0	0	1
<i>Polistes goeldii</i>	1	0	0	0	0	0	1
<i>Polybia chrysothorax</i>	0	0	2	0	0	0	2
<i>Polybia dimidiata</i>	0	0	0	2	2	2	6
<i>Polybia emaciata</i>	0	0	2	0	0	2	4
<i>Polybia erythrothorax</i>	0	1	2	6	0	0	9
<i>Polybia gorytoides</i>	0	1	0	0	3	0	4
<i>Polybia ignobilis</i>	2	0	7	0	0	5	14
<i>Polybia jurinei</i>	0	0	2	5	6	2	15
<i>Polybia liliacea</i>	0	0	0	1	0	1	2
<i>Polybia micans</i>	0	0	0	0	0	1	1
<i>Polybia occidentalis</i>	11	6	1	6	0	0	24
<i>Polybia platycephala</i>	0	1	1	1	1	2	6
<i>Polybia quadricincta</i>	0	0	0	0	0	2	2
<i>Polybia rejecta</i>	0	0	1	1	2	6	10
<i>Polybia ruficeps</i>	0	6	7	0	7	0	20
<i>Polybia scrobalis</i>	0	0	0	0	2	0	2
<i>Polybia sericea</i>	0	3	1	2	0	0	6
<i>Polybia singularis</i>	0	1	0	3	0	1	5
<i>Polybia striata</i>	0	0	0	0	0	2	2
<i>Protopolybia acutiscutis</i>	0	0	0	0	0	1	1
<i>Protopolybia exigua</i>	1	0	0	0	0	0	1
<i>Protopolybia sedula</i>	0	0	1	0	0	1	2
<i>Pseudopolybia compressa</i>	0	0	0	1	0	0	1
<i>Pseudopolybia vespiceps</i>	0	0	0	1	0	0	1

Species	CU	VE	CS	OF	DC	CE	CD	GF	DF	TT
<i>Polistes cinerascens</i>	0	0	0	0	0	1	0	0	0	1
<i>Polistes goeldii</i>	0	0	1	0	0	0	0	0	0	1
<i>Polistes pacificus</i>	0	0	0	0	0	0	0	1	0	1
<i>Polistes subsericeus</i>	4	0	0	0	0	0	0	0	0	4
<i>Polybia chrysothorax</i>	0	0	0	0	0	2	0	0	0	2
<i>Polybia dimidiata</i>	0	0	0	0	0	0	2	2	2	6
<i>Polybia emaciata</i>	0	0	0	0	0	2	0	1	2	5
<i>Polybia erythrothorax</i>	0	0	2	0	1	6	6	0	0	15
<i>Polybia gorytoides</i>	0	0	0	0	1	0	0	3	0	4
<i>Polybia ignobilis</i>	0	0	2	0	0	7	0	0	5	14
<i>Polybia jurinei</i>	0	0	5	0	0	4	5	6	2	17
<i>Polybia liliacea</i>	0	0	0	0	0	0	1	0	1	2
<i>Polybia micans</i>	0	0	0	0	0	0	0	0	1	1
<i>Polybia occidentalis</i>	0	0	11	1	6	3	6	0	0	27
<i>Polybia paulista</i>	0	0	0	0	0	0	0	0	2	2
<i>Polybia platycephala</i>	0	0	0	0	1	1	1	1	2	6
<i>Polybia quadricincta</i>	0	0	0	2	0	0	0	0	2	4
<i>Polybia rejecta</i>	0	0	0	0	0	1	1	2	6	10
<i>Polybia ruficeps</i>	0	0	0	5	6	23	0	9	0	43
<i>Polybia scrobalis</i>	0	0	0	0	0	0	0	2	0	2
<i>Polybia sericea</i>	0	0	0	1	3	3	2	0	0	9
<i>Polybia singularis</i>	0	0	0	0	1	1	3	2	1	8
<i>Polybia striata</i>	0	0	0	0	0	0	0	0	2	2
<i>Protopolybia acutiscutis</i>	0	0	0	0	0	0	0	0	1	1
<i>Protopolybia exigua</i>	0	0	1	1	0	1	0	0	0	3
<i>Protopolybia sedula</i>	0	0	0	0	0	1	0	0	1	2
<i>Pseudochartergus chartergoides</i>	0	0	0	0	0	0	0	1	0	1
<i>Pseudopolybia compressa</i>	0	0	0	0	0	0	1	0	1	2
<i>Pseudopolybia vespiceps</i>	0	0	0	0	0	1	1	0	0	2
<i>Stelopolybia angulata</i>	0	0	0	0	0	0	1	2	1	4
<i>Stelopolybia fulvofasciata</i>	0	0	0	0	0	0	0	0	1	1
<i>Stelopolybia lobipleura</i>	0	0	1	0	0	1	0	0	0	2
<i>Stelopolybia testacea</i>	0	0	0	0	0	0	0	2	1	3
<i>Synoeca chalybea</i>	0	0	0	0	0	0	2	0	0	2
<i>Synoeca surinama</i>	0	0	0	2	0	0	0	6	1	9
Total of nests	08	02	24	12	32	88	39	48	41	299
Total of species	04	02	10	06	14	29	17	19	23	61

CU—Campo úmido

VE—Vereda

CS—Campo sujo

OF—Old field

DC—Dirt roads and clearings

CE—Cerrado *sensu-stricto*

CD—Cerradão

GF—Gallery forest

DF—Dry forest

TT—Total

Table 4. Wasp colonies density in three different habitats in Rio Manso - Chapada dos Guimarães: Mato Grosso, Brazil.

	Campo úmido	Cerrado <i>sensu stricto</i>	Gallery forest
Area (m ²)	500	10000	7500
Number of nests	3	5	6
Nest density/ha	60	5	8
Density of adult wasps/ha	480	1300	50000
Number of species	2	5	5

proximately 50% of wasps were restricted to a single habitat for nesting (Table 3).

Only a few ubiquitous species like *Polybia occidentalis* (5), *Polybia platycephala* (5), *Polybia (Pedothoeca) singularis* Ducke (5), *Chartergellus communis* (4), *Chartergus chartarius* (4), *Polybia erythrothorax* (4), *Polybia rejecta* (4), *Polybia ruficeps* (4) and *Polybia sericea* (4) use more than three habitats for nesting (Table 3).

Substrates for nesting in the cerrado is almost unlimited (Henriques *et al.* 1992), but availability of food, water and protection could be limiting factors.

2. Density

In an area of 2500 m² of the gallery forest (Fig. 5) three colonies of two species of wasps were found, two of *Polybia (Myrapetra) paulista* H.von Ihering and one of *Polybia ruficeps*. In a contiguous area of approximately 5000 m² three colonies of three species (*Polybia (Pedothoeca) emaciata* Lucas, *Polybia (Myrapetra) sp.* and *Polybia (Pedothoeca) singularis* (Ducke) were found, which correspond to an average of eight colonies and five species per ha (Table 4). In an area of 10000 m² of cerrado *sensu stricto* (Fig. 4), near a stream, three colonies of the following species were found: *Mischocyttarus (Kappa) metathoracicus* (deSaussure), *Mischocyttarus (Mischocyttarus) labiatus* (F) and *Polybia ruficeps*.

Colonies of *Brachygastra bilineolata* Spinola and *Stelopolybia lobipleura* Richards were also found on trees close to each other, but away from the stream with an average of colonies of five species per ha (Table 4). A similar result was found in the cerrado *sensu-stricto* of Brasília DF (Ecological Reserve of IBGE), where six colonies were found in an area of 1.5 ha corresponding to an average of five colonies per ha (Henriques *et al.*, 1992).

In an area of 500 m² of campo úmido (Fig. 1), two colonies of *Polistes subsericeus* and one of *Mischocyttarus drewseni* were found. Based on these numbers estimates were 60 colonies per ha for both species, or 40 per ha for *Polistes subsericeus* and 20 per ha for *Mischocyttarus drewseni* (Table 4). Although the colony density in campo úmido was larger than that found in gallery forest and cerrado *sensu-stricto*, the number of individuals per nest was smaller, due to low numbers of adults per nest (eight per nest). In gallery forest and cerrado *sensu stricto*, the colonies of *Syntoeca surinama*, *Epipona tatua* and *Polybia spp.* were larger, with hundreds to thousands of individuals per nest (Table 4).

In a relatively simply-structured habitat, such as campo úmido (Fig. 1) with a small area (500 m²), the density estimate was more accurate than in more complex habitats. A ranking of habitats in order of reliability of estimate is: campo úmido, cerrado *sensu-stricto* and gallery forest.

ACKNOWLEDGMENTS

We acknowledge the contribution made by the late Professor O.W. Richards to studies of social wasps in general. It is not unusual for subsequent workers to discover interesting information in the data he published. Financial support was provided by the North Brazilian Electricity Company (Eletronorte) and the University of Brasilia. We are especially grateful to Dr. Anthony Raw and Dr. Linda Caldas of

the Universidade de Brasilia and the anonymous reviewer for useful comments on the manuscript. Dr. Raw also identified several of the species of wasps. Dr. Paul M. Marsh made some editorial changes on the manuscript. Sra. Beatriz Mossri kindly assisted in the collection of field data. We also thank Dr. Antônio José E. Brussi, for his help and encouragement

LITERATURE CITED

- Eiten, G. 1972. The Cerrado vegetation of Brazil. *The Botanical Review* 38: 201-341.
- Forsyth, A. 1980. Nest site and Habitat selection by the social wasp, *Metapolybia azteca* Araujo (Hymenoptera: Vespidae) *Brenesia* 17: 157-162.
- Gobbi, N. & Machado, V. L. L. 1985. Material capturado e utilizado na alimentação de *Polybia (Myrapetra) paulista* Ihering 1896 (Hymenoptera-Vespidae). *Anais da Sociedade Entomológica do Brasil* 14(2): 189-195.
- Gobbi, N. Machado, V. L. L. & Tavares Filho, J. A. 1984. Sazonalidade das presas utilizadas na alimentação de *Polybia occidentalis* (Olivier 1791) (Hymenoptera: Vespidae). *Anais da Sociedade Entomológica do Brasil* 13(1): 63-69.
- Henriques, R. P. B. Rocha, I. R. D. & Kitayama, K. 1992. Nest density of some social wasps species in Cerrado vegetation of Central Brazil (Hymenoptera: Vespidae) *Entomologia Generalis* 17(4): 265-268.
- Jeanne, R. L. 1975. The adaptiveness of social wasp architecture. *Quarterly Review of Biology* 50: 267-287.
- Kitayama, K. Rocha, I. R. D. & Bulhões B. M. 1989. Densidade de ninhos de vespídeos em diversos habitats de Mato Grosso. I. *Simpósio Latino-americano sobre Inseto Sociais Neotropicais*. Rio Claro SP. R-67 P 44.
- Kojima, J. I. 1982. Nest architecture of three *Ropalidia* species (Hymenoptera: Vespidae) on Leyte Island, The Philippines. *Biotropica* 14(4): 272-280.
- Machado, V. L. L. Gobbi, N. & Simões, D. 1987. Material capturado na alimentação de *Stelopolybia pallipes* (Olivier 1791) (Hymenoptera: Vespidae) *Anais da Sociedade Entomológica do Brasil* 16 (1): 73-79.
- Partridge, L. 1978. Habitat selection In Behavioural Ecology (Eds. J.R. Krebs & N.B. Davies) Blackwell Scientific Publications, Oxford, 351-376.
- Rau, P. 1942. Habitat preferences of *Polistes* wasps (Hymenoptera: Vespidae) *Entomological News* 53: 293-295.
- Raw, A. 1988. Social wasps (Hymenoptera: Vespidae) and insect pests of crops of the Surui and Cinta Larga Indians in Rondônia, Brazil. *The Entomologist* 107: 104-109.
- Reed, H. C. & Vinson, S. B. 1979. Nesting ecology of paper wasps (*Polistes*) in a Texas urban area (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society* 52 (4): 673-689.
- Richards, O. W. 1978. The social wasps of the Americas. *British Museum of Natural History*. London 580 pp.
- Starr, C. K. 1988. The nesting association of the social wasps *Mischocyttarus immarginatus* and *Polybia* spp. in Costa Rica. *Biotropica* 20(2): 171-173.
- Windsor, D. M. 1972. Nesting association between two Neotropical polybiine wasps (Hymenoptera: Vespidae) *Biotropica*. 4: 1-3.

Descriptions of two New Species and Notes on the Genus *Bakeriella* Kieffer from Brazil and Ecuador (Hymenoptera: Bethyliidae)

CELSO OLIVEIRA AZEVEDO

Departamento de Biologia, Universidade Federal do Espírito Santo, Av. Marechal Campos 1468, Maruípe, 29040-090
Vitória, ES Brasil

Abstract.—*Bakeriella incompleta* sp. n., from rubber-tree crops of São Paulo, Brazil and *B. grossensis* sp. n. from Mato Grosso, Brazil are described and illustrated. Taxonomic data on *B. reclusa* (Evans) and *B. montivaga* (Kieffer) are included, and the latter recorded from Brazil for the first time. A key to females with a transverse carina on the pronotal disc is presented.

INTRODUCTION

Bakeriella Kieffer is a neotropical genus, ranging from Southern United States to Northern Argentina (Azevedo 1991). Kieffer (1910a) described this genus based on one species from Pará, Brazil, *B. flavicornis*, which has the pronotum carinate laterally and medially as well as anteriorly. This genus is related to *Epyris* Westwood by having the scutellar groove divided (Evans 1964). Kieffer (1910b) described *B. depressa* from Peru which has a carinate pronotum also. Evans (1964) expanded the definition of *Bakeriella* when he described ten species, in some of which the median or lateral carinae of the pronotum are weak or absent. Evans (1969), in his revision of *Epyris*, pointed out the relationship of the *montivagus*-group of *Epyris* to *Bakeriella* by the fact that both groups have similar scutellar pits. Evans (1979) reviewed *Bakeriella*, providing identification keys for both males and females and arranging the genus into four species-groups. In this revision, Evans described one species, *B. erythrogaster*, which has the scutellar groove similar to the genus *Rhabdepyris* Kieffer. Evans also transferred members of the *montivagus*-group from *Epyris* to *Bakeriella* simply by the fact that they closely resemble each other. Curiously, he did not include *B. subcarinata* Evans 1965 in his revision. Gordh & Moczar (1990) cited in their

catalog 19 species for the world and Azevedo (1991) described *B. dentata* from São Paulo State, Brazil.

The present study focuses on four species of this genus, *B. montivaga* (Kieffer), *B. reclusa* (Evans) and two new species. Ideally what is needed is a complete revision of the genus. Unfortunately, specimens are rare in collections and until more material is available for study, I have chosen to present these notes and new species descriptions.

Specimens for this study belong to the following collections (abbreviations according to Arnett & Samuelson (1986)): IBSP, Instituto Biológico de São Paulo, SP, Brasil; MZSP, Museu de Zoologia da Universidade de São Paulo, SP, Brasil; UFES, Coleção de Entomologia da Universidade Federal do Espírito Santo, Vitória, ES, Brasil. The last collection is not included in Arnett & Samuelson (1986) because it is new.

Abbreviations used follow Evans (1964) and are as follows: LFW, length of forewing; WH, maximum width of head, including eyes; LH, length of head, measured from median apical margin of clypeus to median point of vertex; WF, minimum width of frons; HE, maximum height (or length) of eye; WOT, maximum width of ocellar triangle, including posterior ocelli; OOL, shortest ocellular line. The nomenclature of the integument follows Eady (1968).

Bakeriella incompleta, sp. n.

Figs. 1-2

Holotype female.—Brazil: SP, Ibatinga; 05.X.1988; yellow pan trap, rubber-tree crop, no collector given. (UFES).

Description of holotype female.—Length of body 6.0 mm; LFW 2.85 mm; head and thorax black, abdomen black except tip dark brownish; palpi light brownish; mandible brownish, black at base and with a light brownish spot outside, teeth reddish; antennal scape dark brownish, apex brownish, pedicel and flagellum somewhat infuscated; tegula brownish; fore and hindcoxae black, midcoxa dark brownish; trochanters, femora, tibiae and tarsi dark brownish, the anterior being lighter; wings subhyaline somewhat brownish, veins, prostigma and stigma dark brownish.

Head (Fig. 1). Mandible with 5 teeth, apical tooth largest (Fig. 1). Clypeus with subangulate median lobe, with median carina straight in lateral profile, clypeus forming a small excavated reentrance in the region of contact with frons. WH 1.03 X LH; WF 0.5 X WH; WF 1.34 X HE; WOT 1.33 X OOL. Antennal scrobe not carinate. Posterior ocelli about 3 X their diameter from the vertex. Vertex nearly straight and with lateral angles rounded off. Distance from the top of eyes to crest of vertex about 0.7 X HE. Length of first four antennal segments in a ratio of about 11:5:4:4. Segments 5 to 12 about as wide as long. Temple not carinate. Frons somewhat alutaceous and brilliant.

Mesosoma (Fig. 1). Somewhat more alutaceous than frons, mesoscutum polished anteriorly. Pronotal disc slightly convex anteriorly, transverse anterior carina without teeth, median carina weak, situated in a slight depression and absent anteriorly, not intersecting transverse carina. Posterior margin of pronotal disc paralleled by a series of small foveae; lateral margin of disc somewhat sharpened, not carinate, and slightly diverging posteriorly; median width of the disc slightly greater than its length; disc slightly shorter than mesoscutum and scutellum together. Notauli not reaching the anterior margin of mesoscutum, converging posteriorly, widened posteriorly, and slightly curved anteriorly. Parapsidal furrows straight, somewhat more enlarged posteriorly, occupying only the posterior half of mesocutum

(fig. 1). Scutellar pits transverse, much wider than long, separated by a thin septum which is lower than margin of foveae. Propodeal disc as wide as long, with three discal carinae, median one complete and the others incomplete, occupying about two thirds of disc and converging posteriorly but not reaching median carina; space among discal carinae with transverse striae; disc without sublateral carinae; inner side of lateral carinae paralleled by a series of small irregular depressions; anterior part of space between lateral and discal carinae occupied by a rather large depression; posterior angle of the disc foveolate; declivity of propodeum with median carina and perpendicular striae. Metapleuron with longitudinally sinuous striae. Mesopleuron granulate, with large fovea anteriorly and small, deep pit at anterior margin, with small pentagonal fovea and elongate upper fovea (fig. 2). Mesosternum with small median pit, anterior margin of acetabular carina paralleled by striae. Midtibia spinose. Forefemur 2.0 X as long as thick, midfemur 1.65 X as long as thick. Claw trifid, first tooth rounded off, the others sharp.

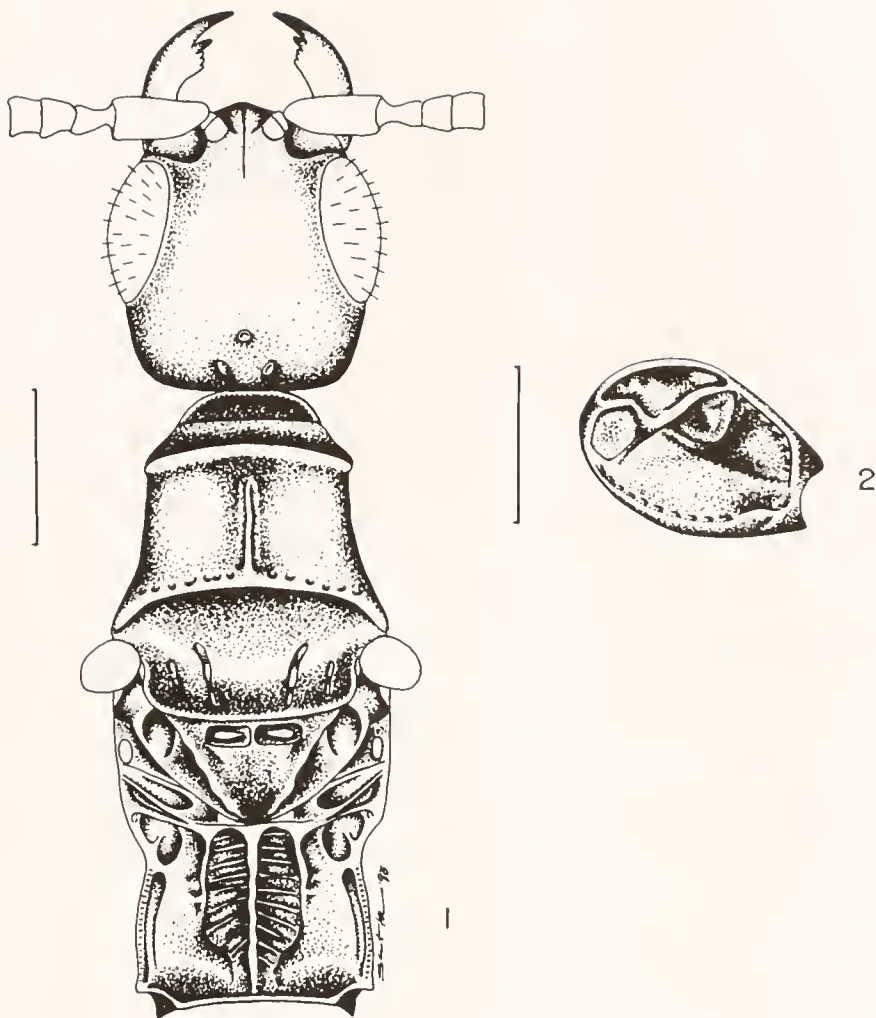
Metasoma. Sterna setose on posterior of each sternum. Terga with few setae on the posterior half of each tergum. Terga I and II with lateral setae. Transverse section of metasoma circular. Length of mesosoma 1.35 X length of metasoma. Valvae III dark brownish with only its end setose, setae range between one third and a half length of the valvae.

Paratype female.—BRAZIL: SP, Bálamo; 21.IX.1988, white pan trap, no collector given. (IBSP).

The paratype differs from holotype as follows: WH 1.00 X LH; WF 0.57 X WH; WF 0.76 X HE; OOL 1.62 X WOT; propodeal disc 1.08 as large as long.

Remarks.—This species is known only from the female. *Bakeriella incompleta* differs from other species in the genus in having the median longitudinal pronotal carina incomplete anteriorly, not reaching the anterior transverse carina, but reaching the posterior margin. In *B. cristata* Evans this carina is incomplete posteriorly.

Etymology.—The specific name refers to the fact that the median longitudinal carina of the pronotal disc is incomplete.



Figs 1-2. *Bakeriella incompleta*, sp. n. 1, head and mesosoma, dorsal view; 2, mesopleurum, lateral view. Scale = 0.5 mm.

***Bakeriella grossensis*, sp. n.**

Holotype female.—Brazil: Barra do Tapirapé, MT; XII.1960; unknown trap; B. Malkin, col. (MZSP).

Description of holotype female.—Length of body 3.75 mm; LFW 2.4 mm; head and mesosoma black, metasoma black with apex somewhat brownish; palpi brownish; mandible yellowish with teeth darker; antenna yellowish with scape darker; tegula yellowish; coxae and femora brown, trochanters, tibiae and tarsi yellowish; wings subhyaline, veins brown.

Head. Mandibles with 5 teeth, the basal teeth small and rounded off, the 2 apical teeth sharp-

ened, anterior tooth largest, the second of median size. Clypeus with median lobe angulate, without median carina, clypeus forming a small excavated reentrance in the region of contact with frons. Eyes with sparse long hairs. WH 1.08 X LH; WF 0.58 X WH; WF 1.16 X HE; WOT 1.62 X OOL. Antennal scrobe not carinate. Distance posterior ocelli from vertex about 2.8 X diameter of ocelli, angle of ocellar triangle less than a right angle. Vertex rounded, very slightly angled laterally. Distance from the top of eyes to crest of vertex about 0.57 X HE. Length of first four antennal segments in a ratio about 20:8:7:7. Temple not carinate. Frons coriaceous with punctures which are separated by 1-3 X their own diameters.

Mesosoma. Pronotal disc coriaceous, punctures similar to frons, with straight anterior transverse carina, without median longitudinal carina, posterior margin paralleled by series of small foveae; sides of disc subparallel; median width of disc 1.17 X its length. Pronotal disc 0.77 longer than mesoscutum and scutellum together. Anterior half of mesoscutum alutaceous, posterior half coriaceous. Notauli straight and very thin, vestigial anteriorly, widened posteriorly, reaching both anterior and posterior margin of mesoscutum. Parapsidal furrows straight, occupying only posterior half of mesoscutum and reaching its posterior margin. Scutellar pits transverse, 2.0 X as wide as long, separated by thin septum. Propodeal disc 1.05 X as wide as long, with three discal carinae, median one complete and lateral ones converging behind, not reaching median carina; space between discal carinae with small transverse striae, space between discal carinae and lateral carina polished; disc without sublateral carinae; lateral carinae bordered by a depression with small transverse striae; posterior angle of disc foveolate; declivity of propodeum with median carina and perpendicular striae. Metapleuron alutaceous, without striae. Mesopleuron coriaceous, with large ventral fovea occupying the lower half of mesopleuron, with deep pit in upper margin of lower fovea, with a fovea in the anterior part of mesopleuron and with long fovea in upper part of mesopleuron opened anteriorly. Mesosternum coriaceous, with pit in the middle of posterior region. Midtibia spinose. Forefemur 2.5 X as long as thick, midfemur 1.7 X. Claws trifid, first tooth rounded off, the others sharpened.

Metasoma. Wholly polished, terga and sterna with few setae. Setae of terga on posterior and lateral margins. Transverse section of metasoma subcircular. Length of mesosoma slightly longer than the metasoma. Valvae III brown with setae on apex.

Remarks.—This species is known only from the holotype. It runs to *B. inconspicua* and *B. polita* in the key written by Evans (1979). *B. grossensis* differs from *B. inconspicua* in having the scutellar pits transverse, the claws trifid, the eyes not strongly setose, the metasoma black with reddish apex and the mandible 5-toothed. *B. grossensis* differs from *B. polita* in lacking a median carina in the clypeus, in lacking a lateral carina on the pronotal disc, the head being not well developed above the eyes and

the occipital carina being obscured in full frontal view of head. In addition, the mandible of *B. grossensis* has two big apical teeth, while *B. polita* has one and *B. inconspicua* has three.

Etymology.—The specific name is in reference to the Mato Grosso State, region of origin of the holotype.

***Bakeriella montivaga* (Kieffer) 1910b**

Epyris montivagus Kieffer 1910b:31; Evans 1969:324

Bakeriella montivaga: Evans 1979:261

This species is recorded from Peru, Colombia (Kieffer 1910b), Bolivia, Ecuador, Venezuela, Panama, Costa Rica, Honduras, Mexico (Evans 1969), and now from Brazil.

Four females have been studied: Bálamo, SP, Brazil, one female, 28.IV.1988, yellow pan trap, rubber-tree crop, no collector given (UFES). The others were from Pichincha, Centro Científico R. Palangue, Ecuador, 21.XII.1980, 1.I.1981, 4.I.1981, forest, S. Sandoval, col. (MZSP).

These specimens are similar to the type; pronotal disc with the sides diverging posteriorly; WH 0.99 to 1.17 X LH; WF 0.53 to 0.59 X WH; WF 1.18 to 1.46 X HE; OOL 1.63 to 1.94 X WOT; propodeal disc slightly wider than long. The line of small foveae near the posterior margin of the pronotal disc is weakly angled anteriorly in the middle. This character is common only in males. Evans (1969) considered the possibility that *B. quinquepartita* (Kieffer) and *B. montivaga* represent variations of a single species. Indeed, both species are very similar and the only differences between them were pointed out in Evans' (1979) key to females.

***Bakeriella reclusa* (Evans) 1969**

Epyris reclusus Evans 1969:329

Bakeriella reclusa: Evans 1979:261

This species was described from Costa Rica and El Salvador. Evans (1979) studied a female from Ecuador. I have examined a male from Ecuador: Morona Santiago, Los Tayos, 3.VIII.1976, DeVries, col. (MZSP). Measurements for this species are: LFW = 2.13 mm, WH 1.2 X LH; WF 0.55 X WH; WF 1.06 X HE; WOT 1.44 X WOT. The pronotal disc is slightly wider than long, and the propodeal disc is as long as wide.

The following key to females with an anterior transverse carina on the pronotal disc is modified from Evans (1979:258) and includes *B. dentata* Azevedo 1991, *B. subcarinata* Evans 1965, *B. incompleta*, sp. n., and *B. grossensis*, sp. n.

1	Pronotum without median longitudinal carina; head black	2
1'	Pronotum usually with complete median carina; head black or dark green	7
2(1)	Legs wholly yellowish; propodeal disc covered with weak transverse striations ... <i>floridana</i> Evans 1964	
2'	Coxae and femora largely black; metapleuron shining, at most with very weak sculpture	3
3(2')	Transverse carina of pronotum weakly angled forward medially; median area of propodeum rather weakly sculptured	4
3'	Transverse carina of pronotum evenly arched; median area of propodeum with strong transverse ridges	5
4(3)	Mandible with 5 teeth, basal 3 small; frons with small punctures which are separated by 1.5-3.0 X their own diameters	<i>olmeca</i> Evans 1964
4'	Mandible with only two large apical teeth; frons with somewhat stronger and more widely spaced punctures	<i>brasiliana</i> Evans 1964
5(3')	Sides of pronotal disc carinate anteriorly; scutellar pits ovoid; mandible with 3 strong apical teeth	<i>inconspicua</i> Evans 1964
5'	Sides of pronotal disc not carinate; scutellar pits transverse; mandible with 1 or 2 strong apical teeth	6
6(5')	Sides of pronotal disc sharpened; mandible with one large apical tooth; scutellar pits slightly wider than long	<i>polita</i> Evans 1964
6'	Sides of pronotal disc angled, but not truly sharpened; mandible with two large apical teeth; scutellar pits 2.0 X wider than long	<i>grossensis</i> , sp. n.
7(1')	Median carina of pronotal disc incomplete	8
7'	Median carina of pronotal disc complete	9
8(7)	Median longitudinal carina of pronotum lacking posteriorly; body black with green metallic reflexions	<i>cristata</i> Evans 1964
8'	Median longitudinal carina of pronotum lacking anteriorly; body black without metallic reflexions	<i>incompleta</i> , sp. n.
9(7')	Internal margin of transverse carina of pronotum with tooth-like emargination	<i>dentata</i> Azevedo 1991
9'	Internal margin not like above	10
10(9')	Median longitudinal carina of pronotum somewhat weak and not paralleled by a depression	<i>subcarinata</i> Evans 1965
10'	Median longitudinal carina of pronotum well evident and situated in a depression	<i>inca</i> Evans 1964

ACKNOWLEDGMENTS

I express thanks to Eliana Bergmann for the loan of material from IBSP and Dr. Carlos Brandão for the loan of material from MZSP. I also thank Oscar Shibatta for preparing the illustrations.

LITERATURE CITED

- Arnett, R. H., Jr & G. A. Samuelson (eds). 1986. *The insect and spider collections of the world*. Gainesville, E.J.Brill/Fauna & Flora Publications, 220p.
- Azevedo, C. O. 1991. Espécie nova e notas sobre *Bakeriella* Kieffer (Hymenoptera, Bethyidae) da região de São Carlos, SP. *Revista Brasileira de Entomologia* 35(3): 535-8.
- Eady, R. D. 1968. Some illustrations of microculpture in the Hymenoptera. *Proceedings of the Royal Entomological Society of London, series A General Entomology* 43(3-6): 66-72.
- Evans, H. E. 1964. A Synopsis of the American Bethyidae (Hymenoptera: Aculeata). *Bulletin of the Museum of Comparative Zoology, Harvard University* 132(1): 1-222.
- Evans, H. E. 1965. Further studies on Neotropical Epyrini (Hymenoptera: Bethyidae). *Psyche (Cambridge)* 72(4): 265-78.
- Evans, H. E. 1969. A revision of the genus *Epyris* in the Americas (Hymenoptera: Bethyidae). *Transactions of the American Entomological Society* 95(2): 181-352.
- Evans, H. E. 1979. A reconsideration of the genus *Bakeriella* (Hymenoptera: Bethyidae). *Journal of the New York Entomological Society* 87(3): 256-66.
- Gordh, G. and L. Moczar. 1990. A catalog of the world Bethyidae (Hymenoptera). *Memoirs of the American Entomological Institute* 46: 1-364.
- Kieffer, J. J. 1910a. Description de Nouveaux Microhymenopteres du Bresil. *Annales de la Societe de Entomologique de France* 78: 287-348.
- Kieffer, J. J. 1910b. Description de Nouveaux Microhymenopteres du Bresil. *Annales de la Societe de Entomologique de France* 79: 31-56.
-

Localization of the Female Sex Pheromone Gland in *Cotesia rubecula* Marshall (Hymenoptera: Braconidae)

SCOTT A. FIELD AND MICHAEL A. KELLER

Department of Crop Protection, University Of Adelaide, Waite Campus, Glen Osmond, South Australia 5064, Australia

Abstract.—A combination of behavioural, histological and electron microscopic techniques was used to localize the female sex pheromone gland in the parasitic wasp *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae). The genital capsule was identified as the source of the sex pheromone by presenting males with a choice of body parts in a flight tunnel. Histological examination and electron microscopy further reduced the possibilities for pheromone production to two structures. One of these was a gland in a position similar to that reported for other braconid wasps, and which was associated with surface pores but lacked any obvious secretory products. The other was an active secretory gland which is associated with the moving parts of the ovipositor. Further studies aimed at isolating and identifying the chemicals involved are required to resolve this issue.

The presence of sex pheromone glands has been demonstrated in a number of species of parasitic wasps (Weseloh 1976, 1980; Tagawa 1977, 1983). Although unable to localize the sex pheromone source more precisely than the abdominal region, Vinson (1978) suggested that Dufour's gland produced a sex identification pheromone in *Cardiochiles nigriceps*. Obara and Kitano (1974) first demonstrated that the source of the female sex pheromone in *Cotesia glomerata* is the tip of the abdomen, near the ovipositor. Tagawa (1977) later described a pair of secretory glands located at the base of the second valvifer on the ninth abdominal tergite of this species, which he suggested was responsible for sex pheromone production. A subsequent study (Tagawa 1983) revealed the existence of similar glands in a corresponding position in all seven braconid species examined. Upon revising his initial findings (Weseloh 1976), Weseloh (1980) likewise concluded that paired epidermal glands on the last abdominal tergite were the sex pheromone source in *Cotesia melanoscelus*.

Previous field observations (Keller unpublished) established that courtship in male *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae) is elicited by a female sex pheromone. The present

study combined behavioural tests with microscopic techniques in order to identify the position of the sex pheromone gland in *C. rubecula*.

MATERIALS AND METHODS

Behavioural Experiments.—*C. rubecula* was reared in the laboratory on larvae of *Pieris rapae* L. using the methods of Keller (1990). Females between one and four days of age were frozen at -15° C for approximately 30 minutes before being dissected.

Using the same experimental protocol, we performed two experiments to test the responsiveness of males to different female body parts. In the first, the head and mesosoma (thorax plus first abdominal segment) were tested against the metasoma (remaining abdominal segments), and in the second the genital capsule (terminal abdominal segment plus ovipositor) was tested against the remaining anterior portion of the metasoma.

A glass microscope slide was divided into two halves and the two body parts being tested were placed randomly in the middle of either half, presenting a choice to the males. The slide was clamped at its midpoint and held horizontally at a

height of 30 cm by a small metal stand. Tests were conducted in a flight tunnel (Keller 1990) at a wind speed of 30 cm/s. Males were kept in a separate cage and removed for testing individually with a minimum of disturbance. They were released 30 cm downwind of the slide and observed to determine (1) which half of the slide they landed on, (2) whether subsequently they oriented to either body segment and performed typical elements of courtship (Field and Keller 1993), and (3) whether they attempted to copulate with either body segment.

The same males were then tested again, but this time the female body segments were washed in diethyl ether prior to testing. This solvent removed all contaminating pheromone from the surface of the body segment (Golub and Weatherston 1984). Therefore any subsequent emission of pheromone could be due only to continued leaking of the pheromone onto the surface from an internal glandular reservoir. The preference of courting males for a particular segment after washing would therefore localize the pheromone gland to somewhere within that segment.

Most males were successful in navigating to the slide; those that did not were discarded after a few attempts. To lessen the effects of pheromone contamination and depletion of pheromone reserves, the stand was washed with diethyl ether and body segments and slides were replaced at regular intervals throughout the course of the experiments. Variation in attractiveness of females was assumed to be negligible. Fifty males were tested in each experiment and data were analysed using two-tailed binomial tests (Zar 1984).

Scanning Electron Microscopy (SEM).—Two methods were used to prepare specimens for SEM observations. In the first, newly-dissected specimens were immersed in Peterson's KAA (kerosene (10%), 95% alcohol (75%), glacial acetic acid (15%)) prior to washing in 0.1 M phosphate buffer and dehydration through an alcohol series. This technique is commonly used to preserve larval insects because it distends structures that may otherwise lose shape (Smithers 1981).

The second method was to "clear" the specimens by gently warming in 10% KOH for 30-60 minutes. This removed most tissue and allowed dissection of the specimens so that both internal and external cuticular structures could be examined under SEM. Following dehydration, the KAA-treated and cleared specimens were critical-point

dried in an EMSCOPE CPD 750 and mounted on TAAB aluminium stubs using Acheson Electrotag 915. They were coated by vacuum evaporation with carbon and gold palladium and examined in an ETEC Autoscan scanning electron microscope at an accelerating voltage of 20 kV.

Light Microscopy (LM).—Genital capsules were removed and immersed for 4 hours in fixative (3% glutaraldehyde/3% formaldehyde made up in 0.1 M phosphate buffer, pH 7.4, to which had been added 2.5% polyvinyl pyrrolidone). They were washed in 0.1 M phosphate buffer overnight and then dehydrated by passing through a series of alcohols. After washing in propylene oxide, they were infiltrated with increasing concentrations of TAAB epoxy embedding resin over 48 hours and then embedded in resin by curing at 60° C for a further 48 hours.

Using glass knives in a Sorvall MT2-B "Porter-Blum" ultramicrotome, serial transverse sections of 0.5 µm thickness were cut, starting from near the base of the ovipositor and proceeding anteriorly. These were stained using 0.025% Toluidine Blue in 0.5% Borate buffer and photographed with a Wild MPS 45 photoautomat on Ilford Pan-f 50 ASA film. Agfa x 3 light green and Wratten 58 filters were used to achieve suitable contrast. Males were also subject to the same processing procedures and serial sections were cut from the posterior tip of the abdomen.

Transmission Electron Microscopy (TEM).—Tissue samples were prepared in the same manner as for LM. Gold to silver sections (0.08 µm) were cut with a Diatome diamond knife using a Reichert-Jung Ultracut and stained with saturated uranyl acetate in 70% alcohol for 20 minutes, followed by lead citrate for 12 minutes (Reynolds, 1963). They were examined in a JEOL 100S transmission electron microscope at an accelerating voltage of 80 kV.

RESULTS

Behavioural Experiments.—In the first experiment, neither the head/mesosoma nor the metasoma was found to be more attractive when the segments had not been washed in ether. However, when surface contamination had been removed with ether, males responded preferentially toward the metasoma, indicating that it was the source of the sex pheromone (Table 1).

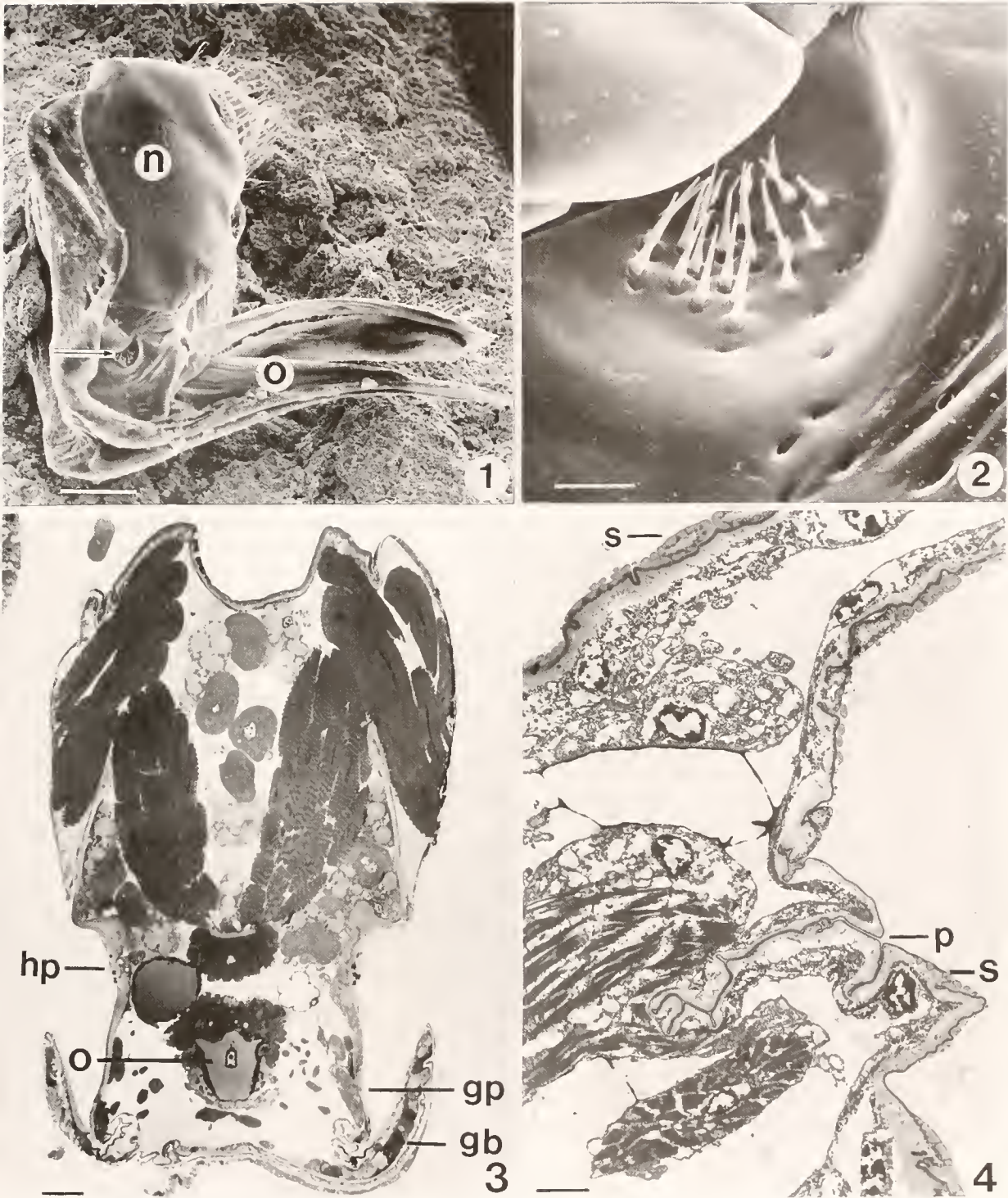


Fig. 1. SEM of lateral view of genital capsule in *Cotesia rubecula*. Arrow indicates position of hair plate and pores (see Fig. 2); n - ninth tergite; o - ovipositor. Scale bar = 100 μ m

Fig. 2. High magnification SEM of hair plate and pores. Scale bar = 10 μ m

Fig. 3. Transverse section of genital capsule, showing under LM two possible sex pheromone-producing glands: gp - glands associated with surface pores; gb - gland at base of genital capsule; hp - hair plate. Scale bar = 30 μ m

Fig. 4. TEM of basal section of genital capsule. p - pore canals; s - secretory droplets. Scale bar = 5 μ m

Table 1. Response of male *Cotesia rubecula* to a choice between the metasoma and the head+mesosoma of females, washed in ether or unwashed. * indicates significant differences ($P < 0.001$).

Treatment	Response	Number Responding	
		Metasoma	Head+Mesosoma
Unwashed	Land	23	27
	Court	23	27
	Copulate	10	22
Washed	Land	36	1*
	Court	36	1*
	Copulate	19	1*

Table 2. Response of male *Cotesia rubecula* to a choice between the genital capsule and the anterior portion of the metasoma of females, washed in ether or unwashed. * indicates significant differences ($P < 0.001$).

Treatment	Response	Number Responding	
		Anterior Metasoma	Genital Capsule
Unwashed	Land	17	31
	Court	18	27
	Copulate	19	1*
Washed	Land	3	28*
	Court	4	21*
	Copulate	3	1

In the second experiment, there was no preference shown by males for either the unwashed genital capsule or the unwashed anterior portion of the metasoma in terms of frequencies of landing and courting (Table 2). Several males moved between the body segments after landing in close proximity to one of them. More males attempted to copulate after courting an unwashed metasoma (18/18, plus one that courted to the genital capsule initially) than an unwashed genital capsule (1/27). After these body parts were washed with ether, males showed a clear preference for the genital capsule in terms of landing and courting, but not copulating.

Microscopy.—Having identified the genital capsule as the source of the sex pheromone, we examined KAA-treated genital capsules under the

SEM to determine whether there were any surface pores that could serve as outlets for pheromone secretion. The only pores found were positioned slightly below and posterior to a mechanosensory hair plate (Figs. 1, 2). Dissection of a cleared specimen revealed the internal attachment site of these mechanosensory hairs to be at the base of the second valvifer, which is an internal cuticular plate comprising part of the ovipositor system (see Snodgrass, 1935).

The LM sections revealed only one region of tissue that was a possible candidate for the sex pheromone source. A pair of glands was located in a position corresponding closely to that of the pores, i.e., just below the hairs and appearing immediately before the hairs in serial transverse sections (Fig 3). No pores were apparent, but this

may have been a result of the small proportion of sections cut (approx. 1/10) that were actually retrieved, stained and mounted for examination. The results of ultrastructural examination of this gland were inconclusive and failed to offer any indication of the organelles present or whether it was secretory in nature.

TEM examination revealed the presence of a second pair of secretory glands (Fig. 4), located at the base of the genital capsule and adjacent to folds of membrane which are presumably stretched and compressed during movements of the ovipositor. The ultrastructure of these glands was also indistinct, but pore canals leading to the surface and an abundance of secretory bodies were visible on or just under the surface of the cuticle.

DISCUSSION

The behavioural experiments clearly demonstrate that the genital capsule is the source of the sex pheromone in *C. rubecula*. With all surface pheromone removed, males were attracted to the metasoma in preference to the head/mesosoma and, when given a further choice, made their initial approach more often to the genital capsule rather than to the anterior portion of the metasoma. This is indicative of the continuous emission of pheromone from an internal reservoir located in the genital capsule, which provides an olfactory cue to the searching wasp.

There are, however, two anomalous results which require explanation. Firstly, a single male chose the washed head/mesosoma over the metasoma in the first experiment. This could have been due to incomplete washing of the body parts. Secondly, although significantly more males landed near and courted the genital capsule as opposed to the anterior portion of the metasoma, they attempted copulation with the genital capsule less frequently. This is not considered to be evidence that the sex pheromone gland is in the anterior portion of the metasoma. Rather, it suggests that a visual cue is involved in triggering attempts at copulation by the male. Upwind flight, landing, orienting and courting all appear to be stimulated entirely by chemical cues. The pres-

ence of a particular threshold amount of chemical may "prime" males so that they are ready to mount and copulate after a certain amount of courtship, but an object of appropriate size, shape and colour in the vicinity of a pheromone source may be required to release copulation behavior. One male did attempt copulation with the tiny genital capsule (0.5 mm in length), so the pheromone alone may be sufficient to elicit attempts at copulation in some cases.

The histology and electron microscopy failed to resolve the exact location of the sex pheromone gland within the genital capsule, but narrowed the possibilities to two structures. One of these is a group of cells located directly underneath surface pores which are adjacent to the mechanosensory hair plate on the genital capsule (Figs. 1-3). The hair plate was in turn juxtaposed to the second valvifer, which places this gland in approximately the same position as the putative pheromone glands indicated by Tagawa (1977, 1983) for a number of other closely-related braconids. Although this constitutes circumstantial evidence that this is the sex pheromone gland in *C. rubecula*, the absence of any clearly defined secretory products in the ultrastructural examinations leaves some uncertainty. The pores associated with these glands required thorough washing before they became visible by SEM.

Another possible source of sex pheromone is a gland located further toward the base of the genital capsule. The most striking feature of this gland is an abundance of associated secretory bodies amassed on and under the surface of the cuticle which are visible under TEM (Fig. 4). One possibility is that these secretions act as a lubricant for the ovipositor as it is extended and retracted from the metasoma. However, if it is the sex pheromone gland, then such movements would undoubtedly smear the secretions over the cuticle, which would be ideal for pheromone dispersal. An additional possibility is that the one secretion has the dual function of lubrication and sex attractant. In the absence of isolation and identification of the pheromone, the question of which of the two glands is the source of sex pheromone in *C. rubecula* will remain unresolved.

ACKNOWLEDGEMENTS

We thank Chris Leigh for the generous use of his facilities for histological processing, preparation of TEM sections and help with the SEM, Dr Adam Lockett for the use of his photographic equipment, Frances FitzGibbon for printing the micrographs and Paul Dangerfield for proofreading the manuscript.

LITERATURE CITED

- Field, S.A. and M.A. Keller. 1993. Courtship and intersexual signalling in the parasitic wasp *Cotesia rubecula*. *Journal of Insect Behaviour* 6: 737-750
- Golub, M.A. and Weatherston, J. 1984. Techniques for extracting and collecting sex pheromones from live insects and from artificial sources. In Hummel, H. and Miller, T., eds., *Techniques in pheromone research*. Springer-Verlag, New York. 464 pp.
- Keller, M.A. 1991. Responses of the parasitoid *Cotesia rubecula* to its host *Pieris rapae* in a flight tunnel. *Entomologia Experimentalis et Applicata*, 57: 243-249
- Obara, M. and Kitano, H. 1974. Studies on the courtship behaviour of *Apanteles glomeratus* L. -1. Experimental studies on releaser of wing-vibrating behaviour in the male. *Kontyu*, 42: 208-214.
- Reynolds, E.S. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *Journal of Cell Biology*, 17: 208-212.
- Smithers, C. 1981 *Handbook of Insect Collecting*. A.H. and A.W. Reed, Sydney. 120 pp.
- Snodgrass, R.E. 1935. *Principles of Insect Morphology*. McGraw-Hill Book Co., New York. 667 pp.
- Tagawa, J. 1977. Localization and histology of the sex pheromone-producing gland in the parasitic wasp, *Apanteles glomeratus*. *Journal of Insect Physiology*, 23: 49-56.
- Tagawa, J. 1983. Female sex pheromone glands in the parasitic wasps, genus *Apanteles*. *Applied Entomology and Zoology*, 18: 416-427.
- Vinson, S.B. 1978. Courtship behavior and source of a sexual pheromone from *Cardiochiles nigriceps*. *Annals of the Entomological Society of America*, 71: 832-837.
- Weseloh, R.M. 1976. Dufour's gland: Source of sex pheromone in a hymenopterous parasitoid. *Science*, 193: 695-697.
- Weseloh, R.M. 1980. Sex pheromone gland of the gypsy moth parasitoid, *Apanteles melanoscelus* : reevaluation and ultrastructural survey. *Annals of the Entomological Society Of America*, 73: 576-580.
- Zar, J.H. 1984 *Biostatistical Analysis*, 2nd edition. Prentice-Hall, Englewood Cliffs. 718 pp.
-

A Review of the World Species of *Orthomiscus* Mason (Hymenoptera: Ichneumonidae: Tryphoninae)*

VIRENDRA K. GUPTA

Entomology and Nematology Department, University of Florida, Gainesville, Florida 32611-0620, U.S.A.

Abstract.—The world species of the exenterine genus *Orthomiscus* Mason are reviewed. *O. amurensis* Kasparyan is transferred to *Kristotomus*, leaving six species under *Orthomiscus* in the Holarctic Region: *O. eridolius* Kasparyan, *medusae* Kasparyan, *pectoralis* (Hellén), *platyura* Mason, *simplex* (Mason) and *unicinctus* (Holmgren). Diagnostic characters, species relationships and a key to the species are given. Diagnostic characters are illustrated by diagrams and photographs.

INTRODUCTION

The genus *Orthomiscus* was described by Mason (1955) to accommodate two new Nearctic species, *O. platyura* and *O. leptura*. It belongs to the *Kristotomus*-Complex of genera in the tribe Exenterini (Gupta 1990), including *Kristotomus* Mason, *Kerrichia* Mason and *Orthomiscus* Mason. This group is characterized by having the apical rim of the hind tibia with a fringe of long, close bristles on the inner side and with a flat polished area on the lower and inner sides between the apical fringe of bristles and the tarsal socket; by having the hind tibia widest at apex and truncate; and by its short ovipositor which hardly surpasses the tip of abdomen. These genera also exhibit the usual exenterine characters such as the presence of only one spur on the middle tibia and the absence of spurs on the hind tibia.

Mason (1962) commented on the relationships of the genus and included two European species: *Exenterus unicinctus* Holmgren, 1858 (with which he synonymized *O. leptura*) and *Cteniscus pectoralis* Hellén, 1951. Kasparyan (1976, 1986, 1990) described three additional new species from Russia:

O. medusae, *O. amurensis*, and *O. eridolius*. Gupta (1990) transferred the Japanese *Kristotomus simplex* Mason, 1962 to this genus. In the present study, *O. amurensis* Kasparyan is transferred to the genus *Kristotomus* as it exhibits most of the characters of that genus, like the tapered and slender ovipositor and sheaths, lower valve of ovipositor without teeth and egg with a simple stalk and anchor. *Orthomiscus* thus is recognized as a Holarctic genus with six species.

Biology.—Not much is known about the biology of *Orthomiscus* except that *O. pectoralis* has been reared from late larval cimbicids (*Trichiosoma lucorum* L. and *T. tibiale* Stephens) that feed on birch and ash (*Betula* and *Crataegus*) in Europe (Jussila 1975).

Material.—This paper is based on the specimens present in the collection of the American Entomological Institute, Gainesville (GAINESVILLE). The types of the Russian species were borrowed from the collections of the Zoological Institute, Russian Academy of Science, St. Petersburg (ST. PETERSBURG) through the kindness of Dr. D. R. Kasparyan. Under synonymy of various species, the location of the type is indicated by the

*Florida Agricultural Experiment Station Journal Series R-03128.

city where the type is housed (see Townes, Momoi & Townes 1965 for details). The key to the species is based on the females which are more diagnostic.

Genus **ORTHOMISCUS** Mason

Orthomiscus Mason, 1955. Canadian Journal of Zoology, 33: 63.

Type: *Orthomiscus platyura* Mason, original designation.

Taxonomy: Mason 1962: 1273; Gupta 1990: 7; Kasparyan 1990: 36.

Diagnostic characters.—Head subcuboidal, swollen behind eyes. Mandibular teeth equal or subequal. Occipital and hypostomal carinae complete. Occipital carina bent inwards, meeting hypostomal carina at a right angle above base of mandible by a distance equal to the basal width of mandible. Epomia distinct. Epicnemial carina extending at least to the middle of hind margin of pronotum. Basal area of propodeum confluent with areola or only partly separated from it. Legs slender, elongate. Tarsal claws with 2-6 basal teeth. Areolet present, oblique, sometimes second intercubitus partly weak. Nervellus inclivous, intercepted in its lower 0.15 to 0.3. Tergite 1 elongate, usually about 2.0x as long as its apical width, its dorsomedian and dorsolateral carinae sharp and distinct; dorsolateral carina usually extending to the entire length of the tergite and passing just dorsad of spiracle and not broken there. Tergite 2 usually with a pair of strong to weak oblique basolateral grooves. Ovipositor short, stout and

decurved, not tapered apically and not extending beyond apex of abdomen. Upper valve of ovipositor flattened dorsally in basal half. Lower valve of ovipositor with an obliquely serrated edge (Figs. 10, 12, 18, 29). Ovipositor sheaths short, broadly triangular or sometimes a little slender. Female subgenital plate thin, creased medially and pinched apically. Egg stalk short, anchor simple, button-like or flattened and enclosing part of the egg (Figs. 4-14).

SPECIES RELATIONSHIPS

On the basis of egg structure, the six species of *Orthomiscus* form two distinct species groups. Group 1 comprises *platyura* Mason (type-species), *medusae* Kasparyan and *eridolius* Kasparyan (Figs. 4, 7, 9), where the egg stalk is short and wide and the anchor is four-pronged and encloses part of the egg. Group 2 comprises *pectoralis* (Hellén), *unicinctus* (Holmgren) and *simplex* (Mason) (Figs. 8, 12, 30) where the egg has a simple short stalk and a short button-like anchor. In the latter group, the stalk arises apicoventrally in *pectoralis* and *unicinctus* while in *simplex* it is central and the anchor is flat and oval.

Gupta (1990) stated that the plesiomorphic state of the egg in Cteniscini was probably an egg with a short stalk and anchor. This type of egg is seen in some generalized members of the genus *Kristotomus* (like *claviventris*, *santoshae* and *ctenonyx*). *Kristotomus* also exhibits more general-

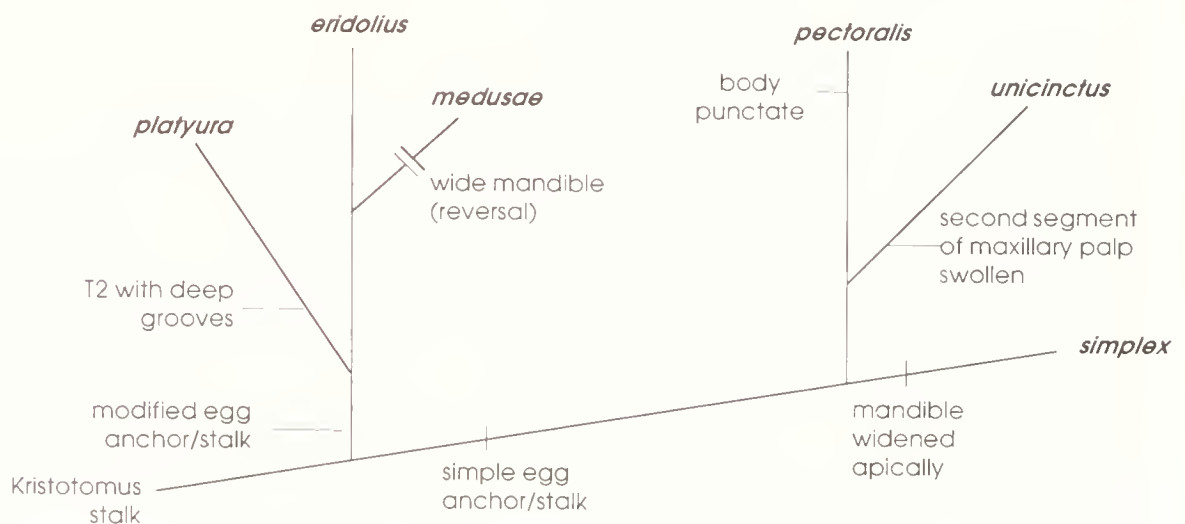


Diagram depicting the relationships of *Orthomiscus* species

ized characters from which *Orthomiscus* and *Kerrichia* may be derived. The *Orthomiscus* species closest to *Kristotomus* appears to be *O. simplex*, which was originally described in *Kristotomus* and considered a primitive member of the genus by Mason (1962), primarily because the mandible is slightly widened apically in this species and in several species of *Kristotomus*. *O. medusae* also exhibits a widened mandible but the egg structure is very different. I consider that the widened mandible of these two species arose by convergence. The relationships of all *Orthomiscus* species may be depicted as follows:

Under group 1, *Orthomiscus platyura* has deep oblique grooves on tergite 2 separating it from *O. medusae* and *eridolius*. In *medusae* the mandibles are widened apically and the lower tooth is longer than the upper (reversal). It also has the basal vein more strongly curved medially (Fig. 38). Under group 2, *O. simplex* has the mandible widened apically with the lower tooth longer than the upper. This is not the condition in *O. pectoralis* and *O. uncinctus*. *O. pectoralis* has the body, including face, punctate and the propodeum rugose and punctate in places. *O. uncinctus* has the second segment of maxillary palp swollen (Fig. 39).

KEY TO THE SPECIES

- 1a Basal vein of fore wing slightly curved close to its junction with the medius vein. Petiolar area of propodeum almost pentagonal, about 0.75x the combined length of areola and basal area (Fig. 3). Apical transverse carina of propodeum angulate at its junction with lateral and median longitudinal carinae (Fig. 23). Mandibular teeth equal in length (Figs. 2, 15). Hypostomal carina not raised at its junction with occipital carina. Egg stalk situated apicoventrally or in the middle 2
- 1b Basal vein of fore wing more strongly curved, curvature in the middle of the vein. Petiolar area of propodeum small, circular, about half the combined length of areola and basal area. Apical transverse carina of propodeum almost evenly curved between the lateral longitudinal carinae. Mandible slightly widened apically and the lower tooth longer than the upper (Figs. 27, 31). Hypostomal carina slightly raised at its junction with occipital carina. Egg stalk situated in the middle of the egg (Figs. 7, 30) ... 5
- 2a Second segment of maxillary palp swollen, about 2.0x as wide as the rest. Abdomen black dorsally, tergites 2-3 often with triangular yellow patches or their apical margins yellow. Pronotum yellow. Mesopleurum partly yellow. Mesosternum yellow. Ovipositor slender (Figs. 20, 21). Egg stalk short and apicoventral (Figs. 6, 11). Egg anchor button shaped. Holarctic 2. *uncinctus* (Holmgren)
- 2b Second segment of maxillary palp similar to the others, not swollen. Abdomen beyond first tergite black or brown with middle segments of ten with large yellowish brown patches. Egg stalk and anchor various (Figs. 4, 8, 9) 3
- 3a Face with definite punctures. Propodeum rugose and punctate in places. Tergites 4-5 as long as wide. Ovipositor sheaths slender. Propleurum yellow. Mesopleurum largely black. Abdominal tergites black with narrow apical yellow stripes. Egg stalk short and apicoventral (Figs. 8, 12). Egg anchor button-shaped. Eurasia, Japan 1. *pectoralis* (Hellén)
- 3b Face polished, only with sparse punctures. Propodeum polished to subpolished, without distinct punctures or rugosities. Tergites 4-5 transverse. Ovipositor thick, its sheaths triangular (Figs. 18, 25). Egg oval, its stalk very short, central. Egg anchor partly enclosing the egg (Figs. 4, 5, 9, 14) 4
- 4a Tergite 2 with deep oblique basolateral grooves. Abdominal tergites beyond first largely reddish brown. Pronotum, mesopleurum ventrally and mesosternum yellow. Nervellus intercepted at its lower 0.25-0.3. Egg stalk short (Fig. 4), anchor 4-pronged (Fig. 5). U.S.A., Canada 5. *platyura* Mason
- 4b Tergite 2 without oblique grooves. Abdominal tergites black, with margins of tergites 2-3 (sometimes 4-5 also) yellow. Mesosternum of female black. Nervellus intercepted at its lower 0.15-0.2. Egg anchor (Fig. 9) broad and partly enclosing the egg. Russia: Far East 6. *eridolius* Kasparyan
- 5a Mesopleurum of female yellow ventrally, in male with yellow spots. Tarsal claws with 4-5 teeth. Female subgenital plate sharply creased medioventrally. Ovipositor slender (Fig. 29). Egg with a simple, oval anchor (Fig. 30). Japan 3. *simplex* (Mason)
- 5b Mesopleurum black. Tarsal claws with a pair of weak teeth. Female subgenital plate convex ventrally, not strongly creased. Ovipositor thick (Fig. 10). Egg with a 4-lobed anchor (Fig. 7). Russia: Far East, Japan 4. *medusae* Kasparyan

1. *Orthomiscus pectoralis* (Hellén)
Figs. 8, 12

Cteniscus pectoralis Hellén 1951. Notulae Entomologicae Helsingfors, 31: 31. F. des. Type: Female, Finland Esbo (HELSINKI). — Kerrich 1952. Bulletin of the British Museum (Natural History) Entomology Series, 2 (6): 432. F. des., distr.

Orthomiscus pectoralis: Mason, 1962. Canadian Entomologist, 94: 1274. n. comb. Japan: Nagano Prefecture: Kamikochi. — Townes, Momoi & Townes, 1965. Memoirs of the American Entomological Institute, 5: 109. cat. — Jussila, 1975. Acta Entomologica Fennica, 41 (2): 53. des. of male, host records. — Kasparyan, 1976. Entomologicheskoe Obozrenie, 55: 137. — Kasparyan, 1977. Nasekomye Mongoliaca, 5: 463. Mongolia. — Kasparyan, 1990. Fauna of USSR Insecta, Hymenoptera, 3 (2): 43. key, des., fig. Russia.

No specimens of this species were available for study. Kerrich (1952) and Kasparyan (1990) have provided detailed descriptions of this species. The description that follows is adapted from Kerrich (1952).

Diagnosis.—This species appears different from the others by having the face and thorax extensively punctate and the propodeum rugoso-punctate (cf. Kerrich, 1952 description). All other species have only weak to indistinct body punctation. Tergites 4-5 as long as wide. The egg has a short apicoventral stalk and a small button-like anchor (Fig. 8).

Male and female.—Face moderately punctate. Clypeus with fine punctures. Epomia short and weak. Mandibular teeth equal in length. Notauli sharply impressed. Scutellum strongly convex, finely punctate. Epicnemial carina incomplete medially. Sternaulus superficially impressed. Propodeum rugose to punctate in places. Areola about as long as wide, confluent with basal area. Abdomen elongate and slender. Abdomen elongate and slender. Tergite 1 about 1.6x as long as its apical width, its dorsomedian and dorsolateral carinae strong. Postpetiole with a pitlike depression bounded by carinae. Tergite 2 with small but distinct thyridia. Tergites 4-5 as long as their basal width. Apical abdominal segments compressed in female. Female subgenital plate less sharply folded than in *O. uncinatus* (with which Kerrich compared this species). Ovipositor sheaths slender. Ovipositor comparatively stout as is usual in the genus (Fig. 12).

Color.—Ground color black. Mouthparts, clypeus, face, and temples broadly, yellow. Scape

and pedicel pale brownish. Thorax and propodeum black, with pronotum, scutellum, metascutellum, a mark above epicnemial carina, mark above middle coxa, tegula and subtegular ridge, yellowish brown. Propleurum yellow. Fore and middle coxae and trochanters yellow. Fore and middle femora yellowish brown, their tibiae and tarsi paler. Hind coxa reddish brown. Hind femur, tibia and tarsus more brownish to reddish brown. Abdomen black above, yellow below. Tergites 1-6 with narrow, pale apical margins and tergite 7 with an obscure, triangular yellow mark. Ovipositor sheaths yellow, infuscate above and rufous towards apex.

Egg.—(Fig. 8) Egg with a short apicoventral stalk and a button-like anchor.

Length.—5.0-10.0 mm. Fore wing 3.8-8.5 mm.; Ovipositor about 0.5 mm.

Distribution.—Europe (Finland), Russia, Mongolia, Japan.

Mason (1962) reported this species from Japan and included two females from Nagano Prefecture: Kamikochi, collected by Townes in 1954. These specimens could not be located in the AEI collections.

2. *Orthomiscus uncinatus* (Holmgren)
Figs. 6, 11, 19-23, 36, 39

Exenterus uncinatus Holmgren, 1858. Svenska Vetensk.-Akad. Handlirsch (n. f.), 1: 234. M, F. key, des. Lectotype (selected by Roman, 1914), Female, Sweden: Lapland-Tarna (STOCKHOLM).

Exenterus macrocephalus Holmgren, 1858. Svenska Vetensk.-Akad. Handlirsch (n. f.), 1: 243. M. des. Type: Male, Sweden (STOCKHOLM). Syn. by Roman, 1914.

Cteniscus macrocephalus: Jacob & Tosquinet, 1896. Annales de la Societe Entomologique Belge, 34: 108. new comb.

Cteniscus uncinatus: Roman, 1914. Arkiv for Zoologie, 9 (2): 17. syn., des. — Kerrich, 1942. Transactions of the Society for British Entomology, 8 (2): 63-64. Britain. — Kerrich, 1952. Bulletin of the British Museum (Natural History) Entomology Series, 2 (6): 434. key, des., fig. Localities in Britain, France, Belgium, Germany, Sweden.

Orthomiscus leptura Mason, 1955. Canadian Journal of Zoology, 33: 64. M, F. key, des., fig. Type: Female, U.S.A.: New Hampshire: Pinkham Notch (AEI, Gainesville). Examined. Syn. by Mason, 1962.

Orthomiscus uncinatus: Mason, 1962. Canadian Entomologist, 94: 1274. syn., distr. Japan: Sapporo. — Townes, Momoi & Townes, 1965. Memoirs of the American Entomological Institute, 5: 109. cat.— Mason, 1966. Canadian Entomologist, 98: 48. key. Japan. — Carlson, 1979. Catalog of Hymenoptera in America North of Mexico, 1: 377. cat. U.S.A., Canada. — Kasparyan, 1990. Fauna of

USSR Insecta, Hymenoptera, 3 (2): 45. key, des., fig. Russia.

Diagnostic features.—Second segment of maxillary palp widened and flat, about 2.0x as wide as the rest (Fig. 39). Oblique impressions on tergite 2 faint. Ovipositor comparatively more slender than in the previous species (Figs. 20, 21). Egg with a short apicoventral stalk and a button-like anchor (Figs. 6, 11). Temple yellow only on its basal half. Scutellum black except at apex. Hind coxa with blackish brown patches. Abdomen largely black and with yellow patches on tergites 2 and 3. Thorax of male largely black, that of female generally yellow in lower half, but color variable.

Male and female.—Flagellum with 23-24 segments in male and 23-26 segments in female. First segment about 1.4x as long as the second. Second segment of maxillary palp widened and flat, about 2.0x as wide as the rest of the segments (Fig. 39). Mandibular teeth equal in length but lower tooth more prominent than the upper. Hypostomal carina of normal shape, not conspicuously raised at its junction with occipital carina. Vertex widened posteriorly. Intercellular distance 0.25x the ocellular distance.

Thorax subpolished. Mesoscutum rather strongly convex. Notauli distinctly impressed up to middle of mesoscutum. Lateral carinae of scutellum distinct only at base of scutellum. Epomia sharp across pronotal collar. Sternaulus and epicnemial carina moderately impressed. Propodeum convex, subpolished. Areola (Fig. 23) widened at its junction with costulae, confluent with basal area. Basal vein of fore wing uniformly but weakly arched (Fig. 36). Nervellus intercepted in its lower 0.25-0.33.

Abdomen subpolished. Tergite 1 slender (Fig. 19), its dorsomedian carinae strong and extending to 0.7-0.8 the length of the tergite, its dorsolateral carina sharp and extending to the entire length of the tergite. Tergite 2 with distinct thyridia and faint oblique grooves. Female subgenital plate folded medially and pointed apically. Ovipositor slender, of uniform diameter (Fig. 21). Ovipositor sheaths (Figs. 20, 21) comparatively narrow. Egg anchor small and situated apicoventrally (Fig. 6).

Color.—Ground color black. Thorax almost wholly black in male and some females. Abdominal tergites largely black. Scape, pedicel below, mouthparts, clypeus, face, inner orbits up to top of

eyes, malar space, and temples on lower half, yellow. Propleurum, lower half of pronotum, its upper margin, tegula, subtegular ridge, tip of scutellum, epicnemium, mesosternum, lower half of mesopleurum, abdominal venter, and sides of abdomen, yellow. Legs yellow to yellowish brown. Fore and middle coxae and trochanters yellow. Hind coxa largely brownish or yellow with large black or brown patches. Hind femur brown. Hind coxa largely yellow in specimens from Ontario and blackish in specimens from Alaska. Tergites 2 and 3 often with triangular yellow patches or with their apical margins yellow. In males the yellow along the inner orbits extending only to the level of antennal sockets, temple yellow on its lower 0.3, and thorax almost wholly black. The color is quite variable.

The European specimens were not examined to ascertain the range of variation. Kerrich (1952: 434) and Kasparyan (1990: 45) have described this species in detail.

Egg.—(Fig. 6, 11, 21). Egg small, oval, with a short apicoventral stalk and a button-like anchor.

Length.—6.0-8.5 mm.; fore wing 5.0-7.0 mm.; ovipositor 0.4-0.6 mm. Kerrich (1952) stated that a female measuring 4.0 mm. was seen from Lapland.

Specimens examined.—CANADA: Quebec: Stoneham, 1 male, 1 female, 21.VI.1938, H. & M. Townes. U.S.A.: New Hampshire: Pinkham Notch, 1 female, 25.VI.1938, H. & M. Townes; Mt. Madison, 3 males, 24.VI.1938, H. & M. Townes. Vermont: L. Willoughby, 2 male, 17, 25.VI.1945, C.P. Alexander. (Types and paratypes in AEI, Gainesville). Non-type material: U.S.A.: Oregon: Corvallis, 2 males, 1 female, V-VII. 1978, H. & M. Townes. Alaska: Anchorage, 1 female, 6-16.VII.1976, Petre Rush. CANADA: Ontario: Cumberland, 1 male, 3 females, VI.1975, L. Ling.

Distribution.—U.S.A., Canada, Europe (Britain, France, Belgium, Germany, Sweden), Russia, Japan.

3. *Orthomiscus simplex* (Mason)

Figs. 26-30, 42

Kristotomus simplex Mason, 1966. Canadian Entomologist, 98: 46. M, F. key, des., fig. Type: Female, Japan: Nagano Prefecture: Kamikochi (GAINESVILLE. Examined. — Kasparyan, 1976. Entomologicheskoe Obozrenie, 55: 150. (Entomological Review, 55: 108). key.

Orthomiscus simplex: Gupta, 1990. Contrib. Amer. Ent. Inst., 25 (6): 8. n. comb. — Kasparyan, 1990. Fauna of USSR Insecta, Hymenoptera, 3 (2): 44. key, des., fig. Japan.

Diagnostic features.—Mandible widened apically, its lower tooth wider and longer than the upper (Fig. 27). Hypostomal carina slightly raised at its junction with occipital carina (Fig. 42). Basal vein of fore wing curved. Egg reniform-ovate, with a short central stalk and a simple anchor. Egg surface coarsely granular. Head and thorax in female yellow on lower half and black on upper half, in male largely black. Abdominal tergites black, their apical margins yellow.

Male and female.—Scape about 1.5x as long as wide. Flagellum with 24 segments. First flagellar segment 1.4x as long as the second. Face (and rest of head also) smooth and shiny. Mandible widened apically, the lower tooth wider and slightly longer than the upper (Fig. 27). Malar space 0.4x the basal width of mandible. Maxillary palp segments normal, not swollen. (Fig. 42). Hypostomal carina slightly raised at its junction with occipital carina (Fig. 42). Vertex widened behind eyes (Fig. 26). Interocellar distance 0.4x the ocellocular distance.

Thorax largely smooth and shiny. Notauli distinct anteriorly. Lateral carinae of scutellum distinct. Epomia normal, not very sharp. Epicnemial carina extending to half the height of mesopleurum. Sternaulus indistinct. Propodeum normally areolated. Petiolar area small and round. Apical transverse carina uniformly curved between its junction with lateral longitudinal carinae. Basal vein in fore wing medially curved, more strongly so than in the preceding species. Second intercubitus of areolet sometimes absent.

Abdomen smooth and shiny. Tergite 1 about 2.25x as long as its apical width, its dorsomedian carinae extending up to about 0.75 its length, its dorsolateral carina complete, sinuate and passing just above the spiracle (Fig. 28). Tergite 2 with weak basolateral oblique grooves. Female subgenital plate strongly creased and pointed apically. Ovipositor (Fig. 29) somewhat slender and cylindrical, its teeth weak but present at the tip. Ovipositor sheaths small and slender. Male claspers broader than in other species.

Color.—Ground color black. Male comparatively darker than the female. Face, clypeus, mandibles, lower half of temples, pronotal collar, hind corner of pronotum, whole of fore and middle legs, hind coxae and trochanters, and abdominal venter, yellow. Ventral side of scape and pedicel and apex of scutellum yellowish-brown. Hind

femur, tibia and tarsus blackish brown (male) to yellowish brown (female). Pronotum of female more extensively yellow and mesosternum and lower part of mesopleurum may also be yellow. Abdominal tergites black with yellow apical stripes, particularly on tergites 2-3.

Egg.—Reniform-ovate (Fig. 30). Stalk shorter than its own diameter, arising near the middle of the egg. Anchor about 0.33 as long as the egg, flat and oval. Egg surface coarsely granular.

Length.—4.5-6.5 mm.; fore wing 4.5-6.0 mm.; ovipositor about 0.5 mm. long.

Specimens examined.—JAPAN: Nagano Prefecture: Kamikochi, 6 males and 2 females (holotype, allotype and paratypes), 23-31.VII.1954, Townes family (AEI, Gainesville).

Distribution.—Japan.

Discussion.—Mason (1966) placed this species under *Kristotomus*, stating that it was the most primitive member of the genus and closely related to *Orthomiscus*, particularly in the structure of the egg and development of the dorsolateral carina of the petiole. Apart from the widened mandible, this species shares most characters of *Orthomiscus*, particularly the structure of the ovipositor, in which the lower valve has teeth-like indentations. The dorsolateral carina of the petiole and the egg structure also relate it to the present genus.

4. *Orthomiscus medusae* Kasparyan Figs. 7, 10, 31, 38, 41

Orthomiscus medusae Kasparyan, 1976. Entomologicheskoe Obozrenie, 55: 140 (Entomological Review, 55 (1): 99). M. F. des., fig. Type: Female, Russia: Sakhalin: Kunashir Island (ST. PETERSBURG). Examined — Kasparyan, 1990. Fauna of USSR Insecta, Hymenoptera, 3 (2): 42. kev., des., fig. Russia.

Diagnostic features.—Mandible widened apically, the lower tooth longer than the upper (Fig. 31). Hypostomal carina raised at its junction with occipital carina. Scutellum subconvex. Basal vein of fore wing strongly curved medially (Fig. 38). Tergite 2 with very faint to indistinct oblique grooves. Female subgenital plate convex ventrally, not sharply creased. Egg (Figs. 7, 10) with a short medioventral stalk and a four-pronged anchor enclosing the egg. Thorax and abdomen black; sometimes pronotal collar and prosternum yellow and tergites 2-3 with yellow marks, particularly in females.

Male and female.—Flagellum with 23-24 segments in male and 25-27 segments in female. First flagellar segment about 1.3x as long as the second. Face and clypeus subpolished, with sparse punctures. Malar space about 0.33–0.4x (male) to 0.4–0.5x (female) the basal width of mandible. Mandible slightly widened apically (Fig. 31), its lower tooth a little longer than the upper. Maxillary palp slender, normal (Fig. 41). Vertex widened posteriorly, smooth and shiny. Interocellar distance 0.25x the ocellocular distance.

Epomia present but not very strong. Notauli distinct to middle of mesoscutum. Scutellum subconvex, its lateral carinae confined to base. Epicnemial carina strong, ending in middle of hind margin of pronotum. Sternaulus weakly indicated anteriorly. Propodeum areolated but its longitudinal dorsal and sublateral carinae quite often erased beyond the costulae or absent; combined length of basal area and areola approximately 1.5x the length of apical area (according to the original description). In one paratype and in the Japanese specimens examined in the AEI collection, the areola is narrow, 2.0x as long as wide, confluent with the basal area, and a little widened at the costulae. Basal vein curved medially (Fig. 38). Tarsal claws with a pair of weak teeth at base.

Tergite 1 2.0x as long as its apical width; its dorsomedian carinae extending to 0.75 its length and its dorsolateral carinae strong and complete. Postpetiole with a median oval depression. Tergite 2 with rather weak oblique basolateral impressions. Female subgenital plate convex, not strongly creased ventrally, apically narrow and pinched. Ovipositor stout (Fig. 10). Ovipositor sheaths broad.

Color.—Ground color black. Scape and pedicel reddish brown dorsally and lighter ventrally. Flagellum yellow. Face, clypeus, mouthparts, and lower half of temple, yellow. Thorax black with pronotal collar and prosternum yellow in female. Apex of scutellum brown. Coxae and trochanters yellow. Fore and middle legs otherwise yellowish brown. Hind femur, tibia and tarsus blackish brown. Abdomen black with tergites 2 and 3 with triangular yellow marks. Tergite 4 with a faint yellow mark in the paratype examined. In one male studied only yellow apical lines are present on the abdominal tergites.

Egg.—Oval in shape (Fig. 7, 10), with a medioventral short stalk, its anchor four-pronged,

enclosing part of the egg, somewhat similar to that seen in *O. platyura*.

Length.—7.0-9.0 mm.; fore wing 5.5-7.0 mm.; Ovipositor about 0.5 mm.

Specimens examined.—RUSSIA: SAKHALIN: Kunashir Island: Sernovodsk, 1 female (paratype), 26.VIII.1973, D. R. Kasparyan. JAPAN: Nagano Prefecture: Kamikochi, 1 male, 22.VII.1954, 1 male, 24.VII.1954 (labeled *O. uncinatus* Tow.), Townes family (AEI, Gainesville).

Distribution.—Russia, Japan.

Relationships.—Structurally this species is close to *O. simplex* (Mason) from which it differs mainly in the complex structure of the egg anchor, black mesopleurum, male tarsal claws with a pair of weak teeth at base, female subgenital plate convex but not strongly creased ventrally and by possessing a comparatively thicker ovipositor. The egg structure relates it to *O. platyura*.

5. *Orthomiscus platyura* Mason

Figs. 1-5, 15-18, 37, 40

Orthomiscus platyura Mason, 1955. Canadian Journal of Zoology, 33: 66. M, F. key, des., fig. Type: Female, U.S.A.: Rhode Island: Westerly (GAINESVILLE). Examined. — Carlson, 1979. Catalog of Hymenoptera in America North of Mexico, 1:377. cat. U.S.A. New Hampshire, Vermont, California. Canada: Quebec, Ontario.

Diagnostic features.—Areola narrow, parallel-sided and confluent or partly separated from the basal area. Tergite 2 with rather deep oblique basolateral grooves. Ovipositor stout, its sheaths broadly triangular. Egg with a four-lobed anchor, as large as the egg. Scutellum mostly yellow. Hind coxa yellow. Abdominal tergites beyond first reddish brown to reddish yellow.

Male and female.—Scape about 1.5x as long as wide. Flagellum with 24 segments in male and 26 segments in female. First segment 1.32 to 1.35x as long as the second segment. Face (Fig. 15) polished, depressed laterally. Clypeus convex and polished. Mandibular teeth subequal, upper tooth slightly longer than the lower. Malar space 0.45x the basal width of mandible. Second segment of maxillary palp slender and similar to other segments (Fig 40). Vertex polished, quadrate, widened behind eyes, 1.75x as wide as eye in dorsal view. Interocellar distance 0.22x the ocellocular distance. Temple in lateral view 1.7x to 1.75x as wide as eye.

Thorax mostly smooth and shiny. Mesoscutum convex, pubescent. Notauli deep and distinct to middle of mesoscutum. Scutellum flat, with lateral carina confined to base. Pronotum somewhat dull, epomia strong and extending close to upper edge of pronotum. Epicnemium dull, epicnemial carina strong and extending to 0.75 the height of mesopleurum. Sternaulus indicated on anterior 0.4 of mesopleurum. Propodeum convex, shiny. Areola narrow, parallel-sided, about 2.0x as long as wide (Fig. 3), confluent with basal area or only partly separated from it.

Abdomen shiny. Tergite 1 2.0x as wide at apex as at base, about 2.0x as long as its apical width, its dorsomedian carinae extending up to about 0.8 its length (carinae weaker apically, widened, and enclosing a depressed area between them), its dorsolateral carina complete and strong (Fig. 17). Tergite 2 with deep, oblique, basolateral grooves. Ovipositor thick, decurved (Fig. 18). Ovipositor sheaths short, broadly triangular.

Color.—Black and yellow. Lower 0.66 of head, scape, flagellum beyond 4th segment, pronotum, scutellum, metascutellum, prosternum, mesosternum, lower part of mesopleurum, fore and middle coxae and trochanters, sternites, ovipositor sheaths, and subgenital plate, yellow. Legs otherwise and abdomen (except tergite 1), yellowish brown. Tergite 1 black. Brown to blackish patches present on abdominal tergites and pronotum. Wings hyaline.

Egg.—(Figs. 4, 5, 18). Short, oval, ventrally flat and bearing on nearly half its length a short but wide stalk; egg anchor large and enclosing most of the egg. Anchor bearing two long posterior and two long anterolateral arms that extend toward the dorsal surface of the egg.

Length.—6.0-8.0 mm.; fore wing 5.0-6.5 mm.; ovipositor about 0.4 mm.

Specimens examined.—CANADA: Ontario: Cumberland, 1 female, 11.VI.1975, L. Ling. U.S.A.: Rhode Island: Westerly, 1 male, 2 females, 9-11.VI.1936, M. Chapman. New York: McLean Bogs, Tompkins Co., 1 female, 30.VI.1939, J. G. Franclemont. New Jersey: Tabernacle, 1 male, 11.VI.1939, H. K. Townes; Millwood, 1 female, 21.VI.1936, H. K. Townes. Maryland: Takoma Park, 1 male, 2.VII.1944, H. & M. Townes. Pennsylvania: Trout Run, 1 female, 29.V.1938, H. K. Townes; Spring Brook, 1 female, 27.VI.1945, H. K. Townes; Michigan: Huron Mts., 2 males, 2 females, VI.1961, H. & M. Townes; Iron River, 1 female, 23.VI.1969,

H. & M. Townes. South Carolina: Cleveland, 3 females, V-VI.1971, G. Townes. Alabama: Gulf Shores, 1 male, 22.IV.1968, H. & M. Townes. All these specimens are in the AEI collection at Gainesville, and those collected prior to 1955 are paratypes (see Mason, 1955: 67). Additional paratypes were described by Mason from Maine, Vermont, New Hampshire, Massachusetts, Connecticut, and Quebec.

Distribution.—U.S.A., Canada.

6. *Orthomiscus eridolius* Kasparyan Figs. 9, 14, 24-25

Orthomiscus eridolius Kasparyan, 1990. Fauna of USSR Insecta, Hymenoptera, 3(2):44. M, F. key, des., fig. Type: Female, Russia: Far East: Khabozavodsk Region (ST. PETERSBURG). Paratypes examined.

This species has been described in detail by Kasparyan (1990). Structurally it resembles *O. simplex* (Mason) but shows differences in the curvature of the basal vein, shape of the areola, shape of tergite 2, and in the egg structure. The diagnostic features are given below.

Diagnosis.—Temple more buccate than in *O. simplex*. Mandibular teeth equal. Epomia present, moderately strong. Areola slightly widened at its junction with costulae and confluent with basal area. Apical transverse carina of propodeum angulate at its junction with lateral and median longitudinal carinae. Petiolar area appearing pentagonal. Basal vein of fore wing only slightly curved near its junction with the medius vein. Nervellus intercepted at its lower 0.15-0.2. Tergite 2 without oblique grooves. Ovipositor short and thick (Fig. 25). Ovipositor sheaths short, tapered. Egg (Figs. 9, 14, 25) oval, with a ventral flattened anchor that encloses almost half of the egg.

Coloration essentially similar to that of *O. simplex*. Head and thorax in female yellow in lower half and black in upper half. Mesosternum of female black or brownish-black. Face of male partly yellow. Abdomen beyond tergite 1 brownish black, with yellow spots. Mesosternum black in female. Face of male largely black.

Length.—4.5-6.0 mm.; fore wing 3.8-4.8 mm.; ovipositor about 0.4 mm.

Distribution.—Russia: Far Eastern Region.

Orthomiscus amurensis Kasparyan, 1986 is hereby transferred to *Kristotomus*.

**Kristotomus amurensis (Kasparyan),
new combination**
Figs. 13, 32-35

Orthomiscus amurensis Kasparyan, 1986: 55. Kasparyan, 1990. Fauna of USSR Insecta, Hymenoptera, 3 (2): 40. key, des., fig. Type: Female, Russia: Far East: Khabovodsk Region (ST. PETERSBURG). Examined.

The holotype of this species was examined in 1992. The ovipositor and its sheaths are tapered and slender and both extend beyond the apex of abdomen. The lower valve of the ovipositor is without teeth. The egg has a simple stalk and anchor. The interocellar distance is about 0.8x the ocellocular distance. The malar space is 0.5x the basal width of mandible. The temple is moderately swollen, and is about as wide as the eye width. The dorsolateral carina of tergite 1 is interrupted just above the spiracle.

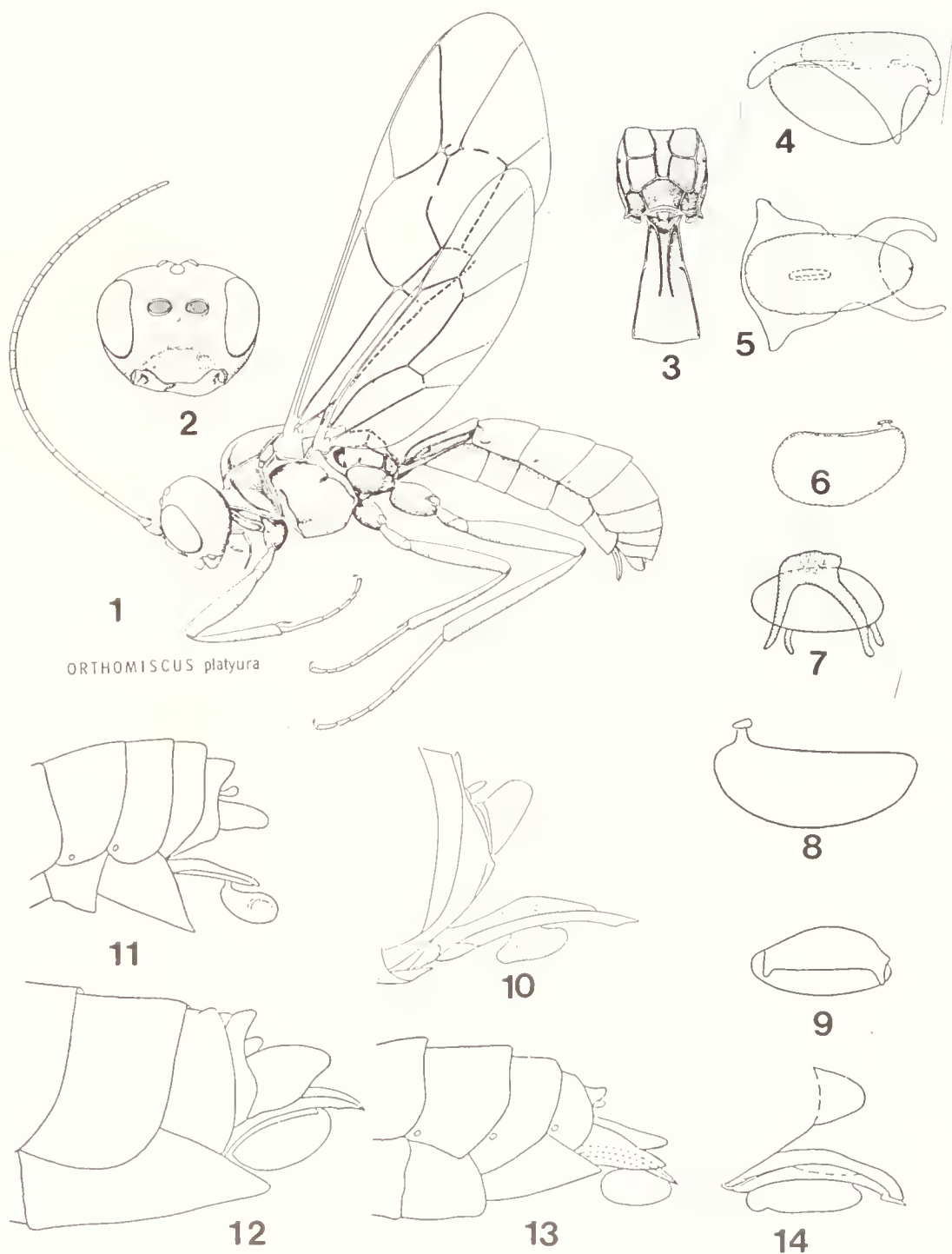
The above mentioned characters and the general body form would place this species in *Kristotomus*, to which genus this species is hereby transferred. It appears related to *Kristotomus buccatus* Kasparyan.

ACKNOWLEDGMENTS

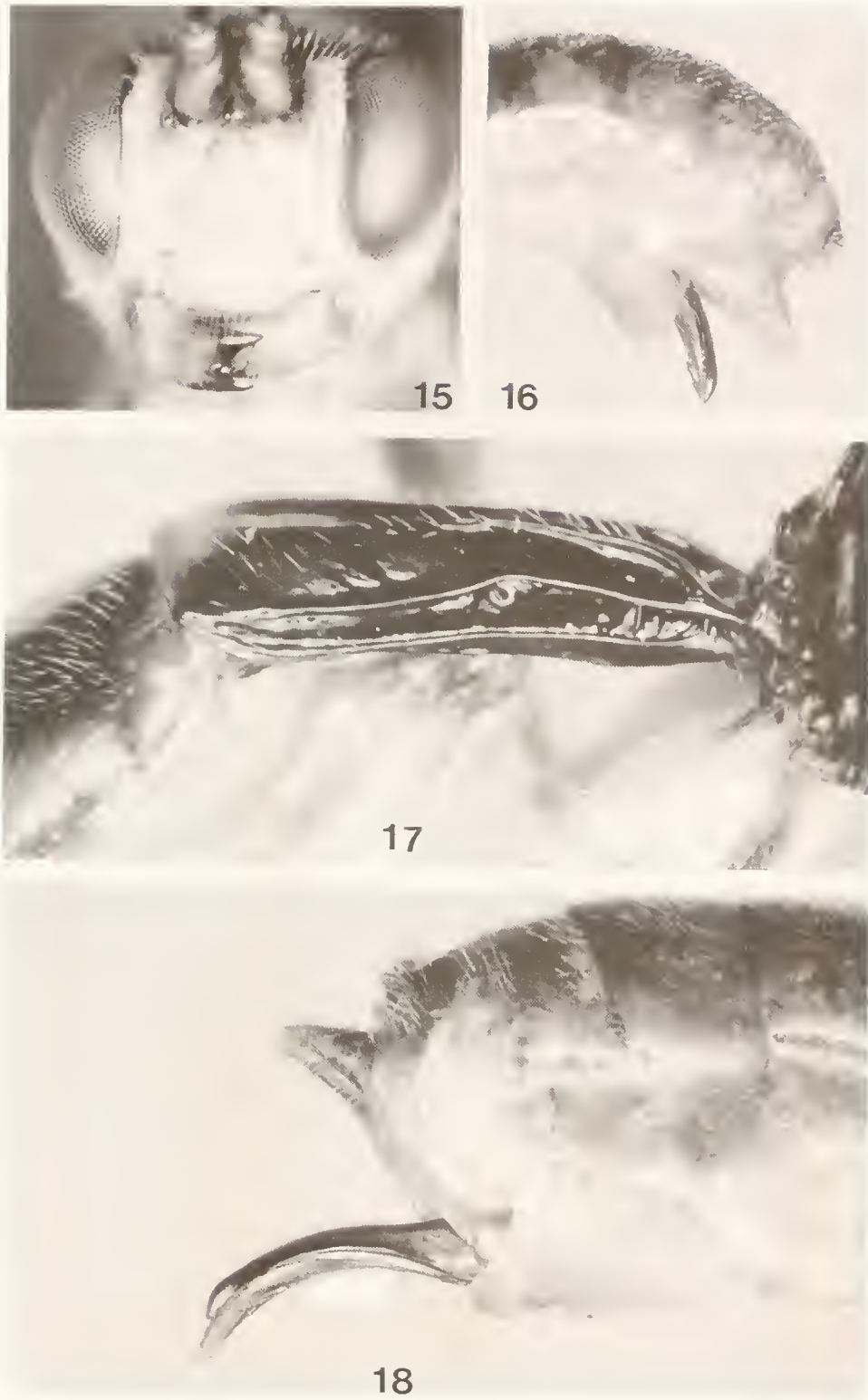
My thanks are due to Dr. D. R. Kasparyan (St. Petersburg) for the loan of the type specimens and for his comments. The collections of the American Entomological Institute (AEI) were readily available for my studies, for which I am thankful to the President of the Institute. The draft of the paper was kindly read by and commented upon by Drs. John Barron and Charles Porter and their comments have been incorporated. I am also thankful to Mr. Andrei Sourakov for translating Kasparyan's key to the Russian species of the genus for my use. Subsequently I received a similar translation from Dr. Kasparyan. The use of published figures from the works of Henry Townes, D. R. Kasparyan and W. R. M. Mason is duly acknowledged and the source is cited under figure legends.

LITERATURE CITED

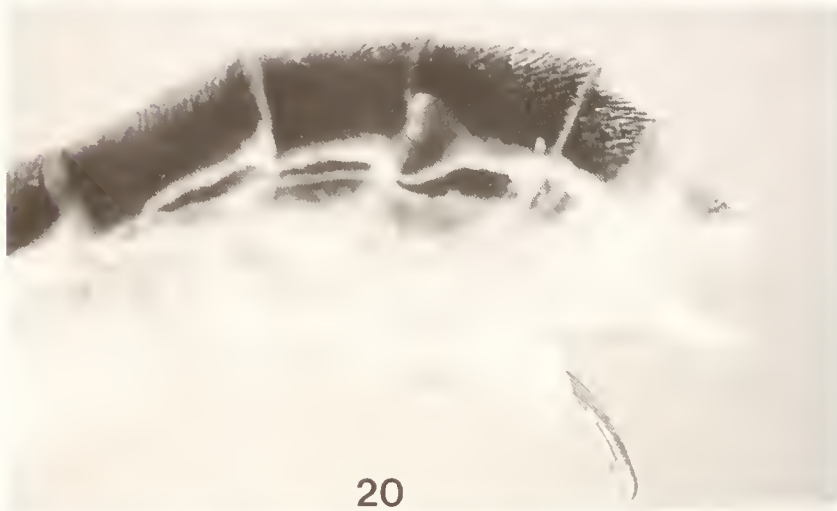
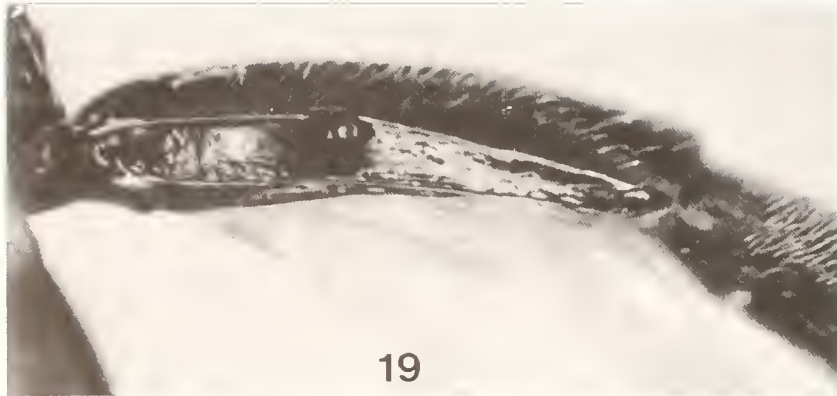
- Carlson, R. W. 1979. Family Ichneumonidae. In: Krombein, Smith & others, *Catalog of Hymenoptera in America North of Mexico* 1: 315-741 (Ichneumonidae pages). Washington, D.C.
- Gupta, Virendra K. 1990. The taxonomy of the *Kristotomus*-Complex of genera and a revision of *Kristotomus* (Hymenoptera: Ichneumonidae: Tryphoninae). *Contributions of the American Entomological Institute* 25 (6): 1-88.
- Hellén, W. 1951. Neue Ichneumoniden aus Ostfennoskandien. I. *Notulae Entomologicae* 31: 25-31.
- Holmgren, A. E. 1858. Forsök till uppställning och beskrifning av de i Sverige fauna Tryphonider [Monographia Tryphonidum Sueciae]. *Svenska Vetensk.-Akad. Handlirsch (N.F.)* 1: 93-246, 305-394.
- Jacob, J. C. and J. Tosquinet. 1890. Catalogue des Ichneumonides de la Belgique appartenant au groupe des Tryphonides. *Annales de la Societe Entomologique Belge* 34: 44-135.
- Jussila, R. 1975. Ichneumonological (Hym.) reports from Finland III. *Annales Entomologici Fennici* 41: 49-55.
- Kasparyan, D. R. 1976. [New species of ichneumonids of the tribe Cteniscini (Hymenoptera, Ichneumonidae) from eastern Asia. The genera *Cycasis* Townes, *Orthomiscus* Mason and *Kristotomus* Mason.] *Entomologicheskoe Obozrenie* 55(1): 137-150. [English translation in *Entomological Review* 55 (1): 99-108.]
- Kasparyan, D. R. 1977. [Ichneumonids of the subfamilies Pimplinae and Tryphoninae (Hymenoptera, Ichneumonidae) new for Mongolia and Transbaikalia.] *Nasekomye Mongolica [Insects of Mongolia]* 5: 456-470.
- Kasparyan, D. R. 1986. [Two new species of the tribe Exenterini (Hymenoptera, Ichneumonidae) of the Far East.] In: Ler, P. A. (Editor) *[Systematics and ecology of insects from the Far East.]* *Academiya Nauk SSSR, Vladivostok*, 155 pages. (Pp. 54-57).
- Kasparyan, D. R. 1990. *Fauna of USSR Insecta, Hymenoptera* Vol. III, No. 2. Ichneumonidae, Subfamily Tryphoninae: Tribe Exenterini, Subfamily Adelognathinae. Leningrad: Nauka Publishing House. 340 pages.
- Kerrich, G. J. 1942. Second review of literature concerning British Ichneumonidae (Hym.), with notes on palaeartic species. *Transactions of the Society for British Entomology* 8 (2): 43-77.
- Kerrich, G. J. 1952. A review, and a revision in greater part, of the Cteniscini of the Old World. *Bulletin of the British Museum (Natural History) Entomology Series* 2 (6): 305-460.
- Mason, W. R. M. 1955. A revision of the Nearctic Cteniscini (Hymenoptera: Ichneumonidae) I. *Eudiaborus* Kerrich and a new genus. *Canadian Journal of Zoology* 18-73.
- Mason, W. R. M. 1962. Some new Asiatic species of Exenterini (Hymenoptera: Ichneumonidae) with remarks on generic limits. *Canadian Entomologist* 94: 1273-1296.
- Mason, W.R.M. 1966. A primitive new species of *Kristotomus* Mason (Hymenoptera: Ichneumonidae). *Canadian Entomologist* 98: 46-49.
- Roman, A. 1914. Beitrage zur schwedischen Ichneumonidenfauna. *Arkiv for Zoologie* 9 (2): 1-40.
- Townes, H. 1969. The genera of the Ichneumonidae Part I. *Memoirs of the American Entomological Institute* 11: 1-300.
- Townes, H., S. Momoi and M. Townes. 1965. A Catalog and reclassification of the Eastern Palearctic Ichneumonidae. *Memoirs of the American Entomological Institute* 5:1-671.



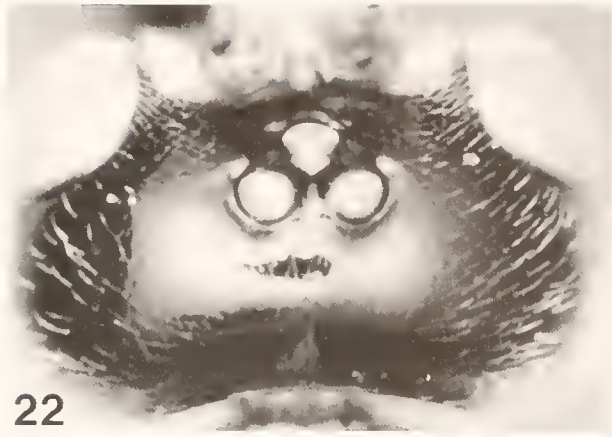
Figs. 1-14 1-5 *Orthomiscus platyura* Mason: 1, habitus, 2, head; 3, propodeum and tergite 1; 4, lateral view of egg, 5, ventral view of egg. Figs. 6-9 Lateral view of egg of 6, *O. uncinatus* (Holmgren); 7, *O. medusae* Kasparyan; 8, *O. pectoralis* Hellén; 9, *O. eridolius* Kasparyan. Figs. 10-14. Apex of abdomen showing subgenital plate, ovipositor and ovipositor sheath of: 10, *O. medusae*; 11, *O. uncinatus*; 12, *O. pectoralis*; 13, *O. [=Kristotomus] amurensis* (Kasparyan); 14, *O. eridolius*. [Figs. 1-3 after Townes, 1969; 4-6 after Mason, 1955, 7-14 after Kasparyan, 1990.]



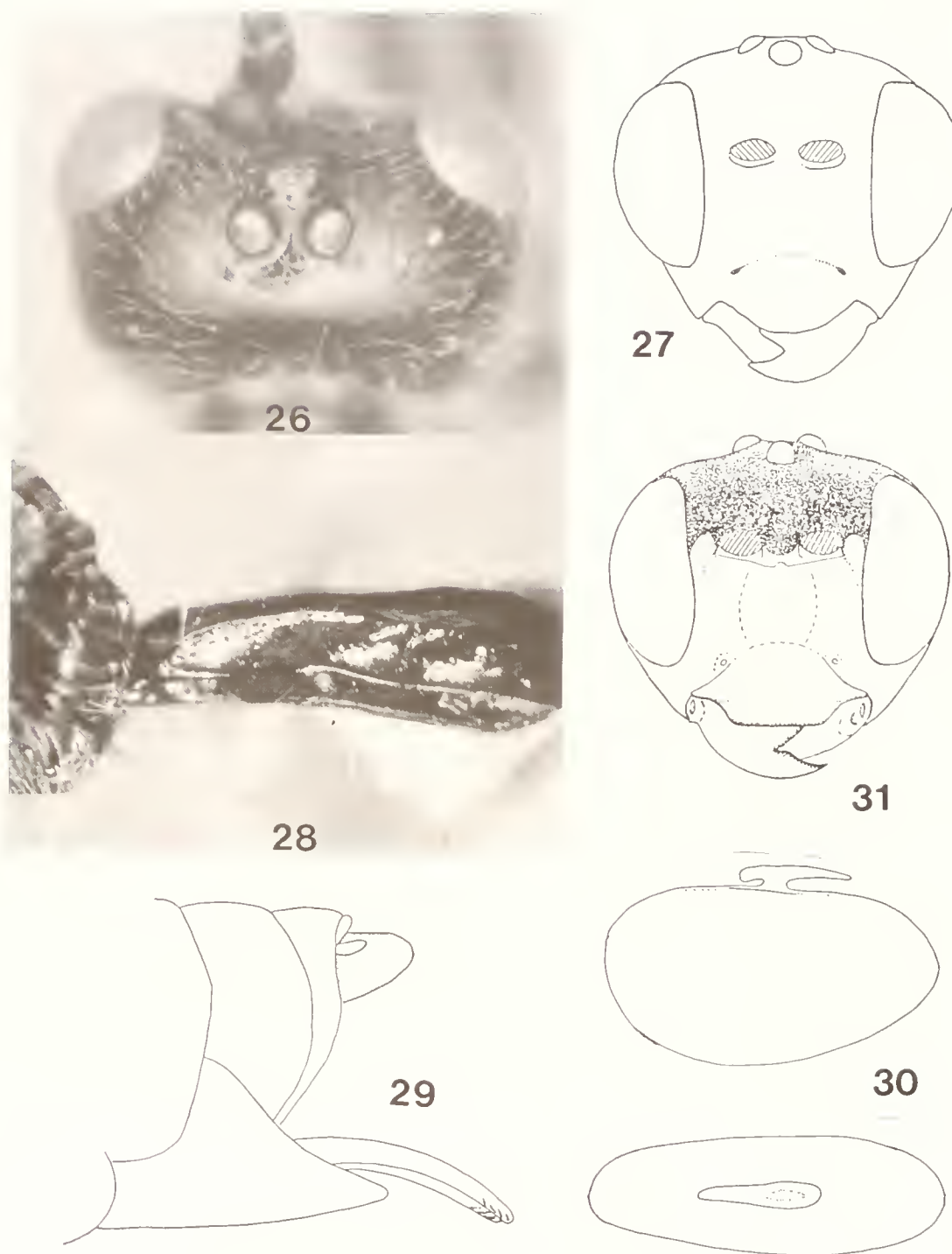
Figs. 15-18. *O. platyura*: 15, face and mandible; 16, tip of abdomen showing ovipositor, subgenital plate and ovipositor sheath; 17, tergite 1; 18, enlarged view of ovipositor + egg.



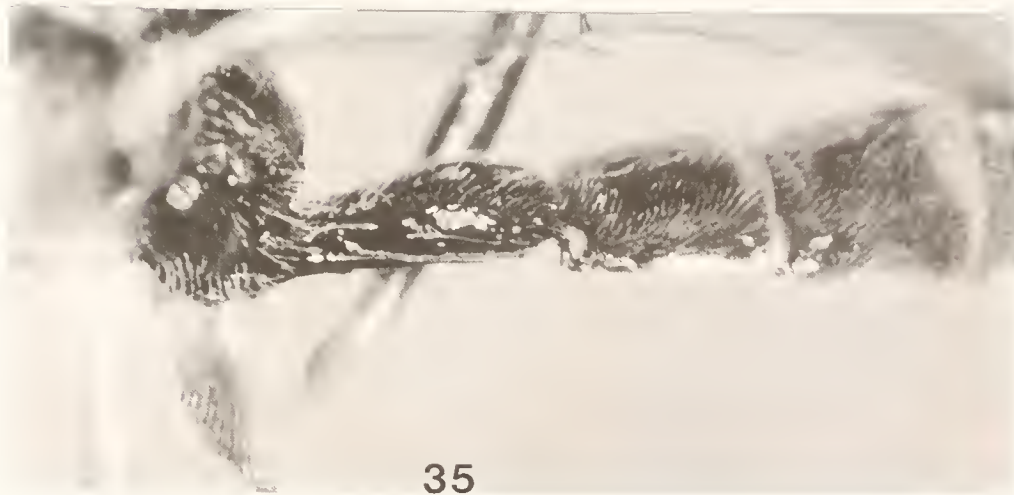
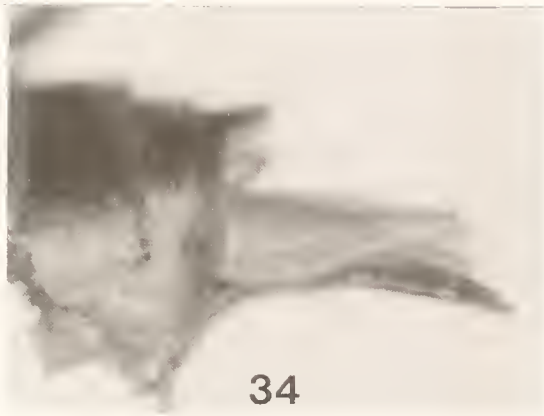
Figs. 19-21. *Orthomiscus uncinatus*: 19, tergite 1; 20, apical half of abdomen; 21, ovipositor with egg, ovipositor sheath and subgenital plate. [Photos taken from specimens of *O. leptura* Mason.]



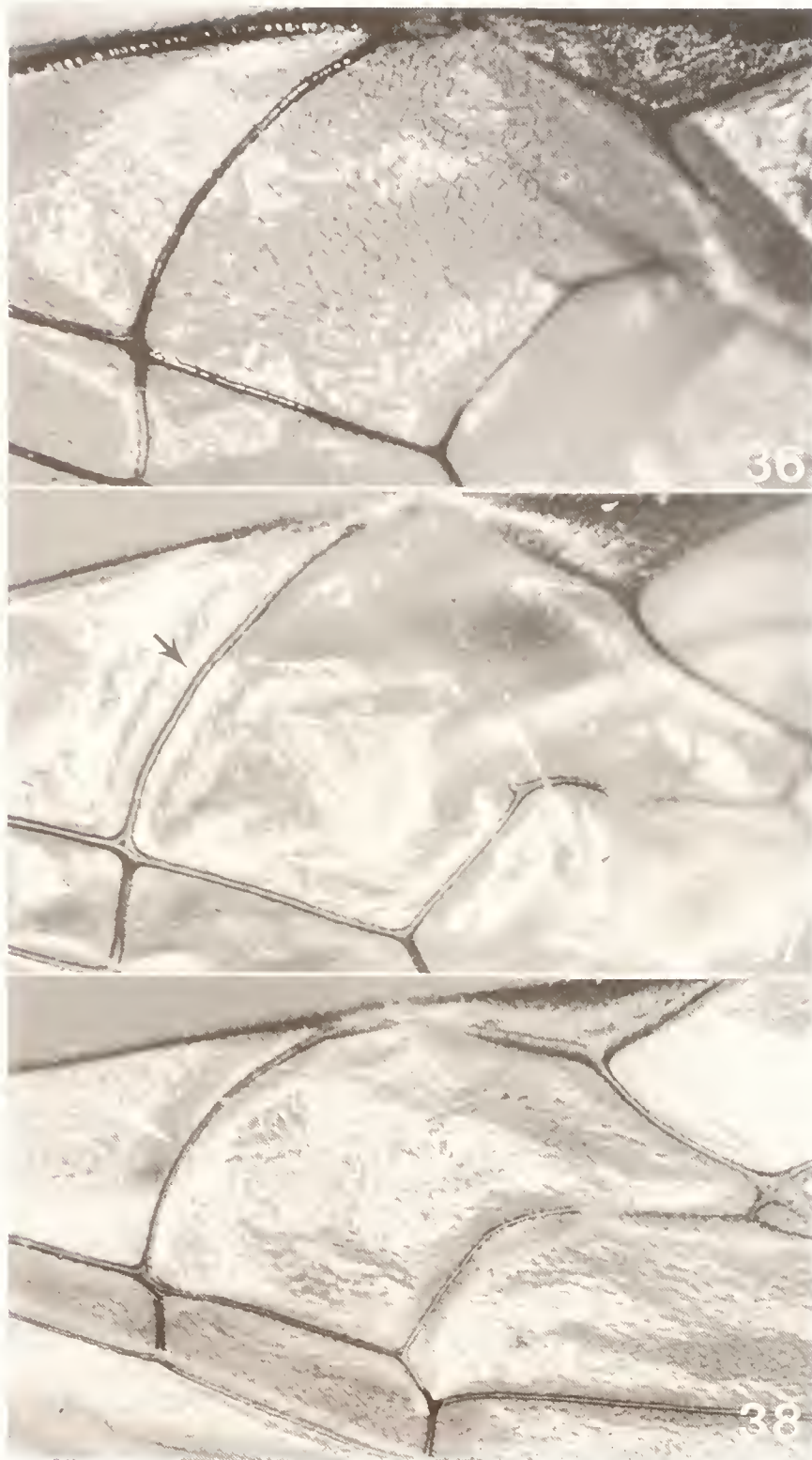
Figs. 22-25. 22, vertex of *Orthomiscus uncinatus*; 23, propodeum of *O. uncinatus*; 24, vertex of *O. eridolius*; 25, ovipositor + egg of *O. eridolius*. [22-23 of *O. leptura* Mason; 24-25 from holotype of *eridolius*.]



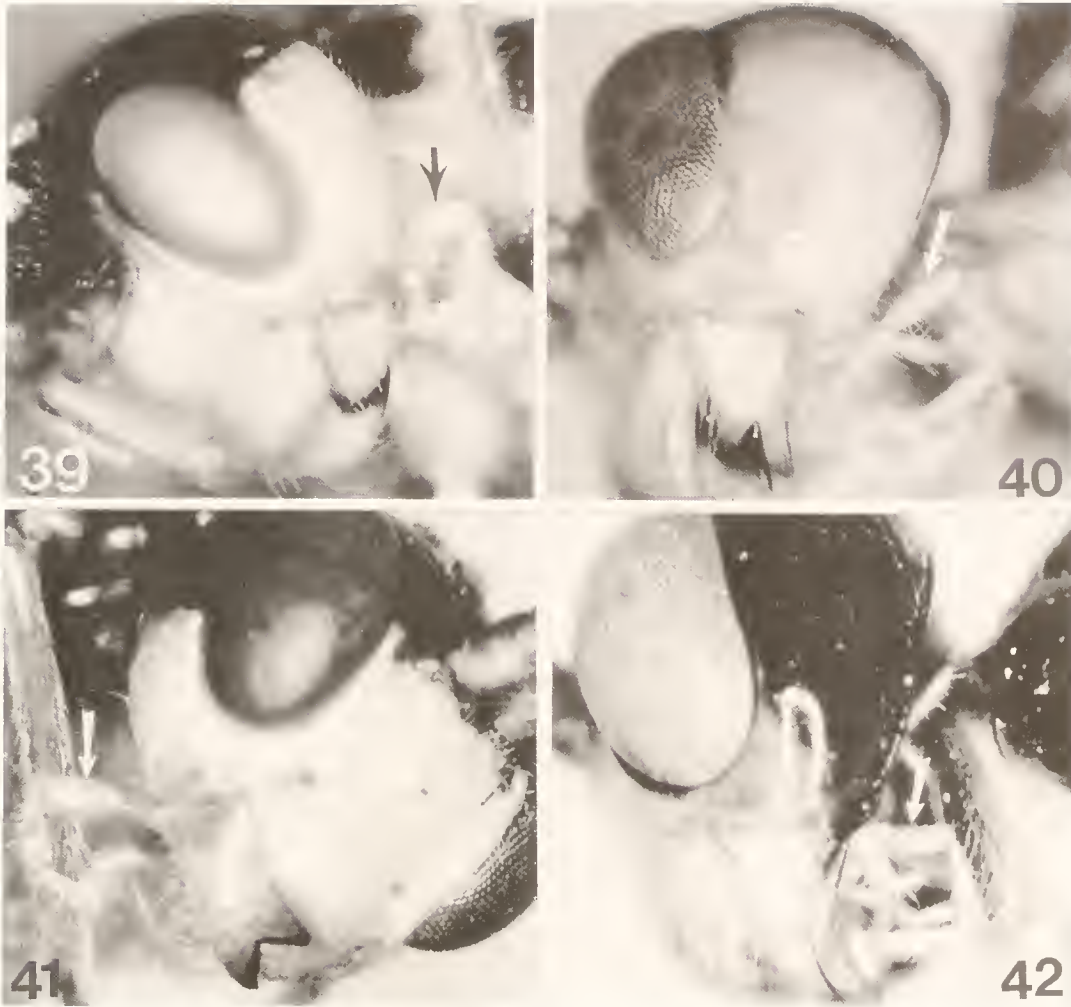
Figs. 26-31. 26-30. *Orthomiscus simplex* (Mason): 26, vertex, 27, face and mandible; 28, tergite 1; 29, tip of abdomen showing ovipositor and subgenital plate; 30, egg. 31, Face and mandible of *O. medusae*. [Figs. 27, 29, 30 after Mason, 1966; 26 and 28 of paratype and 30 after Kasparyan, 1990.]



Figs. 32-35. *Kristotomus amurensis* (Kasparyan): 32, habitus; 33, face; 34, ovipositor and sheaths; 35, abdomen. [Photos of holotype, *Orthomiscus amurensis* Kasparyan.]



Figs. 36-38. Fore wing showing the curvature of the basal vein in: 36, *Orthomiscus uncinatus*; 37, *O. platyura*; 38, *O. medusae*.



Figs. 39-42. Maxillary palp: 39, *Orthomiscus uncinatus*; 40, *O. platyura*; 41, *O. medusae*; 41, *O. simplex*.

Revision of West-European Genera of the Tribe Aylacini Ashmead (Hymenoptera, Cynipidae)

J. L. NIEVES-ALDREY

Museo Nacional de Ciencias Naturales (Biodiversidad), c/José Gutierrez Abascal 2, 28006 Madrid, Spain

Abstract.—The west European genera of Aylacini Ashmead (Hym., Cynipidae) and the genus *Antistrophus* Walsh from North America are reviewed. Diagnoses of all the genera are presented and an illustrated key for the identification of the genera is provided. Four genera are described as new: *Barbotinia* gen. n., *Hedickiana* gen. n., *Iraella* gen. n. and *Neaylax* gen. n. The genus *Timaspis* Mayr is resurrected and the following synonymies are proposed: *Aylacopsis* Hedicke 1923 = *Timaspis* Mayr 1881; *Weldiella* Ionescu and Roman 1962 = *Cecconia* Kieffer 1902 and *Endocaulonia* Ionescu and Roman 1960 = *Panteliella* Kieffer 1902. Five species are redescribed and figured and lectotypes for six species are designated. Nine new combinations are proposed as well as new synonymies for three species. A check list of the west European species of Aylacini is presented.

INTRODUCTION

The Cynipidae or gall wasps is one of the better known families of Cynipoidea. It is estimated that there are around 1,800 species distributed mainly in temperate areas of the northern hemisphere (Dalla Torre and Kieffer 1910, Nordlander 1984). More than 250 species have been recorded in Europe (Nieves-Aldrey 1987). Galls of this group of parasitic wasps are counted among the most specialized and morphologically complex of all zooecidia. About 75% of all known cynipids are gall inducers associated with Fagaceae, almost exclusively with *Quercus*; another large group is associated with Rosaceae and Asteraceae, while a few species are linked to Lamiaceae, Papaveraceae, Valerianaceae, Aceraceae, Fabaceae, and Apiaceae.

With regard to the higher classification of the Cynipidae, the family is divided here into six tribes, on the basis of the five tribes proposed by Ashmead (1903); see also Kinsey (1920). All the tribes but one, viz Eschatocerini, are present in west-Europe. Eschatocerini is only represented by the Neotropical *Eschatocerus* Mayr, gall maker on species of *Acacia* and *Prosopis*. This genus presents an axilla large, triangular and situated in the same plane as scutellum; scutellar foveae and notauli absent and reduced wing venation; all of them very distinctive apomorphic morphological fea-

tures, supporting its monophyly. Pediaspidini includes only one genus of palaeartic distribution: *Pediaspis*, Tischbein gall maker on *Acer* (Aceraceae). Some authors (Weld 1952, Weidner 1968, Askew 1984) include this genus within the Aylacini but since it exhibits a specialized scutellar morphology and has a heterogenic life-cycle, it is better placed in a separate tribe. Rhoditini is composed of two genera: *Diplolepis* Fourcroy and *Liebelia* Kieffer (Ronquist, "in press") which induce galls on *Rosa* (Rosaceae). Cynipini comprises of oak gall inducers and they are associated exclusively with Fagaceae, mainly *Quercus*. The inquiline group is composed of genera which do not produce galls, living as inquilines in the galls of other Cynipidae. Some authors, especially in North America, have given subfamily status to this group (Ashmead 1903, Burks 1979); more frequently it has been included together with the gall inducers in a large group without subdivisions (Weld 1952, Eady and Quinlan 1963). Here it is regarded as a tribe.

Recent studies on phylogenetic relationships within Cynipidae (Ritchie 1984, Ronquist in press) support the monophyly of Synergini as well as that of Cynipini and Rhoditini. On the other hand, Aylacini appears to be based on symplesiomorphy and would be an unnatural paraphyletic group. Nevertheless, for historical reasons and considering biological characters, I prefer to treat them here as a tribe.

KEY TO THE TRIBES OF CYNIPIDAE

- 1 Pronotum dorsally longer, in median dorsal line at least one-sixth, usually one-third as long as greatest length on outer lateral margin, and frequently with truncation and pits forming pronotal plate (Figs. 1, 2); projection of ventral spine of gaster of female always short. Species usually fully alate, except male of *Phanacis centaureae* and some forms of *Synergus thaumacerus*, which are brachypterous 2
- Pronotum dorsally very short, in medial dorsal line one-seventh or less as long as outer lateral margin, and without truncation or pits (Fig. 3); projection of ventral spine of gaster of female usually longer than broad, viewed laterally. Agamic forms of some species apterous 4
- 2 Scutellum dorsally flat and trapezoidal with a large, heart-shaped impression on the disk; scutellar foveae absent (Fig. 4). One species with heterogonic life cycle, associated with Aceraceae (*Acer* spp) **Pediaspidini**
- Scutellum oval or rounded, always dorsally convex; scutellar foveae usually present, sometimes reduced to an arched depression. Inquilines or gall makers associated with plants other than *Acer* 3
- 3 Gula (Fig. 5) reduced to a long, narrow median strip; gular sulci united well before reaching hypostomata; metasomal tergites 2+3 (third and fourth abdominal terga) (Fig. 8) fused, at least in the female, into one large segment occupying nearly the whole of the gaster in the female; if showing only a false suture in either sex (Fig. 6), then the face usually has two vertical and parallel carinae (Fig. 7); face and thorax sculptured, sometimes very lightly, but never smooth and shining; Maxillary palps with 5 palpomeres with 1 and 2 fused. Inquilines in galls of *Quercus* and *Rosa* **Synergini**
- Gular sulci (Fig. 9) usually free or meeting near the hypostomata; metasomal tergites 2-7 (Fig. 10) free in most cases; if metasomal tergites 2+3 fused in the female into one large segment then head and thorax almost smooth and shining; pits of pronotum usually present and sometimes associated with a light pronotal plate; maxillary palps 5-segmented. Gall makers on plants other than *Quercus*, *Rosa*, and *Acer* **Aylacini**
- 4 Axilla large, triangular and situated in the same plane as scutellum; scutellar foveae (Fig. 11) absent; notauli absent; wing venation (Fig. 12) reduced; Rs+M and R1 not visible; radial cell of forewing with radius quite separate from anterior margin of wing; frons (Fig. 13) with a strong medial keel. One genus from South America, gall maker on *Acacia* **Eschatocerini**
- Axilla much smaller; not situated at the same level as the scutellum; scutellar foveae present or forming a shallow arcuate transverse depression; (Rs+M) of fore wing present and Rs reaching or almost reaching to anterior margin of wing; frons without medial keel or with a much weaker keel 5
- 5 Mesopleuron (Fig. 14) with longitudinal furrow; hypopygium of female (Fig. 15) ploughshare-shaped; radial cell of wing usually closed anteriorly. Gall makers on *Rosa* **Rhoditini**
- Mesopleuron without longitudinal furrow; hypopygium of female never shaped as above; radial cell open anteriorly. Gall makers on *Quercus*, *Castanea* and *Lithocarpus* **Cynipini**

The tribe Aylacini comprises a group of primitive genera of cynipid gall-inducers associated mainly with herbaceous plants. Most of their representatives are linked with species of Asteraceae producing milky juice, but some genera and species are associated with Papaveraceae, Lamiaceae, Valerianaceae and Apiaceae. Galls of the species of this tribe are not complex; they are produced mainly in twigs or fruits and are not detachable from the host plant tissues. The life cycles are uni- or bivoltine but without heterogony or alternation of generations (Folliot 1964, Askew 1984). There is no previous full revision of the genera of this tribe. Some partial revision of genera included in Aylacini were made by Weld (1952), Eady and Quinlan

(1963), Quinlan (1968) and Kovalev (1982), but as far as I know no entire revision of the group has been accomplished.

The group appears to be particularly abundant and species-rich in the far east of Europe where many taxa have been described recently (Zerova et al. 1988) (see also Belizin 1959). Unfortunately I have failed to obtain type material of these taxa to be included in this revision.

MATERIAL AND METHODS

This study is supported by the examination of the types of almost all the genera represented in western Europe. The initial purpose was to in-

clude all the genera described from the western Palaearctic region but since I failed to borrow the type material of some genera from eastern Europe, mainly Russia, Ukraine and Rumania, the work was finally restricted to west-Europe. It was also necessary, in order to clarify the taxonomic status and relationships of some genera, to examine some Nearctic material. These were: *Antistrophus*, *Gillettea* and the type species of *Aulacidea* Ashmead. Type species of genera of Aylacini are cited according to Rohwer and Fagan (1917). The list of collections from which material have been examined for this study is as follows:

MCNM	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHP	Museum National d'Histoire Naturelle, Paris, France (Mme Casevitz-Weulersse)
MZLU	Museum of Zoology and Entomology Lund University, Lund, Sweden (R. Danielsson)
NHML	The Natural History Museum (British Museum), London, England (N. Fergusson)
NHMW	Naturhistorisches Museum, Vienna, Austria (M. Fischer)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (A. Menke)
ZMHB	Zoologisches Museum, Humboldt-Universitat, Berlin, Germany (F. Koch)
ZMH	Zoologisches Museum Hamburg, Hamburg, Germany (R. Abraham)
ZSBS	Zoologische Sammlungen des Bayerischen Staates, Munich, Germany (E. Diller)

MORPHOLOGICAL TERMS

The terminology mostly follows that used by Eady and Quinlan (1963), Ritchie (1984) and Ronquist and Nordlander (1989). The term "thorax" as used here includes the propodeum and thus is an equivalent to the "mesosoma" of the mainly American literature. Measurements and abbreviations used here are as follows: A3 and A4, third and fourth antennomeres; POL (post-ocellar distance) is the distance between the inner margins of the posterior ocelli; OOL (ocell-ocular distance) is the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; *transfacial line* is the shortest distance across the face between the antennal sockets. Abbreviations of forewing venation are used as Eady and Quinlan (1963). Supraclypeal area is the medial area between the clypeus and the antennal sockets. Length and width of the radial cell of the forewing are measured following Wiebes-Rijks (1979).

AYLACINI (Ashmead 1903)

Aulacini Ashmead 1903:147

Aylaxini (Ashmead): Quinlan 1968:275

Aylacinae (Ashmead): Kovalev 1982:85

Aulacideini (=Aylaxini) Fergusson 1988:143

Type genus: *Aylax* Hartig 1840 (= *Aulax* Hartig, 1843 (unjustified emendation)). orig. desig.

Insects of relatively small size; 1-5 mm. Coloration usually black, brown or red-brown. Head viewed dorsally transverse; usually two times broader than long; in frontal view usually slightly broader than high or as broad as high; temples not expanded behind the eyes; ocelli small; face with radiating striae from clypeus to antennal sockets weak to moderately developed, medially usually absent; subocular sulcus absent. Frons and vertex usually with dull sculpture, coriaceous, alutaceous or reticulate; rarely smooth and shining; frontal carina not present; supraclypeal area raised or slightly protuberant; antenna filiform with 12 to 14 antennomeres in females, 13 to 15 in males. Pronotum dorsally long; in median dorsal line one-sixth at least, usually one-third as long as greatest length on outer lateral margin, frequently with truncation and submedial pits forming a light pronotal plate; sides of pronotum usually pubescent; mesoscutum usually with coriaceous, alutaceous or reticulate sculpture, less frequently transversally rugulose or almost smooth; notauli complete to almost absent; median mesoscutal impression, if present, usually impressed only in posterior third or less of mesoscutum; scutellar foveae usually present, sometimes confluent and not well defined posteriorly; mesopleuron usually longitudinally striated, reticulate or rugose-reticulate. Wings well developed except the brachypterous males of *Phanacis centaureae* Förster; radial cell of forewing open or closed in the margin. Abdominal tergites 3 to 7 free; third abdominal tergum covering 1/3 to 1/8 of the whole length of gaster, laterally with or without a pubescent patch; tergites with or without punctures. Ventral spine of hypopygium very short. Tarsal claws simple, rarely with acute basal lobe or tooth.

KEY TO WEST-PALAEARCTIC GENERA OF AYLACINI
(INCLUDING NEARCTIC GENUS *ANTISTROPHUS* WALSH)

- 1 All claws with distinct basal lobe or tooth (Figs. 16, 18). Mesopleuron, mesoscutum and vertex smooth and shining. Associated exclusively with *Rubus* and *Potentilla* (Rosaceae) 2
- All claws simple (Figs. 19, 20). Mesoscutum and vertex rather dull, sculptured, striate or reticulate; mesopleuron striate or reticulate. Genera not associated with Rosaceae 3
- 2 Claws weakly lobed (Figs. 17, 18). Subcosta and radius reaching to anterior margin of wing; radial cell sometimes partly closed anteriorly (Fig. 21). Third and fourth abdominal terga completely fused in females, separated in males. Gall-maker on *Potentilla* *Xestophanes* Foerster
- Claws strongly lobed (Fig. 16). Subcosta and radius not reaching to anterior margin of wing (Fig. 22); radial cell open anteriorly. Third and fourth abdominal terga completely free in both sexes. One genus associated with *Rubus* and *Potentilla* *Diastrophus* Hartig
- 3 Mesopleuron longitudinally striated. Pronotum always with two distinct submedial pits 7
- Mesopleuron reticulate (Figs. 24, 28, 41), rugulose-reticulate (Fig. 116) or rugulose-striate. Pronotum with or without submedial pits 4
- 4 R1 and Rs not quite reaching to anterior margin of wing (Fig. 42); wing fringe absent (Fig. 42). Third antennal segment shorter than fourth (Fig. 37) *Antistrophus* Walsh
- R1 and Rs reaching to anterior margin of wing and hair fringe distinct, usually long. Third antennal segment as long as or longer than fourth 5
- 5 Pronotum (Fig. 23) with two distinct submedial pits. Pronotum, mesoscutum and mesopleuron strongly reticulate (Fig. 24). Radial cell (Fig. 25) clearly open anteriorly. Radiating striae on face absent (Fig. 26). Third antennal segment as long as fourth (Fig. 27). Gall-maker on *Papaver somniferum* L. *Iraella* gen. n.
- Pronotum usually without submedial pits, rarely with two rather small and indistinct pits. Mesopleuron reticulate or rugulose-reticulate. Radial cell usually closed, at least partially. Radiating striae on face present, sometimes weak or faint. Third antennal segment longer than fourth 6
- 6 Mesopleuron reticulate (Fig. 28). Notauli usually faint or absent anteriorly. Gall inducer on Asteraceae .. *Phanacis* Foerster
- Mesopleuron rugulose-reticulate (Fig. 116) or rugulose-striated. Notauli complete. Gall inducer on Asteraceae *Timaspis* Mayr
- 7 Head, in frontal view, as high as broad, slightly higher than broad in male (Fig. 29); malar space at least as long as the height of an eye in the female, longer in male. Scutellar foveae shallow and indistinct. Hair fringe on apical margin of forewing long (Fig. 30). Gall-maker on *Valerianella* (Valerianaceae) *Cecconia* Kieffer
- Head in frontal view broader than high (Figs. 44, 57); malar space usually shorter than height of an eye. Scutellar foveae distinct. Wing fringe on apical margin, if present, usually not as long 8
- 8 R1 and Rs of forewing not quite reaching to anterior margin of wing; radial cell clearly open at base and along margin (Figs. 62, 79, 110) 9
- Rs almost reaching to anterior margin of wing and R1 continuing more or less along margin of wing (sometimes R1 only touching the margin); radial cell closed, partially closed or obsoletely closed (Figs. 34, 50, 55, 103) 12
- 9 Pronotum shorter medially (Fig. 60). Mesopleuron (Fig. 62) striate with some reticulation between striae. Third abdominal tergum without lateral pubescent patch. Gall maker on *Papaver* (Papaveraceae) *Barbotinia* gen. n.
- Pronotum longer medially (Figs. 75, 107). Mesopleuron (Fig. 77) finely or strongly striate. Third abdominal tergum usually with lateral pubescent patch 10
- 10 Pronotum longitudinally striate and strongly pubescent (Fig. 31). Mesoscutum finely reticulate (Fig. 32). Third female antennal segment longer than fourth (Fig. 33). Third abdominal tergum with a distinct lateral pubescent patch (Fig. 31). Hair fringe on margin of forewing moderately long. Associated with *Glechoma* (= *Nepeta*) (Papaveraceae) *Liposthenus* Förster
- Pronotum without longitudinal striae (Fig. 77), coriaceous or reticulate, only moderately pubescent. Mesoscutum coriaceous or rugulose-coriaceous. Third female antennal segment shorter than fourth (Fig. 73). Third abdominal tergum with or without lateral pubescent patch. Hair fringe on margin of forewing absent or very short 11

- 11 Hair fringe on wing margin completely absent (Fig. 110). Mesoscutum coriaceous, with scattered piliferous punctures (Fig. 108); notauli distinct only in posterior half of mesoscutum. Gaster laterally smooth, without punctures (Fig. 109). Gall inducer on *Phlomis* (Lamiaceae) *Rhodus* Quinlan
- Hair fringe on wing margin very short or absent. Mesoscutum without punctures (Fig. 76). Notauli almost complete. Fourth to seventh abdominal tergites finely punctate (Fig. 78). Associated with *Centaurea* (Asteraceae) *Isocolus* Foerster
- 12 R1 of forewing continuing along margin of wing almost completely closing radial cell; sometimes vein is very lightly pigmented on the margin and radial cell appears obsoletely closed (Figs. 50, 55, 69). Pronotum always dorsally quite long 13
- R1 usually not continuing along margin of wing, occasionally slightly so; radial cell appearing open, at least anteriorly (Figs. 34, 103) 14
- 13 Mesopleuron clearly striate (Figs. 49, 54). Third abdominal tergum with lateral pubescent patch. Antenna of female 13-segmented. Notauli usually complete. Hair fringe on margin of forewing moderately long. Associated with Asteraceae and Lamiaceae *Aulacidea* Ashmead
- Mesopleuron not clearly striate (Fig. 68), with some striae on alutaceous sculpture. Third abdominal tergum without lateral pubescent patch (Fig. 70). Antenna of female 12-segmented (Fig. 65). Hair fringe on margin of forewing absent (Fig. 69). Gall inducer on *Salvia* (Lamiaceae) *Hedickiana* gen. n.
- 14 Notauli weak or obsolete even in posterior half of mesoscutum. Third abdominal tergum without lateral pubescent patch. Gall maker on *Phlomis* (Lamiaceae) *Panteliella* Kieffer
- Notauli clearly impressed, at least in posterior half of mesoscutum. Third abdominal tergum with or without lateral pubescent patch 15
- 15 Pronotum dorsally relatively short and pits narrowly separated, more strongly transverse (Fig. 1). Scutellar foveae smaller, sculptured. Female antenna 13-segmented. R1 partially closing the radial cell (Fig. 34). Gall maker on *Papaver* (Papaveraceae) *Aylax* Hartig
- Pronotum dorsally longer and pits rounder and more broadly separated (Fig. 100). Scutellar foveae larger, rounded and smooth (Fig. 101). Female antenna 12-13 segmented. R1 not partially closing the radial cell (Fig. 103). Associated with *Salvia* (Lamiaceae) *Neaylax* gen. n.

ANTISTROPHUS Walsh

Antistrophus Walsh 1869:74. Type species: *Antistrophus ligodesmiae-pisum* Walsh. Monotypic (examined)

Asclepiadiphila Ashmead 1897b:263. Type species: *Asclepiadiphila stephanotidis* Ashmead. Monotypic.

Diagnosis.—Head, viewed dorsally two times broader than long; viewed frontally, slightly broader than high; temples slightly expanded behind the eyes. Frons and vertex strongly reticulate; radiating striae present; supraclypeal area reticulate, slightly protuberant; antenna 13-14 segmented in female, 14-segmented in male; A3 clearly shorter than A4. Pronotum strongly reticulate, in dorsal view, long; submedial pits conspicuous. Mesoscutum reticulate; notauli slightly faint anteriorly; median mesoscutal impression weakly impressed posteriorly; scutellar foveae large, rounded, confluent; scutellum strongly reticulate; mesopleuron reticulate. Wings hyaline; R1 not quite reaching the margin of wing; radial cell open, nearly three times as long as broad, without hair fringe on distal margin. Third abdominal tergum without lateral pubescent patch; follow-

ing tergites not punctate.

Comments.—The structure of the antenna, pronotum and radial cell relate it to the European genus *Isocolus*, but it differs from *Isocolus* in the strongly reticulate sculpture of the mesopleuron and mesoscutum. This feature relates it to *Phanacis* but it differs from that genus in important traits such as the presence of submedial pits in the pronotum, scutellar foveae distinct, third antennal segment shorter than fourth, radial cell open, and hair fringe on distal margin of forewing absent.

Distribution and Biology.—*Antistrophus*, in spite of being cited in Weld (1952) as a genus confined to North America, is mentioned in the generic keys of the same work as also present in Greece, galling plants of *Salvia* (Lamiaceae). Later on, Quinlan (1968) reiterates, without questioning it, the record. But the truth is that there is no correct distribution record of this species for that country, therefore Quinlan's citation is quite clearly erroneous and the occurrence of the genus in Europe quite unlikely. All data suggest that it is a genus of exclusively Nearctic distribution.

The genus comprises nearly 10 species in North America, associated with species of *Silphium* and *Chrysothamnus* (Asteraceae), in the stems of which they produce galls.

REVISED SPECIES

Antistrophus pisum Ashmead

Antistrophus pisum Ashmead 1885:294
Antistrophus ligodesmia-pisum Walsh 1869:74 (invalid name).
Asclepiadiphila stephanotidis Ashmead 1897b:263

Examined material.—Walsh's type series of *A. pisum* in the USNM consists of 34 syntypes: 11 ♂, 23 ♀, part of them mounted on micro-pins and part on cards. 4 ♀, with red labels printed "Type No 1523 U.S.N.M." and white handwritten "*Antistrophus pisum* Walsh"; the female in better condition, only missing the last segments of the right antenna, is designated lectotype; 7 ♂, glued on a single card, with labels number 208, red "Type No 1523 USNM"; white "*Lygodesmia* gall", are designated paralectotypes. The type series of *A. stephanotidis* Ashmead comprises 4 ♂ and 7 ♀; 1 ♀, set on card point, with labels: white "4780 4-0-91" and red "Type No 3737 USNM", is designated lectotype.

Redescription.—FEMALE. (Figs. 35-42). Length 3 mm. Yellow-red or amber with darkened parts mainly in vertex, mesoscutum, scutellum and upper part of gaster; antenna and legs concolorous with the body. Head scarcely pubescent and strongly reticulate, viewed dorsally (Fig. 35) two times broader than long, viewed frontally (Fig. 36) 1.1 times broader than high. POL slightly shorter than OOL and about three times greatest diameter of lateral ocellus; transfacial line around 2.4 times height of eye; temples moderately expanded behind eyes; malar space 1.2 times height of eye; face laterally with radiating striae; supraclypeal area reticulate, only slightly prominent; antenna (Fig. 37) relatively long, slightly shorter than body, filiform, with 13-14 antennomeres; if only 13, then top segment is very long; third segment clearly shorter than fourth, slightly excavated in middle. Pronotum (Fig. 39) reticulate and pubescent; dorsally long, with distinct submedial pits associated to clearly visible pronotal plate; mesoscutum (Fig. 40) strongly reticulate; notauli faint in anterior third; moderately convergent posteriorly; median mesoscutal impression indistinct, weakly im-

pressed in posterior fourth of mesoscutum; scutellar foveae large, confluent, rounded; scutellum rounded, strongly reticulate; mesopleuron (Fig. 41) reticulate; propodeum reticulate and laterally pubescent; propodeal carinae slightly divergent. Wings hyaline with pale venation; R1 and Rs of forewing not quite extending to wing margin, radial cell open (Fig. 42); Rs rather curved; length of the radial cell about 2.8 times the width; areolet indistinct; cubitalis (Rs + M) joining the basalis (Rs+M) at a point close to junction of basalis with Cu₁; fore-wing without distinct hair fringe on wing margins. Gaster, viewed laterally, slightly longer than head + thorax; third abdominal tergum (Fig. 41) basally smooth without sculpture or pubescence, following segments not punctate nor pubescent; ventral spine of hypopygium very short. MALE. differs from female in darker coloration, mainly rufo-brown; antenna longer (Fig. 38), with 14 antennomeres.

AULACIDEA Ashmead

Aulacidea Ashmead 1897a:68. Type species: *Aulax mulgeducola* Ashmead (= *Aulax harringtoni* Ashmead 1877) Original designation

Diagnosis.—Head, viewed dorsally, about two times broader than long; viewed frontally slightly broader than high; temples not expanded or slightly expanded behind eyes; Frons and vertex coriaceous; radiating striae present laterally on face; supraclypeal area raised, coriaceous; antenna 13-segmented in female, 14-segmented in male, A3 slightly shorter than A4. Pronotum long dorsally and submedial pits present, broadly separated; mesoscutum coriaceous, granulate or finely rugulose; notauli usually complete; median mesoscutal impression usually present posteriorly; scutellar foveae distinct, usually large and rounded; mesopleuron longitudinally striated. Radial cell of forewing entirely closed on margin; hair fringe present, moderately long. Third abdominal tergum, in females, with lateral pubescent patch; following tergites usually punctate.

Comments.—Morphologically, the genus is well distinguished by its closed radial cell and striate mesopleuron. The type species was described from North America and is redescribed below.

Distribution and Biology.—Genus of holarctic distribution. The genus is represented in West-

Europe by 12 species. Most of European species induce galls on stems and leaves of species of Asteraceae specially on *Hieracium*; one species produce galls in achenes of *Nepeta* (Lamiaceae).

Aulacidea harringtoni (Ashmead)

Aulax harringtoni Ashmead 1887:146

Aulax mulgediicola Ashmead 1896:133 (examined)

Type material.—Series composed of 75 specimens, individually set on card points. 1♀, with labels: red printed "Type No 3092 USNM"; white handwritten "*Aulax mulgediicola*", is designated lectotype.

Redescription.—FEMALE. Figs. 43-50. Length: 2.4 mm. Reddish yellow or orange, darker on dorsum; antenna and legs entirely yellow. Head, in dorsal view (Fig. 43), a little less than two times broader than long; in frontal view (Fig. 44) 1.2 times broader than high; POL: OOL as 10:9; OOL slightly more than three times greatest diameter of lateral ocellus; transfacial line about 1.4 times height of eye; temples slightly expanded behind eyes; frons and vertex finely coriaceous; face laterally with incomplete radiating striae; supraclypeal area not prominent; antenna (Fig. 45) filiform with 13 antennomeres, third segment shorter than fourth. Pronotum (Fig. 47) coriaceous and scarcely pubescent; dorsally long, with distinct submedial pits broadly separated; mesoscutum (Fig. 48) finely rugulose or granulate; notauli complete; median mesoscutal impression visible in posterior 1/3 of mesoscutum; scutellar foveae ovate, well defined, separated by a septum relatively broad posteriorly; scutellum weakly rugose; mesopleuron (Fig. 49) finely striated longitudinally. Wings hyaline; radial cell of forewing (Fig. 50) closed on the margin; length of the radial cell about 2.4 times width; areolet indistinct; hair fringe on wing apical margin distinct. Gaster (Fig. 49), viewed laterally, as long as head + thorax; third abdominal tergum basally with lateral pubescent patch, following segments finely punctate; ventral spine of hypopygium very short. MALE. Differs from female in antenna (Fig. 46), with 14 antennomeres.

Comments.—The morphological features of the type species are congruent with those exhibited by the species represented in Europe.

Distribution and Biology.—Nearctic. The species makes galls in stems of *Lactuca spp*, mainly *L. villosa* (Burks, 1979).

SPECIES FROM WESTERN EUROPE

The species of this genus recorded in Western Europe are listed in the check list (see Appendix). The novelties are represented by some species described by Thomson which are considered either good species or represent new synonymies (Nieves-Aldrey, in press). The following are other new combinations or redescrptions of poorly known species:

Aulacidea kernerii (Wachtl) comb. n.

Aylax kernerii Wachtl 1891:277

Examined material.—I have been not able to examine the type material of this species. Observations come from specimens reared from galls on *Nepeta spp* collected in Spain.

The following characters advise the transfer of this species to the genus *Aulacidea* Ashmead: pronotum relatively long dorsally (Fig. 52); 13-segmented antenna, with A3 slightly shorter than A4 (Fig. 51); mesoscutum with complete notauli (Fig. 53); longitudinally striated mesopleuron (Fig. 54); closed radial cell, although R1 is slightly pigmented on margin (Fig. 55).

Aulacidea scorzonerae (Giraud)

Aulax scorzonerae Giraud 1859:370

Aulacidea scorzonerae (Giraud): Kieffer 1902:96

Examined material.—The type material, sent by the MNHP, comprises 66 specimens set on micropins isolated or in pairs. Most specimens are complete and in good condition. All the specimens carry a white label "Museum Paris, coll. Giraud" and some carry labels handwritten by Giraud. 1♂, complete, set next to a male, is hereby designated lectotype.

Redescription.—FEMALE. Figs. 88-95. Length: 2 mm. Coloration variable, from almost entirely red-brown with darker thorax, antenna orange or dark-yellow and legs entirely red-yellow except coxae and base of femora darkened to dark-brown or black with legs darker too. Head scarcely pubescent and finely coriaceous; viewed dorsally (Fig. 88) two times broader than long; viewed frontally (Fig. 89) 1.2 times broader than high. POL:OOL as 10:7; OOL about 3.5 times the greatest diameter of lateral ocellus; transfacial line around 1.8 times

height of eye; temples not expanded behind eyes; face laterally with incomplete radiating striae; supraclypeal area only slightly prominent; Antenna (Fig. 90) filiform, relatively short, about 0.6 times length of the body; with 13 antennomeres, A3 clearly longer than A4. Thorax scarcely pubescent; pronotum (Fig. 91) dorsally long; submedial pits clearly visible, slightly transverse; pronotum with coriaceous sculpture; mesoscutum (Fig. 92) finely coriaceous-alutaceous sculptured; notauli faint anteriorly, posteriorly not broad; median mesoscutal impression weakly impressed in posterior 1/6 of mesoscutum; scutellar foveae shallow, shining and almost smooth, ovate, separated by septum broader posteriorly; scutellum rounded with coriaceous-alutaceous sculpture; mesopleuron (Fig. 93) with fine longitudinal striae; propodeum with subparallel lateral carinae; median area scarcely pubescent, almost smooth. Forewings slightly longer than body, hyaline; radial cell (Fig. 94) closed on front margin, about 2.3 times longer than broad; hair fringe relatively short; areolet inconspicuous. Gaster as long as head+thorax; third abdominal tergum with a slight lateral pubescent patch (Fig. 93); following tergites without visible punctures; ventral spine of hypopygium quite short. Tarsal claws simple.

MALE. Differs from female in 14-segmented antenna (Fig. 95), A3 slightly broadened apically.

Comments.—The species had been very seldom recorded and, consequently, was poorly known having been incompletely described. After examination, I confirm that it belongs to *Aulacidea*. It is a species which is closely related to *A. tragopogonis* Thomson, from which it differs in host plant as well as in its incomplete notauli, less pronounced scutellar foveae, relatively shorter radial cell and invisible gastral punctuation.

Distribution and Biology.—Only recorded from Austria and Hungary. Reared from galls in the stems of *Scorzonera austriaca* Willd and *S. humilis* L.

AYLAX Hartig

Aylax Hartig 1840(1839):186, 195. Type species: *Cynips rhoeadis* Bouche. Desig. by Ashmead 1903 (not seen)
Aulax Hartig 1843:412. Emendation.

Diagnosis.—Head, viewed dorsally, about two times as broad as long; viewed frontally slightly broader than high; temples not or slightly expanded behind eyes; radiating striae present later-

ally on face; supraclypeal area slightly prominent; antenna of female with 13 antennomeres; A3 as long as A4; antenna of male with 14 segments. Pronotum relatively short dorsally and submedial pits strongly transverse and slightly separated; mesoscutum coriaceous-granulate; notauli complete or faint anteriorly; median mesoscutal impression present in posterior 1/2 or more of mesoscutum; scutellar foveae small, slightly transverse and confluent; mesopleuron longitudinally striated. Radial cell of forewing only partially or obsoletely closed on the margin; R1 reaching to anterior margin of wing; hair fringe present, moderately long. Third abdominal tergum of females with lateral pubescent patch; following tergites without punctures.

Comments.—The genus was originally very heterogeneous. Later on, some species were set apart and transferred to such new genera as *Aulacidea* Ashmead and *Isocolus* Förster. My present conception of the genus is very restricted and I limit it to the species which are gall makers on seed capsules of *Papaver* and maybe also of *Hypecoum*.

Distribution and Biology.—The genus is represented in Europe by two species: *A. papaveris* (Perris 1839) and *A. minor* Hartig 1840. *Aylax hipecoi* Trotter 1912, described from Northern Africa (Tripoli), with galls in *Hypecoum* fruits, also found in Greece and Algeria, could also be assigned to this genus. However, the species has not been recorded again and I am ignorant as to the location of the types, so I have not been able to study the species.

BARBOTINIA gen. n.

Figs. 56-62

Type species.—*Aylax oranensis* Barbotin 1964:152. Herein designated. Derivation: Feminine gender. Dedicated to the French cynipidologist Mr. Barbotin, discoverer of the type species.

Description.—Head transverse; viewed dorsally (Fig. 56) more than two times as broad as long; temples not expanded behind eyes; viewed frontally (Fig. 57) trapezoid-shaped; transfacial line almost two times height of eye; malar space longer than height of eye; radiating striae on face strong, complete, laterally reaching the antennal sockets, medially absent; face without subocular sulcus; mandibles large; frons and vertex minutely alutaceous; antenna filiform, females with 14 antennomeres (Fig. 58), male with 15 antennomeres

(Fig. 59); pedicel as long as broad; A3 as long as A4. Pronotum (Fig. 60) dorsally relatively short; in median dorsal line, not more than 1/4 as long as greatest length on outer lateral margin; submedial pits clearly visible slightly transverse and moderately separated; mesoscutum (Fig. 61) granulate-punctate but punctures very obsolete or indistinct; notauli complete; median mesoscutal impression impressed in about the posterior half of mesoscutum; scutellar foveae large, rounded, contiguous, shining and almost smooth; scutellum granulate-rugulose; mesopleuron (Fig. 62) irregularly longitudinally striated but some reticulation present between the striae. Wings hyaline; R_1 not quite reaching the margin and radial cell of forewing open (Fig. 62); distal wing margins with short hair fringe. Gaster as long as head+thorax; third abdominal tergum covering about 1/3 of the gaster, basally smooth without punctures or pubescence; ventral spine of hypopygium short. Legs with simple tarsal claws.

Comments.—The proposed genus is closely related to *Aylax* Htg. these two genera having in common a pronotum which is relatively short medially and submedial pits which are transverse and scarcely separated. However, *Barbotinia* differs from *Aylax* in that the head has a trapezoidal shape with a relatively long malar space in relation to the height of an eye; the conformation of the scutellar foveae, very large and rounded; the striate-reticulated sculpture of the mesopleuron; the radial cell of the forewing completely open on the margin, with the R_1 vein hardly reaching the wing margin and the absence of a lateral pubescent patch, in the third abdominal tergum.

Distribution and Biology.—The new genus comprises a single known species: *Barbotinia oraniensis* (Barbotin 1964) comb. n., gall maker on capsules of *Papaver* species (Papaveraceae). Its known distribution area includes the mediterranean region and Northern Africa (Barbotin 1964). In Spain it is relatively frequent (Nieves-Aldrey 1984). In the NHML there are six specimens and galls of this species collected in Italy, Moladi Baxi, 1974, identified by Quinlan as *Aylax* sp.

CECCONIA Kieffer

Cecconia Kieffer 1902:7, 93. Type species: *Aylax valerianellae* Thomson 1877. Monobasic and original designation (examined)

Weldiella Ionescu and Roman 1962:551. Type species: *Weldiella aequalis* Ionescu and Roman 1962. Monobasic and original designation (not seen)

Diagnosis.—Head slightly less than two times broader than long viewed dorsally; in frontal view as broad as high or slightly higher than broad; malar space as long as height of eye; clypeus subquadrate; radiating striae well impressed; supraclypeal area slightly prominent; female antenna with 13 segments; A3 shorter than A4 or as long as A4; male antenna with 14 antennomeres. Pronotum dorsally not very long with distinct submedial pits; mesoscutum with alutaceous sculpture; notauli very lightly impressed, absent in anterior half of mesoscutum; median mesoscutal impression absent; scutellar foveae confluent, rounded, not well defined posteriorly; scutellum dorsally convex, with reticulate sculpture; mesopleuron finely striated longitudinally. Wings hyaline; radial cell of forewing open on the margin; about three times longer than broad; wing margins with long hair fringe. Third abdominal tergum with a lateral pubescent patch; following segments not punctate.

Comments.—The genus is easily distinguished morphologically: the head shape higher than broad viewed frontally; presence of long hairs in the distal wing margin; the shape of the scutellar foveae and notauli conformation. *Weldiella* was erected by Ionescu and Roman (1962) for the species *W. aequalis* found in Rumania, also gall-maker on fruits of species of *Valerianella* (Valerianaceae). On the basis of the original description (since I have not had the chance to examine the type species) I consider the differences used to differentiate that genus from *Cecconia* insufficient to support the description of a separate genus. At most, the mentioned features could indicate the existence of a second species, different from *C. valerianellae*, within the genus *Cecconia*.

Distribution and Biology.—The genus comprises two known species which produce galls in the fruits of species of *Valerianella* (Valerianaceae). *C. valerianellae* (Thomson) is widely distributed in Europe from Sweden to Rumania, through the Iberian Peninsula; *C. aequalis* (Ionescu & Roman), is only recorded from Rumania.

DIASTROPHUS Hartig

Diastrophus Hartig 1840 (1839):186. Type species: *Diastrophus rubi* Hartig. Monotypic

Type material of *D. rubi* Hartig, is housed in Munich (ZSBS). It is composed of 1 ♂ and 5 ♀. Lectotype ♀, mounted on micro-pin, designated by Weld (1931) (examined).

Diagnosis.—Head slightly more than two times broader than long viewed dorsally; in frontal view slightly broader than height; malar space slightly shorter than height of eye; transfacial line 1.5 to 2 times height of eye; supraclypeal area rugose-punctate with some striae; radiating striae incomplete; female antenna with 13 segments, male antenna with 14 antennomeres; A3 slightly longer than A4. Pronotum dorsally long with distinct submedial pits associated with a distinct pronotal plate; mesoscutum mostly smooth and shining; notauli well impressed and complete; median mesoscutal impression variable as to its length; scutellar foveae deep, rounded, smooth and shining; scutellum with a longitudinal furrow; mesopleuron almost entirely smooth and shining, medially with some fine longitudinal striae. Wings weakly infuscate; radial cell of forewing open on the margin; wing apical margin with hair fringe moderately long. Third abdominal tergum without lateral pubescent patch; following segments punctate. Tarsal claws of the legs with conspicuous acute basal lobe or tooth.

Comments.—The genus is quite distinct morphologically and together with *Xestophanes* Förster 1869 and *Gonaspis* Ashmead 1897 it forms a separate group within Aylacini. In fact, morphologically, they are distinguished from the rest of the genera of this tribe because they exhibit claws having a basal lobe or tooth; in the biological aspect, both genera are also well characterized by their association with species of *Rubus* and *Potentilla* (Rosaceae). Their special position within Aylacini has been pointed out by recent phylogeny studies of some genera of cynipids, mainly inquilines, by Ritchie (1984) and Ronquist (in press). The latter study indicates that *Diastrophus* is the genus of gall-wasps most closely related to the inquilines, which form a monophyletic group.

Distribution and Biology.— In Europe *Diastrophus* is represented by only two species: *D. rubi* Hartig, gall-inducer in species of *Rubus* and *D. mayri* Reinhart, 1876, which forms galls in the stems of *Potentilla argentea* L. In contrast with

Europe, the genus comprises many species in North America, most of them also associated with species of *Rubus*, the others associated with *Potentilla* and *Fragaria*.

HEDICKIANA gen. n.

Figs. 63-70

Type species: *Aulacidea levantina* Hedicke 1928:81. By present designation. Derivation: Feminine gender. Dedicated to the German entomologist Hedicke, discoverer of the type species.

Examined material.—4 ♀ (paratypes) deposited in the NHML. The holotype stated by the author to be deposited in his collection, has not been found and is probably lost. Consequently, we designate a lectotype amongst the studied paratypes: 1 ♀, mounted on micro-pin on card point, red label "paratypus"; handwritten labels "*Aulacidea levantina* 1928 Hedicke det" and "Tel Aviv Palestine Bodenheimer".

Description.—FEMALE. Head transverse; viewed dorsally (Fig. 63) more than two times broader than long; POL almost equal to OOL; temples slightly expanded behind eyes; viewed frontally (Fig. 64) clearly broader than high; transfacial line slightly more than 1.5 times height of eye; malar space shorter than height of eye; radiating striae on face well impressed laterally; supraclypeal area slightly protuberant, without striae; frons and vertex with coriaceous-alutaceous sculpture; antenna (Fig. 65) 12 segmented, A3 slightly more slender at the base; as long as A4. Pronotum (Fig. 66) dorsally relatively long; submedial pits clearly visible, broadly separated; mesoscutum (Fig. 67) coriaceous-punctate; notauli posteriorly broad but impressed only in posterior 3/4 of mesoscutum; median submedial impression visible in posterior 1/4 of mesoscutum; scutellar foveae large, rounded, contiguous, shining and finely coriaceous; scutellum rugulose; mesopleuron (Fig. 68) longitudinally striated but some reticulation present between the striae. Wings slightly infuscated; radial cell of forewing (Fig. 69) closed on front margin; distal wing margins with hair fringe quite short. Gaster as long as head+thorax; third abdominal tergum covering about 1/3 of gaster; basally smooth without punctures or pubescence; following segments punctate; ventral spine of hypopygium short. Tarsal claws simple.

Comments.—The genus is erected for the single species: *H. levantina* (Hedicke), described within *Aulacidea* Ashmead. In common with *Aulacidea*, the new genus exhibits a closed radial cell but it can be distinguished from *Aulacidea* as follows: antenna with 12 segments; mesopleuron not clearly longitudinally striated, in part irregularly reticulate; incomplete notauli and mesoscutum sculptured with piliferous punctures; base of third abdominal tergum lacking lateral pubescent patch.

Distribution and Biology.—Eastern Mediterranean; recorded from Crete, Syria and Israel (Hedicke 1928). The only known species, *Hedickiana levantina* (Hedicke), induces conspicuous juicy galls in stems of *Salvia triloba* L. (Lamiaceae).

IRAELLA gen. n.
Figs. 23-27

Type species: *Aulax luteipes* Thomson 1877:807. (= *Timaspis papaveris* Kieffer in Goury et Gignon). By present designation (examined)

Derivation: Feminine gender. Dedicated to my wife Ira.

Description.—Head viewed dorsally scarcely less than two times broader than long; temples not expanded behind eyes; viewed frontally (Fig. 26) slightly broader than high; transfacial line slightly more than height of eye; radiating striae on face absent; clypeus trapezoid-shaped, moderately projecting anteriorly, supraclypeal area slightly prominent, reticulate; frons and vertex with reticulate-coriaceous sculpture; female antenna, 13-14-segmented, male antenna 14-15-segmented; A3 almost of equal length to A4 (Fig. 27). Pronotum (Fig. 23) dorsally relatively short; submedial pits present; mesoscutum reticulate-coriaceous; notauli faint in anterior one third of mesoscutum; median mesoscutal impression visible in posterior 1/3 of mesoscutum; scutellar foveae transverse, confluent; scutellum reticulate; mesopleuron (Fig. 24) reticulate. Wings hyaline; radial cell of forewing (Fig. 25) open; three times longer than wide; distal wing margins with hair fringe long. Third abdominal tergum basally with lateral pubescent patch; following segments without punctures.

Comments.—The following morphological features define this new genus: face lacking visible radiating striae; clypeus projecting anteriorly; pronotum relatively short dorsally but with visible submedian pits; mesopleuron entirely reticulate; radial cell open on front margin. Some char-

acters, like the general body shape, face and mesopleuron sculpture and shape of the scutellar foveae, approach the new genus to the *Timaspis-Phanacis* complex, but the presence of submedian pits in the pronotum is a differentiating trait; other features that distinguish them are: the entirely reticulate face with total absence of radiating striae; clypeus projecting anteriorly; third antennal segment being of almost the same length as fourth and radial cell of the forewing open on front margin.

The genus is erected for a single species: *Iraella luteipes* (Thomson) comb. n. (= *Timaspis papaveris* Kieffer). Redescription of *Aulax luteipes* Thomson including statement of the synonymy indicated above was recently published (Nieves-Aldrey, in press).

Distribution and Biology.—Genus distributed from Sweden to Spain and Iran. The only known species of the genus is associated with *Papaver somniferum* L. (Papaveraceae), on the stems of which it produces inconspicuous galls. I have had the chance to examine in the Natural History Museum of London some specimens from Iran obtained from stems of *Papaver pseudorientale* and *P. bracteatum* Lindley, which might correspond to a different species within the same genus.

ISOCOLUS Förster

Isocolus Förster 1869:330, 334 (= *Eubothrus* Förster). Type species: *Diastrophus scabiosae* Giraud 1859. Monobasic and original designation (examined)

Diagnosis.—Head, viewed dorsally, about two times broader than long; temples at most only slightly expanded behind eyes; viewed frontally 1.3 times broader than high; transfacial line around 1.5 times the height of eye; malar space shorter than height of eye; radiating striae visible laterally, usually incomplete, sometimes present even in the supraclypeal area; antenna of female with 13 antennomeres, A3 shorter than A4; antenna of male with 14 segments. Pronotum dorsally long and submedial pits conspicuous, broadly separated; mesoscutum with coriaceous-rugulose sculpture, sometimes with transverse rugae; notauli usually complete; median mesoscutal impression usually visible at least in posterior one third of mesoscutum; scutellar foveae distinct, well defined; scutellum rugulose; mesopleuron with conspicuous longitudinal striae; wings hya-

line; radial cell of forewing open; R1 and Rs not quite reaching anterior margin of wing; distal margin of wing with hair fringe very short. Third abdominal tergum usually without lateral pubescent patch, rarely with pubescence; abdominal tergites usually punctate, sometimes weakly, from fourth tergite; ventral spine of hypopygium short. Tarsal claws simple.

Comments.—The genus is defined mainly on the basis of wing characters as follows: R1 and Rs not quite reaching to anterior margin of wing, radial cell clearly open and wing fringe absent or very short.

Distribution and Biology.—The distribution is Palearctic: five species are known in Western Europe. From the biological point of view the genus is associated with Asteraceae; the species inducing galls in stems, achenes or involucre bracteae of species of *Centaurea* and *Serratula* (Asteraceae).

Redescription Of Some Species

Isocolus scabiosae (Giraud)

Diastrophus scabiosae Giraud 1859:368

Diastrophus areolatus Giraud 1859:369. Syn. n.

Isocolus scabiosae (Giraud): Förster 1869:334

Isocolus rogenhoferi Wachtl 1880:542. Syn. n.

Aulax scabiosae (Giraud): Mayr 1882: 10

Aylax scabiosae (Giraud): Dalla Torre and Kieffer 1910:671

Isocolus scabiosae (Giraud): Rohwer and Fagan 1917:369

Isocolus scabiosae (Giraud): Weld 1952:271

Material examined.—The type series of *D. scabiosae* Giraud, in the MNHP, comprises 63 specimens: 30♂, 33♀, mounted on micro-pins, as well as some galls on achenes of *Centaurea scabiosa*. 1♀, set next to a male, with handwritten label "3 mai" and "Museum Paris, coll. GIRAUD", is hereby designated lectotype. Paralectotypes, 18♂ and 12♀

Redescription.—FEMALE. (Figs. 71-79). Length 2.8-3.3 mm. Black; gaster red-brown to black; antenna and legs red brown; coxa, base of femora and first two segments of antenna darker. Head viewed dorsally (Fig. 71) 2.2 times broader than long; viewed frontally (Fig. 72) 1.3 times broader than high; temples only slightly expanded behind eyes; frons and vertex with sculpture coriaceous-alutaceous; POL slightly shorter than OOL, OOL about four times greatest diameter of lateral ocellus; transfacial line around 1.6 times height of eye; malar space slightly shorter than height of eye;

face laterally with radiating striae; supraclypeal area slightly raised, with some striae; antenna (Fig. 73) about 2/3 the length of the body, with 13 antennomeres, A3 slightly shorter than A4. Pronotum (Fig. 75) coriaceous, laterally pubescent; dorsally long, with distinct submedial pits; mesoscutum (Fig. 76) with coriaceous-rugulose sculpture posteriorly with some conspicuous transverse rugae; notauli complete, well impressed posteriorly; median mesoscutal impression distinct in posterior half of mesoscutum; scutellar foveae large, rounded; shining and almost smooth; separated by broad posteriorly septum; scutellum ovate, rugulose with the posterior half more or less flat and sloping backwards; mesopleuron (Fig. 77) longitudinally striated. Wings hyaline or very lightly infuscated; R1 and Rs of forewing not quite extending to wing margin and radial cell open (Fig. 79); Rs slightly curved apically; length of the radial cell about 3 times the width; areolet indistinct; fore wing without distinct hair fringe on wing margins. Third abdominal tergum (Fig. 78) basally smooth without sculpture or pubescence; posterior third of third tergite and following segments conspicuously punctate; ventral spine of hypopygium very short; tarsal claws simple. MALE. differs from female in antenna (Fig. 74) with 14 antennomeres; A3 slightly curved in the middle.

Comments.—The complete series from the Giraud Collection, sent by the MNHP, comprises 63 individuals. In contrast with the specimens predominantly black described above, other individuals of a lighter, chestnut-reddish shade and some completely reddish individuals are included in the series. The latter also exhibit other morphological differences such as a stronger mesoscutal sculpture and less impressed notauli and medial mesoscutal impression. Also included in the series are some galls consisting of transformed achenes from flower heads of *Centaurea scabiosa* L. and in compliance with the handwritten labels from Giraud: "caput centaureae scabiosae" and the date, at least part of the specimens of the series should have been obtained from these galls. Giraud originally described the species *Diastrophus scabiosae* as obtained from conspicuous galls in the stems of *Centaurea scabiosa* L. (Giraud 1859), but these galls are not included in the series. The specimens obtained from galls in achenes could belong to *Isocolus rogenhoferi* Wachtl. However, the status of the

latter has not been clear, since only differences in the coloration of the antennal flagellum together with the different position of the galls have been pointed out in the literature (Kieffer 1901, Eady and Quinlan 1963) to separate it from *I. scabiosae*. For these reasons, I consider that there is only one species with a wide morphological variability being capable of inducing galls on both stems and flower heads of species of *Centaurea*, mainly *C. scabiosa* L. It is possible that the two types of galls correspond to two different generations of the same species. In the same work, Giraud described another species, *Diastrophus areolatus*, from 2 females caught by netting near Vienna. The differences between the latter and *I. scabiosae* were stated to be reddish coloration of the antennal flagellum and presence of areolet in the fore-wings. In the examined series, I found 2 specimens which could correspond to *D. areolatus* labeled "captur 13 juill, Turksch". The presence or absence of the areola, as well the general coloration, is quite variable in the whole of the series, so I consider *D. areolatus* as conspecific with *I. scabiosae* and, therefore, I establish the corresponding new synonymy.

Isocolus serratulae Mayr comb. n.

Aulax serratulae Mayr 1882:9

Aylax serratulae (Mayr): Kieffer 1901:313

Type material.—Series composed of 31 specimens: 12♂, 19♀, most of them set on micro-pins (NHMW). 1♀, with handwritten labels "*serratulae* y det Rogenhofer" and "Luxemburg, Rogenh 1881", hereby designated lectotype. Other specimens carry handwritten labels "*Aul. serratulae* det. G. Mayr" and "*Serratula heterophylla*"; designated paralectotypes.

Redescription.—(Figs. 80-87). FEMALE. Length 2.5 mm. Black; gaster red-brown to dark-brown; antenna and legs light brown; coxa, base of femora and two first segments of antenna darker. Head viewed dorsally (Fig. 80) about 2 times broader than long; viewed frontally (Fig. 81) 1.2 times broader than high; temples not expanded behind the eyes; frons and vertex with sculpture minutely coriaceous-reticulate; POL:OOL as 11:9; OOL about three times the greatest diameter of lateral ocellus; transfacial line around 1.5 times the height of eye; malar space around 0.6 times the height of eye; face laterally with radiating striae; supraclypeal

area slightly raised, without striae; antenna (Fig. 82) with 13 antennomeres, A3 clearly shorter than A4. Pronotum (Fig. 83) reticulate-coriaceous, laterally pubescent; dorsally long, with distinct submedial pits; mesoscutum (Fig. 84) with reticulate-coriaceous sculpture; notauli complete, well impressed posteriorly; median mesoscutal impression distinct in posterior 1/5 of mesoscutum; scutellar foveae large, subtriangle-shaped; not smooth; separated by a posteriorly broader septum; scutellum reticulate-coriaceous, with longitudinal furrow variably impressed; mesopleuron (Fig. 85) longitudinally striated. Wings hyaline, slightly longer than the body; R1 and Rs of forewing not quite reaching to wing margin and radial cell open (Fig. 86); length of the radial cell about 2.6 times the width; areolet indistinct; fore wing without distinct hair fringe on wing margins. Third abdominal tergum (Fig. 85) basally with a lateral pubescent patch; posterior third of third tergite and following segments conspicuously punctate; ventral spine of hypopygium very short; tarsal claws simple. MALE. Differs from female in antenna with 14 antennomeres (Fig. 87), A3 not modified only slightly curved.

Comments.—This species was described by Mayr from material collected by Rogenhofer on *Serratula heterophylla* auct non (L.) Desf. The gall is probably produced on this plant, but it has not been described. Since the description, the species has been recorded once from Ukraine, including galls Zerova et al. (1988), so it is only known from Austria and that country. The features of this species fit well in the genus *Isocolus*, except for the third abdominal tergum with basal pubescent patch, so I transfer it to this genus.

Isocolus lichtensteini (Mayr) comb. n.

Aulax lichtensteini Mayr 1882:7

Aylax lichtensteini (Mayr): Kieffer 1901:297

Isocolus tavaresi Nieves-Aldrey 1984:243. Syn. n.

Type material.—Type series composed of 2♀; 1♀, mounted on micro-pin, with handwritten labels "*Aulax lichtensteini*, det. G. Mayr" and "*Centaur. gall lich*" designated lectotype. Paralectotype, one female with label "*Centaur. salmant. gall Lich*".

Comments.—This species was described from material collected in Montpellier (France), producing galls in the stems of *Centaurea salmantica* L.

(=*Microlonchus salmanticus*) (Mayr, 1882). *Isocolus tavaresi* Nieves-Aldrey, described from material reared from galls on *Centaurea aspera* L. in Spain (Nieves-Aldrey, 1984), later also found on *Centaurea melitensis* L., (Nieves-Aldrey, unpublished), is conspecific with the two type specimens studied and, therefore, I establish the corresponding synonymy.

The type specimens differ from individuals collected in Spain (Nieves-Aldrey 1984) only in their lighter chestnut-reddish coloration, also extended for antenna and legs, including the coxae. Therefore, the types exhibit only a slight colour contrast between the two first antennal segments and the flagellum, and the longitudinal furrow of scutellum is more pronounced compared to the Spanish specimens collected.

LIPOSTHENES Förster

Liposthenus (!) Förster 1869:332.

Liposthenes Förster 1869:336. Type species: *Aulax glechomae* Hartig. Monotypic and orig. desig. (examined). The types of *Aulax glechomae* Hartig, in the ZSM, consist of 4 ♀, mounted on pins. One of them carry label of lectotype ♀ designated by Weld in 1931 (Weld 1952).

Diagnosis.—Head, viewed dorsally, slightly less than two times broader than long; in frontal view slightly broader than high; transfacial line 1.5 times height of eye; malar space shorter than height of eye; frons and vertex finely reticulate; radiating striae incomplete, weakly impressed; antenna of female with 13 segments, A3 slightly longer than A4; male antenna 14-segmented. Pronotum dorsally long, laterally strongly pubescent and with some longitudinal striae or rugae; submedial pits conspicuous, associated with a distinct pronotal plate; mesoscutum regularly coriaceous and shining; notauli well impressed and complete; median mesoscutal impression very short; scutellar foveae deep, rounded, smooth and shining; mesopleuron finely and clearly striated longitudinally. Wings hyaline; radial cell of forewing open on front margin; length of radial cell slightly less than three times width. Third abdominal tergum with conspicuous lateral pubescent patch; following segments not punctate. Tarsal claws simple.

Comments.—The genus is morphologically similar to *Isocolus* Förster, but can be separated by the pronotum being strongly pubescent laterally;

presence of wing fringe on distal margin; third antennal segment being longer than fourth; third abdominal tergum having a lateral pubescent patch and in general sculpture and biology.

Distribution and Biology.—The genus comprises a single known species from Western Europe which causes the formation of galls in the runners, stems and leaves of *Nepeta* (= *Glechoma*) *hederacea* L. (Lamiaceae).

NEAYLAX gen. n.

Type species: *Aylax salvuae* (Giraud 1859):369. By present designation. (examined)

Derivation: from Neos and Aylax (new Aylax)

Description.—Head, viewed dorsally, two times broader than long; temples not expanded behind the eyes; radiating striae on face well impressed laterally; supraclypeal area raised, without striae; frons and vertex with coriaceous or alutaceous sculpture; antenna 12-13-segmented in females; 14-15-segmented in males; A3 as long as A4 or shorter than A4. Pronotum dorsally long; submedial pits clearly visible, not broadly separated; mesoscutum coriaceous or alutaceous, sometimes punctate; notauli complete or faint anteriorly; scutellar foveae large, rounded; mesopleuron longitudinally striated. Wings hyaline; radial cell of forewing open on front margin but R₁ reaching margin; distal wing margins with hair fringe moderately long. Third abdominal tergum basally smooth or with a lateral pubescent patch; following segments finely punctate but punctures not conspicuous; ventral spine of hypopygium short. Legs with tarsal claws simple.

Comments.—*Neaylax* is erected to comprise some species formerly included in *Aylax* Htg, but which do not fit well in that genus. The new proposed genus is closely related to *Isocolus* Förster, from which it differs as follows: radial cell of forewing not completely open along the margin and at the base; first abscissa of radius reaching the wing margin and presence of hair fringe on the distal margin of the wing (absent in *Isocolus*). Biologically *Neaylax* differs from *Isocolus* in its association with Lamiaceae rather than with Asteraceae. The dorsally long pronotum, the rounded scutellar foveae, and the association with Lamiaceae and not with Papaveraceae separate it from *Aylax* Htg.

Distribution and Biology.— The genus comprises two species distributed in centre and south of Europe which produce galls on species of *Salvia* (Lamiaceae) and a third species, only recorded from the Iberian Peninsula whose host plant and gall are unknown.

REVISED SPECIES

***Neaylax salviae* (Giraud), comb. n.**

Aulax salviae Giraud 1859:369

Isocolus salviae (Giraud): Nieves-Aldrey 1988:224. Syn. n.

Type material.—The type series of *A. salviae*, in the NHMW, sent to me by M. Fischer, consists of 12 specimens. 1♂, mounted on a rectangular card with labels: red "Type" and white handwritten "*Aulax salviae* Giraud", is designated lectotype. 1♂, 1♀, mounted on micro-pin, with labels "Collect. Mayr" and "*Aulax salviae* Gir, det. G. Mayr" clearly do not belong to the type series, although they are conspecific with *A. salviae* Giraud. In the same series 1♂, 2♀, collected by Mayr, determined as *Aulax salviae* Giraud, are cynipids but do not correspond to that species. Finally 2 specimens, identified as *A. salviae* by Fahringer, belong to the family Eucoilidae.

Redescription.—MALE. (Figs. 96-103). Length 1.8 mm. Red-brown; antenna red-brown; legs with coxae red-brown, tibiae and tarsi paler. Head viewed dorsally (Fig. 96) about 2 times broader than long; temples not expanded behind the eyes; frons and vertex with sculpture coriaceous-alutaceous; POL as long as OOL; OOL about 4 times the greatest diameter of lateral ocellus; face laterally with radiating striae; supraclypeal area almost raised, without striae; antenna (Fig. 98) with 14 antennomeres, A3 clearly shorter than A4. Pronotum (Fig. 100) coriaceous; dorsally long, with distinct submedial pits; mesoscutum (Fig. 101) finely alutaceous and with some obsolete punctures medially; notauli relatively expanded posteriorly, complete but slightly faint anteriorly; median mesoscutal impression indistinct in posterior 1/4 of mesoscutum; scutellar foveae large, rounded, smooth and shining, separated by a narrow septum; scutellum weakly rugulose, with a weak longitudinal furrow; mesopleuron (Fig. 102) longitudinally striated. Wings hyaline; radial cell of forewing (Fig. 103) open on front margin but

R₁ reaching margin; length of radial cell about three times the width; hair fringe on distal margin of wing long. FEMALE. differs from male as follows: antenna with 13 antennomeres (Fig. 98); third abdominal tergum without lateral pubescent patch; following segments with fine and inconspicuous punctures; ventral spine of hypopygium short.

Distribution and Biology.— The species was described from specimens collected in Dalmatia, reared from galls in the fruits of *Salvia officinalis* L. Species of apparently Eastern Mediterranean distribution.

SPECIES TRANSFERRED TO
NEAYLAX GEN. N.***Neaylax verbenacus* (Nieves-Aldrey), comb. n.**

Isocolus verbenacus Nieves-Aldrey 1988:221. Syn. n.

This species is closely related to *N. salviae* (Giraud). It was described within *Isocolus* from Spain. Its galls are produced in fruits of *Salvia verbenaca* L.

***Neaylax versicolor* (Nieves-Aldrey), comb. n.**

Aylax versicolor Nieves-Aldrey 1985:122. Syn. n.

This species was described under *Aylax* (Nieves-Aldrey 1985). It is known only from Spain. Gall unknown.

PANTELIELLA Kieffer

Pantelia Kieffer 1901:248 (non Bolivar 1887, Orthopt.)

Panteliella Kieffer 1901:324. Type species: *Aulax fedtschenkoi* (Rubsamen 1896). Monobasic

Endocaulonia Ionescu and Roman 1960:222. Type species: *Endocaulonia bicolor* Ionescu and Roman 1960. By original designation.

Weld (1952), stated that the types, consisting of slide-mounts of two adults in balsam, were in the Berlin Museum. Later on, Quinlan (1968) stated that the type material consisted of two specimens deposited in the Vienna Museum but Dr. Fischer informed me that the only material of *A. fedtschenkoi* housed in that museum consisted in galls. I have had the chance to examine one of the preparations of the Berlin Museum, consisting of a head in bad condition, with one of the two antennae being

complete, a leg and the gaster. The preparation has a red type label and is printed "*Aulax fedtschenkoi*; Bijuk Onlar, juni 1893; Blattgallen on *Phlomis tuberosa*". The type species was redescribed by Weld (1930) and by Quinlan (1968).

Endocaulonia was described by Ionescu and Roman in 1960 based on *E. bicolor*, a species discovered by these authors in Rumania producing galls in the stems of *Phlomis tuberosa* L. Although I have not been able to examine the types, it seems clear from the detailed description that this genus is very similar to *Panteliella* Kieffer only differing slightly in the relative lengths of pedicel and third antennal segment. The descriptions of the two genera, except for the mentioned feature, are fully coincident, as is the gall and the host plant, which makes me consider that *Endocaulonia* Ionescu and Roman is synonymous with *Panteliella* Kieffer. The type species of *Endocaulonia* appears to be synonymous with *Panteliella fedtschenkoi*, although in this case I do not venture to formally establish the synonymy without a previous examination of the type.

I present the following diagnosis of the genus based on Quinlan's redescription (1968).

Diagnosis.—Female antenna 14-segmented; male 15-segmented; A3 and A4 of same length in the two sexes. Mesoscutum reticulate; notauli and median mesoscutal impression very faintly indicated; scutellar foveae distinct separated by a broad and striate septum; mesopleuron longitudinally striated. Radial cell of forewing open on the margin; wing fringe on distal margin distinct. Third abdominal tergum without lateral pubescent patch; following tergites weakly punctate on lateral margins. Tarsal claws simple.

The genus is close to *Neaylax* Nieves-Aldrey and to *Rhodus* Quinlan. It can be separated from the former by the obsolete notauli, scutellar foveae broadly separated and female antenna 14-segmented. From *Rhodus* it is distinguished by the distinct fringe on distal margin of forewing, the obsolete notauli and A3 not being shorter than A4.

Distribution and Biology.—Only one known species: *Panteliella fedtschenkoi* (Rübsaamen, 1896) distributed in central and eastern Europe and eastern Mediterranean. It produces galls in the leaves and stems of *Phlomis tuberosa* L. (Lamiaceae). *Panteliella bicolor* (Ionescu and Roman) is possibly a second species of the genus, only known from Rumania.

PHANACIS Förster

Phanacis Förster 1860:145. Type species: *Phanacis centaureae* Förster 1860. Monobasic.

Gillettea Ashmead, 1897:69. Type species: *Gillettea taraxaci* Ashmead 1897. Original designation.

Weld (1952) pointed out that Förster's types in the Berlin Museum were destroyed by dermestids but he could observe good specimens of *P. centaurea* in Vienna. However, I have abundant Iberian material of the type species at my disposal from which I have produced the diagnosis of the genus.

Gillettea Ashmead was synonymized with *Phanacis* Förster by Eady and Quinlan (1963). I have examined the type species of *Gillettea* and I confirm the synonymy.

Diagnosis.—Head, viewed dorsally two times broader than long; viewed frontally slightly broader than high; frons and vertex reticulate-coriaceous; radiating striae of face weakly impressed, incomplete; female antenna 13-segmented; male antenna with 14 antennomeres; A3 clearly longer than A4. Pronotum dorsally moderately long, without distinct submedial pits; mesoscutum reticulate-coriaceous; notauli usually faint anteriorly; scutellar foveae transverse, confluent, not well defined or indistinctly closed posteriorly; mesopleuron reticulate. Wings fully developed in females, sometimes reduced in males; radial cell of forewing usually closed, sometimes incompletely on the margin; hair fringe on distal wing margins moderately long. Third abdominal tergum without lateral pubescent patch. Tarsal claws simple.

Comments.—*Phanacis* is easily distinguished from other genera of Aylacini excepting *Timaspis* by the absence of pronotal submedian pits on the pronotum and the reticulate sculpture of the mesopleuron. The genus was considered by Eady and Quinlan (1963) to comprise also the species included in *Timaspis* Mayr. However, when some species of the latter genus not examined by Eady and Quinlan, are included in *Phanacis*, the heterogeneity of the grouping becomes evident. This is the case with, e.g., *Timaspis cichorii* Kieffer and *T. phoenixopodos* Mayr. The boundary between the two genera does not, however, seem clearly defined and some species, particularly *P. caulicola* (Hedicke), *P. hypochoeridis* (Kieffer) and *Timaspis lampsanæ* Perris, are not easily assigned to one or

the other genus. All the known species of *Phanacis* (*s. str.*) produce galls on plants of the family Asteraceae.

Distribution and Biology.—The genus has a palaeartic distribution with two species introduced in North America. All the known species are associated with Asteraceae. Galls are produced mostly on stems.

Phanacis taraxaci (Ashmead)

Gillettea taraxaci Ashmead 1897:69.

Phanacis taraxaci (Ashmead): Eady and Quinlan, 1963:18.

Examined material.—The type material consists of two female specimens; one in the USNM and the other in the NHMW (both examined); the specimen from Wien, in better condition, is designated lectotype.

The species is being studied in detail by Shorthouse (personal communication). Apparently the species has been introduced in North America, together with the host plant *Taraxacum*, from Europe. But the existence of the species in Europe is documented only by a few gall records, so the European origin of this species does not seem clear. The species is widely distributed and relatively abundant in North America (Shorthouse, pers. comm.).

RHODUS Quinlan

Rhodus Quinlan 1968:282. Type species: *Rhodus oriundus* Quinlan 1968. Monotypic and original designation (examined)

Diagnosis.—Figs. 104-110. Head viewed dorsally (Fig. 104) two times broader than long; viewed frontally (Fig. 105) clearly broader than high; frons and vertex with reticulate sculpture; radiating striae of face present laterally; supraclypeal area raised; female antenna (Fig. 106) 13-segmented; male with 14 antennomeres; A3 clearly shorter than A4. Pronotum (Fig. 107) dorsally long, with distinct submedial pits; mesoscutum (Fig. 108) with dull reticulate sculpture and some scattered piliferous punctures; notauli distinct in posterior 3/4 of mesoscutum; faint or obsolete anteriorly; scutellar foveae large, rounded, sculptured; septum relatively broad; mesopleuron (Fig. 109) longitudinally striated. R1 and Rs not quite reaching anterior margin of wing; radial cell of forewing

(Fig. 110) open; hair fringe on distal wing margins absent. Third abdominal tergum without lateral pubescent patch. Tarsal claws simple.

Comments.—The genus was based on one species, *Rhodus oriundus* Quinlan, found in Rhodes Island, galling apical buds of *Phlomis cretica* Presl (Quinlan 1968). Its morphological features relate it to the genera *Isocolus* Förster and *Neaylax* Nieves-Aldrey; it differs from the former in the conformation of the notauli, the sculpture of the mesoscutum and the distal margin of the wing completely lacking hairs. The wing venation with R1 and Rs not quite reaching the anterior margin of wing and the absent hair fringe on distal wing margin separate it from *Neaylax*.

Distribution and Biology.—The genus comprises one described species, only recorded from Rhodes (Greece) associated with *Phlomis* (Lamiaceae).

TIMASPIS Mayr

Timaspis Mayr 1881:18. Type species: *Diastrophus lampsanae* Karsh. Monotypic. (Type.—*Timaspis phoenixopodos* Mayr 1882. Designated by Ashmead 1903 p.214).

Phanacis Förster (part): Eady and Quinlan 1963:18.

Aylacopsis Hedicke 1923:81. Syn. n. Type species: *Aylacopsis heraclei* Hedicke 1923. Monotypic and original designation.

The type material of *Timaspis lampsanae*, in the Museum of Vienna, consists of a ♀ mounted on micro-pin on polyporous strip labeled "*Tim. lampsanae* det Karsch Type"; "*lampsanae* Karsch Type"; "collect G. Mayr" and red label "Holo-type".

Diagnosis.—Radiating striae present laterally on the face; incomplete. Female antenna of 13-14 segments; 14-15 in males; A3 relatively long; at least 1.5 times longer than A4. Pronotum dorsally moderately long, without distinct submedial pits; notauli usually complete but often not well impressed anteriorly; median mesoscutal impression usually present; scutellar foveae small, confluent, usually indistinctly closed posteriorly; mesopleuron reticulate-rugulose, rugulose-alutaceous or striate-alutaceous. Radial cell of forewing closed on the margin, sometimes incompletely so anteriorly; hair fringe on distal margins of wing long. Third abdominal tergum without lateral pubescent patch. Tarsal claws simple.

Comments.—*Timaspis* can be distinguished from *Phanacis* on the basis of its rugulose-reticu-

late sculpture of the mesopleuron and complete notauli. *Timaspis* was synonymized with *Phanacis* Förster by Eady and Quinlan (1963) but these authors' concept of *Timaspis* was incomplete because it was limited to the type species of the genus, *T. lampsanae*. But if other species described within *Timaspis* are considered, especially *T. phoenixopodos* Mayr, I consider it advisable to keep the genera separate. It must be emphasized, however, that the boundary between the two genera is not clearly defined and some species are difficult to assign to one genus or the other.

Aylacopsis Hedicke, was described from a species that produces galls in the stems of *Heracleum sphondylium* L. (Apiaceae) (Hedicke 1923). After having examined the type species, I consider that it fits well within *Timaspis* Mayr. Consequently, I synonymize *Aylacopsis* with *Timaspis* Mayr.

Distribution and Biology.—As understood herein, the genus comprises 9 species in West-Europe. All the species, excepting one, are associated with Asteraceae

Timaspis heraclei (Hedicke), comb. n.

Aylacopsis heraclei Hedicke 1923:81. Syn. n.

The type of *Aylacopsis heraclei* Hedicke in the Berlin Museum consists of a ♀ specimen glued on a card triangle. The specimen carries the following labels: white handwritten "Doicul, Leipzig 26-2-15"; "Aylacopsis heraclei ♀ Hedicke" and red printed "Type".

We can contribute the following complementary data to the original description: Figs. 111-118. Head, viewed dorsally (Fig. 111), about two times broader than long; viewed frontally (Fig. 112) slightly broader than high; frons and vertex finely coriaceous; POL slightly less than two times OOL; transfacial line about 1.6 times height of eye; face laterally with radiating striae; supraclypeal area without striae; with weak median protuberance; malar space about 0.7 times height of eye; antenna (Fig. 113) slender, filiform, with 14 antennomeres; A3 slightly curved in the middle, about 1.7 times longer than A2; 1.3 times longer than A4. Pronotum (Fig. 114) dorsally only moderately long; scarcely pubescent, without submedial pits; mesoscutum (Fig. 115) finely reticulate-coriaceous; notauli complete; median mesoscutal impression impressed in posterior 1/3 of mesoscutum; scutellar foveae confluent, indistinctly closed posteri-

orly; scutellum ovate, weakly rugulose; mesopleuron (Fig. 116) reticulate-rugulose. Forewing with radial cell (Fig. 117) open anteriorly on margin but R₁ clearly reaching wing margin; length of radial cell 2.6 times width; hair fringe on wing margins long. Third abdominal tergum (Fig. 118) without lateral pubescent patch; following segments not punctate; ventral spine of hypopygium quite short, slightly visible. Tarsal claws simple.

Comments.—Within *Timaspis* Mayr this species is morphologically close to *Timaspis cichorii* from which it is differentiated by the coloration, sculpture of the mesoscutum and conformation of the scutellar foveae. According to the original description, this species produces galls in the stems of *Heracleum sphondylium* (Apiaceae) at that time being the first cynipid species demonstrated to be associated with this family of plants. Afterwards this species has not been recorded again and, consequently, the host has not been confirmed. It may, however, be pointed out that *Phanacis eryngii* Diakonchuk, another Aylacini species, was recently found in Eastern Europe associated with Apiaceae (*Eryngium*) (Diakonchuk 1984).

Timaspis lusitanica Tavares

Timaspis lusitanicus Tavares 1904:301

Timaspis lusitanica Tavares 1904: D T. and Kieffer 1910. Emend. *Phanacis crepidos* Weidner 1965:1. Syn. n.

Timaspis lusitanica Tavares was described from Portugal (Tavares 1904) reared from galls on *Barkausia taraxacifolia* DC. (Asteraceae). More recently, it has been recorded from Spain, on the same host plant (Nieves-Aldrey 1992). *Phanacis crepidos* was described from Germany (Weidner 1965) from material reared from galls on *Crepis biennis* L. (Asteraceae). Having examined the type material from the Museum of Hamburg, I have concluded that it is the same species described by Tavares, so I establish the corresponding new synonymy.

XESTOPHANES Förster

LITERATURE CITED

Xestophanes Förster 1869:332, 337. Type species: *Cynips potentillae* De Villers. Monotypic and original designation.

Diagnosis.—Face laterally with radiating striae; supraclypeal area without striae; with weak median protuberance; frons and vertex almost smooth and shining; antenna of female 13-segmented, A3 as long as or slightly longer than A4; antenna of male 14 segmented. Pronotum dorsally long, laterally pubescent; submedial pits conspicuous; mesoscutum smooth and shining; notauli complete or faint anteriorly; median mesoscutal impression slightly indicated; scutellar foveae smooth; mesopleuron smooth and shining. Forewing with radial cell open on the margin but R₁ reaching to wing margin; hair fringe moderately long. Third abdominal tergum laterally smooth and glabrous. Tarsal claws with weakly developed basal lobe or tooth.

Comments.—The genus, together with the allied genus *Diastrophus*, form a distinct unit within the Aylacini: morphologically, by the tarsal claws having an acute basal lobe or tooth and frons, vertex and mesopleuron without sculpture; biologically, by their association exclusively with Rosaceae (the genera *Potentilla* and *Rubus*). The genus is very likely monophyletic, based on the fusion of third and fourth abdominal terga in the females

Distribution and Biology.— Two species of *Xestophanes* are known in Western Europe, both gall makers on stems and runners of species of *Potentilla*.

ACKNOWLEDGMENTS

I am very grateful to the curators of the collections listed under materials for the loan of type material and other specimens. Special thanks to A. Menke (USNM) and R. Danielsson (MZLU) also for sending some interesting bibliography. I am also most indebted to one anonymous reviewer and specially to F. Ronquist for a critical revision of the manuscript including linguistic suggestions. M. A. Alonso-Zarazaga helped with nomenclatorial questions. I would like to thank Iñiqui Diez for the rotulation of the drawings made by myself. Financial support was provided by the Research project "Fauna Ibérica II", DGICY PB89 0081.

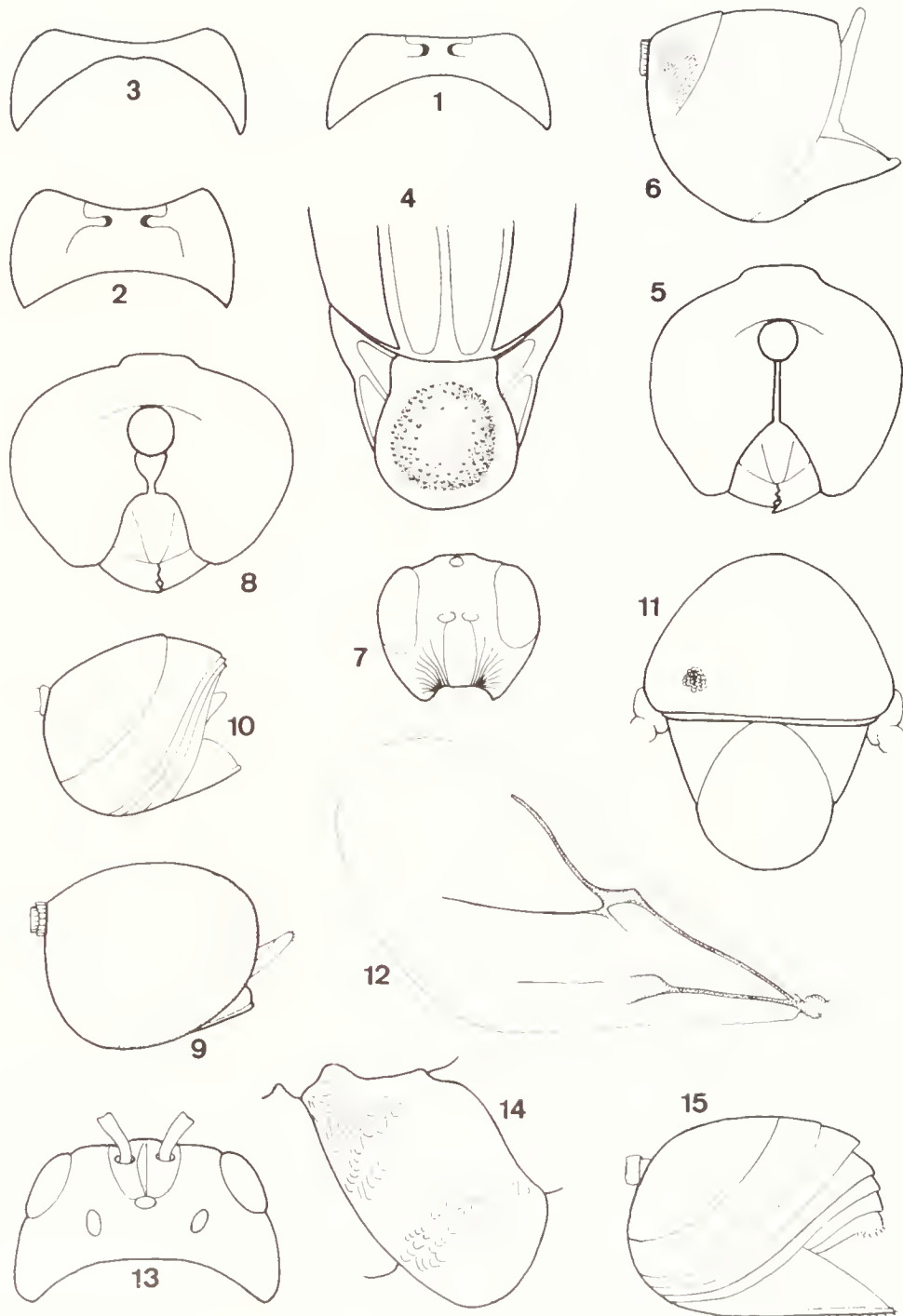
- Ashmead, W. H. 1885. A Bibliographical and Synonymical Catalogue of the North American Cynipidae, with description of new species. *Transactions of the American Entomological Society* 12: 291-304.
- Ashmead, W. H. 1887. On the Cynipidous galls of Florida, with descriptions of new species and synopses of the described species of North America. *Transactions of the American Entomological Society* 14: 125-158.
- Ashmead, W. H. 1896. Description of new cynipidous galls and gall wasps in the United States National Museum. *Proceedings of the United States National Museum* 19: 113-136.
- Ashmead, W. H. 1897a. Description of some new genera in the family Cynipidae. *Psyche* 8: 67-69.
- Ashmead, W. H. 1897b. Description of five new genera in the family Cynipidae. *Canadian Entomologist* 29: 260-263.
- Ashmead, W. H. 1903. Classification of the gall-wasps and the parasitic cynipoids, or the super-family Cynipoidea. 1-IV. *Psyche* 10: 140-155
- Askew, R. R. 1984. *The biology of gall wasps*, pp. 223-271. In T. N. Ananthakrishnan (ed.), *Biology of Gall Insects*. Edward Arnold, London.
- Barbotin, F. 1964. Sur une nouvelle galle et deux cynipides en provenance d'Algerie. *Marcellia* 31: 151-157.
- Belizin, V. I. 1959. Gall wasps of the tribe Aylaxini (Hymenoptera, Cynipoidea) new for the fauna of the USSR. *Entomologicheskoe Obozrenie* 38: 662-674.
- Burks, B. D. 1979. Cynipoidea, pp. 1045-1107. In K. V. Krombein, P. D. Hurd Jr., D. R. Smith, and B. D. Burks (eds), *Catalog of Hymenoptera in North America North of Mexico*. Volume 1, Smithsonian Institution Press, Washington, DC.
- Dalla Torre, C. W. and J. Kieffer. 1910. *Cynipidae*. *Das Tierreich* 24: 1-891.
- Diakonchuk, L. A. 1984. New species of Cynipidae (Hymenoptera) from Georgian SSR. *Vestnik Zoology* 3: 74-77 (In Russian).
- Eady, R. D. and J. Quinlan. 1963. Hymenoptera: Cynipoidea. Key to families and subfamilies and Cynipinae (including galls). *Handbooks for the Identification of British Insects* 8(1a): 1-81.
- Folliot, R. 1964. Contribution a l'étude de la biologie des cynipides gallicoles (Hymenopteres, Cynipoidea). *Annales des Sciences Naturelles, Zoologie, Paris*. 12 ser. 6: 407-564.
- Förster, A. 1860. Die zweite Centurie neuer Hymenoptera (*Eucoela* et *Phanacis*). *Verhandlungen der Naturhistorischen Vereins der Preussischen Rheinlande und Westphalens* 17: 143-146.
- Förster, A. 1869. Ueber die Gallwespen. *Verhandlungen der kaiserlich-koeniglichen zoologisch-botanischen Gesellschaft in Wien* 19: 327-370.
- Giraud, J. 1859. Signalements de quelques especes nouvelles de cynipides et de leurs galles. *Verhandlungen der kaiserlich-koeniglichen zoologisch-botanischen Gesellschaft in Wien* 9: 337-374.
- Hartig, T. 1840. Über die familie der Gallwespen. *German Entomologische Zeitung* 3: 322-358.
- Hartig, T. 1843. Zweiter nachtrag zur naturgeschichte der

- Gallwespen. *Zeitschrift für Entomologie* 4: 395-422.
- Hedicke, H. 1923. Beiträge zur Kenntnis der cynipiden (Hym.) XII. Ein neues Cecidozoon an *Heracleum spondylium* *Zeitschrift für Pflanzenkrankheiten* 33(1-2): 81-83.
- Hedicke, H. 1928. Beiträge zur Kenntnis der cynipiden (Hym.) XIV. Der Erzeuger der levantinischen salviagalge. *Deutsche Entomologische Zeitschrift* 14: 81-85.
- Ionescu, M. A. and N. Roman. 1960. Un genre nouveau de Cynipides gallicoles *Endocaulonia bicolor* n. g., n. sp. (Hymenoptera, Cynipoidea). *Revue de Biologie Academici Republicii Populare Romine Bucuresti* 5(3): 221-225.
- Ionescu, M. A. and N. Roman. 1962. New genera of gall maker Cynipidae in the fauna of the rumanian people's republic: *Weldiella aequalis* n. gen. and *Cecconia valerianellae* Thomson. *Revue de Biologie Academici Republicii Populare Romine Bucuresti* 7: 551-559.
- Kieffer, J. J. 1901. *Monographie des Cynipides d'Europe et d'Algerie*. Hermann edit. Paris, t.1, 687 pp.
- Kieffer, J. J. 1902. Revision du genre *Aulax* et des genres limitrophes d'*Aulax*, avec quelques notes sur divers autres Cynipides. *Bulletin de la Societe d'Histoire Naturelle de Metz*. 10: 91-97.
- Kinsey, A. C. 1920. Phylogeny of cynipid genera and biological characteristics. *Bulletin of the American Museum of Natural History* 62: 357-402.
- Kovalev, O. B. 1982. Cynipid gall-makers of the subfamily Aylacinae (stat. n.) (Hym., Cynipidae) and their species described within the family Figitidae. *Trudy Zoologicheskogo Instituta Akademiyi Nauk SSR* 110: 85-93. (in russian)
- Mayr, G. 1881. Die Genera der gallenbewohnenden Cynipiden. 20. *Jahresberichte der Communal-Oberrealschule im I. Bezirke* pp. 1-38.
- Mayr, G. 1882. Die europaischen arten der gallenbewohnenden cynipiden. 21. *Jahresberichte der Communal-Oberrealschule im I. Bezirke* pp. 1-44
- Nieves-Aldrey, J. L. 1984. Notas sobre los Aylaxini (Hym., Cynipidae, Cynipinae) de la Peninsula Iberica con descripción de una nueva especie de *Isocolus*. *Eos* 60: 235-250.
- Nieves-Aldrey, J. L. 1985. Nuevos Aylaxini (Hym., Cynipidae) para la Peninsula Iberica con descripción de una nueva especie de *Aylax* Htg. *Boletim da Sociedade Portuguesa de entomologia, suppl. 1, Actas do II Congresso Iberico de Entomologia* 117-128.
- Nieves-Aldrey, J. L. 1987. Estado actual de conocimiento de la subfamilia Cynipinae (Hym., Parasitica, Cynipidae) en la Peninsula Iberica. *Eos* 63: 179-195.
- Nieves-Aldrey, J. L. 1988. Descripción de una nueva especie de *Isocolus* Förster con notas de otras especies de Aylaxini nuevas para la Peninsula Iberica (Hym., Cynipidae). *Eos* 64: 221-227.
- Nieves-Aldrey, J. L. 1992. Adiciones a la lista de cinipidos ibéricos, especialmente Aylaxini, incluyendo la descripción de una nueva especie de *Aulacidea* Ashmead (Hymenoptera, Cynipidae). *Boletim da Sociedade portuguesa de entomologia, suppl n°3, Actas do II Congresso Iberico de Entomologia v. 1*: 493-500.
- Nieves-Aldrey, J. L. "In press". The types of *Aylax* Hartig described by C. G. Thomson (Hymenoptera, Cynipidae). *Entomologica Scandinavica*.
- Nordlander, G. 1984. Vad vet vi om parasitiska Cynipoidea?. *Entomologisk Tidskrift* 105: 36-40
- Quinlan, J. 1968. Cynipinae (Hymenoptera) occurring on *Phlomis* L. *Transactions of the Royal Entomological Society of London* 120: 275-286.
- Ritchie, A. J. 1984. *A revision of the higher classification of the inquiline gall-wasps (Hymenoptera: Cynipidae) and a revision of the Nearctic species of Periclistus Förster*. Ph. D. Thesis, Carleton University, Ottawa, ON. 368 pp.
- Rohwer, S. A. and M. M. Fagan. 1917. The type-species of the genera of the Cynipoidea, or the gall wasps and parasitic cynipoids. *Proceedings of the United States National Museum*, 53: 357-378.
- Ronquist, F. In press. Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquiline in gall wasps (Hymenoptera, Cynipidae). *Evolution*.
- Ronquist, F. and G. Nordlander 1989. Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibalidae). *Entomological scandinavica Suppl.* 33: 1-60.
- Tavares, J. da S. 1904. Descripcão de un Cynipide novo. *Broteria* 3: 301-302.
- Thomson, C. G. 1877. Oefversigt af sveriges Cynyps Arter. *Opuscula Entomologica* 8: 732-841.
- Wachtl, F. 1880. Beiträge zur Kenntnis der gallenerz. *Insecten Europas. Verhandlungen der kaiserlich-koeniglichen zoologisch-botanischen Gesellschaft in Wien* 30: 531-545.
- Wachtl, F. 1891. Eine neue Gallwespe. *Wiener Entomologische Zeitung* pp. 277-280.
- Walsh, B. D. 1869. Galls and their architects. *The American Entomologist* 2: 70-74
- Weidner, H. 1965. *Phanacis crepidos* sp. nov., eine neue gallwespe an *Crepis biennis* L. *Entomologische Mitteilungen* 52: 1-7.
- Weidner, H. 1968. Zur Kenntnis der Gallwespentribus Aulacini (Hymenoptera, Cynipidae). *Entomologische Zeitschrift* 10: 105-120.
- Weld, L. H. 1930. Notes on Types (Hymenoptera: Cynipidae). *Proceedings of the Entomological Society of Washington* 32: 8.
- Weld, L. H. 1952. *Cynipoidea (Hym.) 1905-50*. Privately printed, Ann Arbor, MI, 351 pp.
- Wiebes-Rijks, A. A. 1979. A character analysis of the species of *Synergus* Hartig, Section II (Mayr, 1872) (Hymenoptera, Cynipidae). *Zoologische mededelingen* 53(28): 297-321.
- Zerova, M. D., Diakonchuck, L. A. and V. M. Ermolenko. 1988. *Gall-formers of the european part of the USSR. Part 1 Hymenoptera*. Naukova Dumka, Kiev. 180 pp.

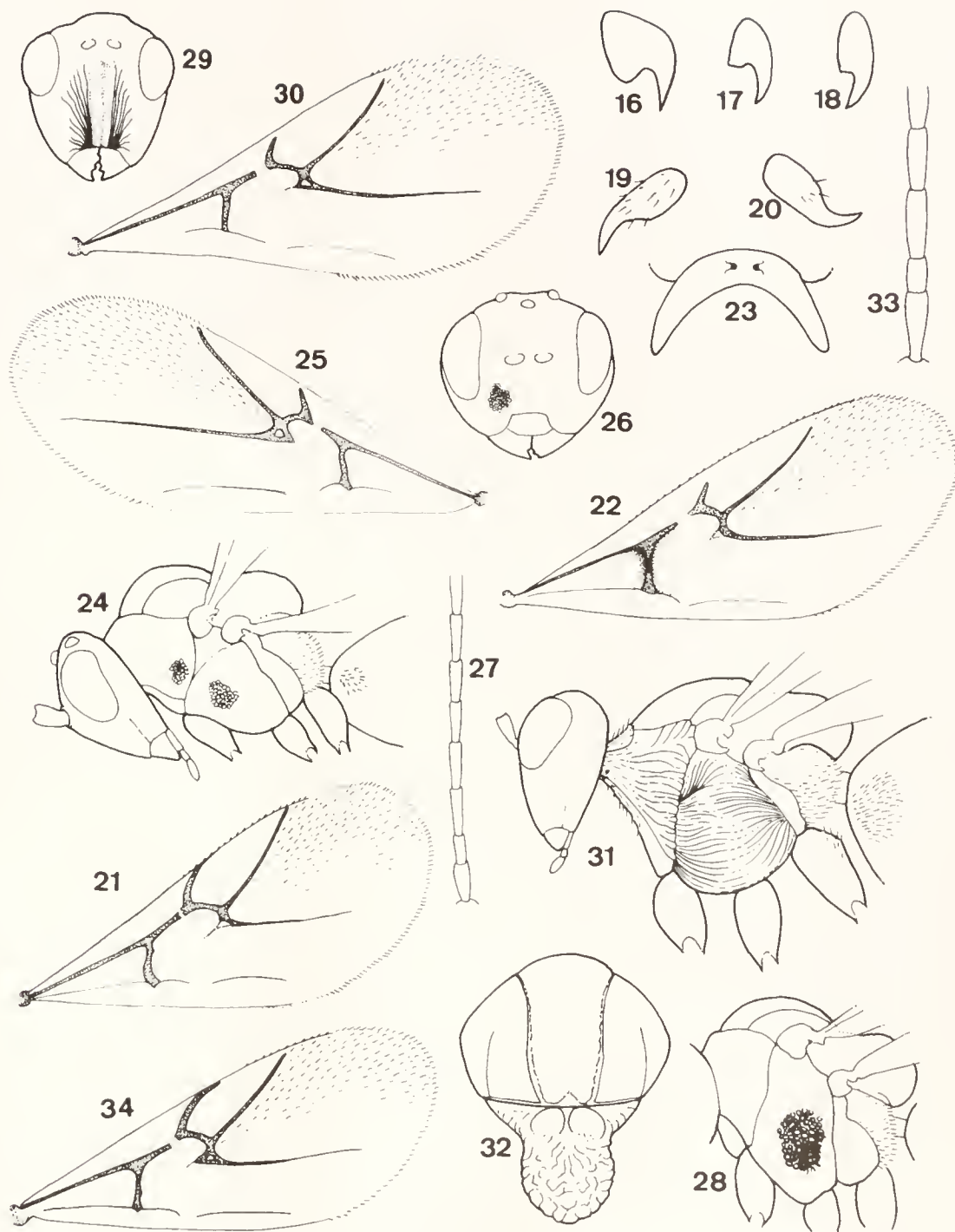
APPENDIX

Check list of the west-European genera and species of Aylacini including their host plant genera.

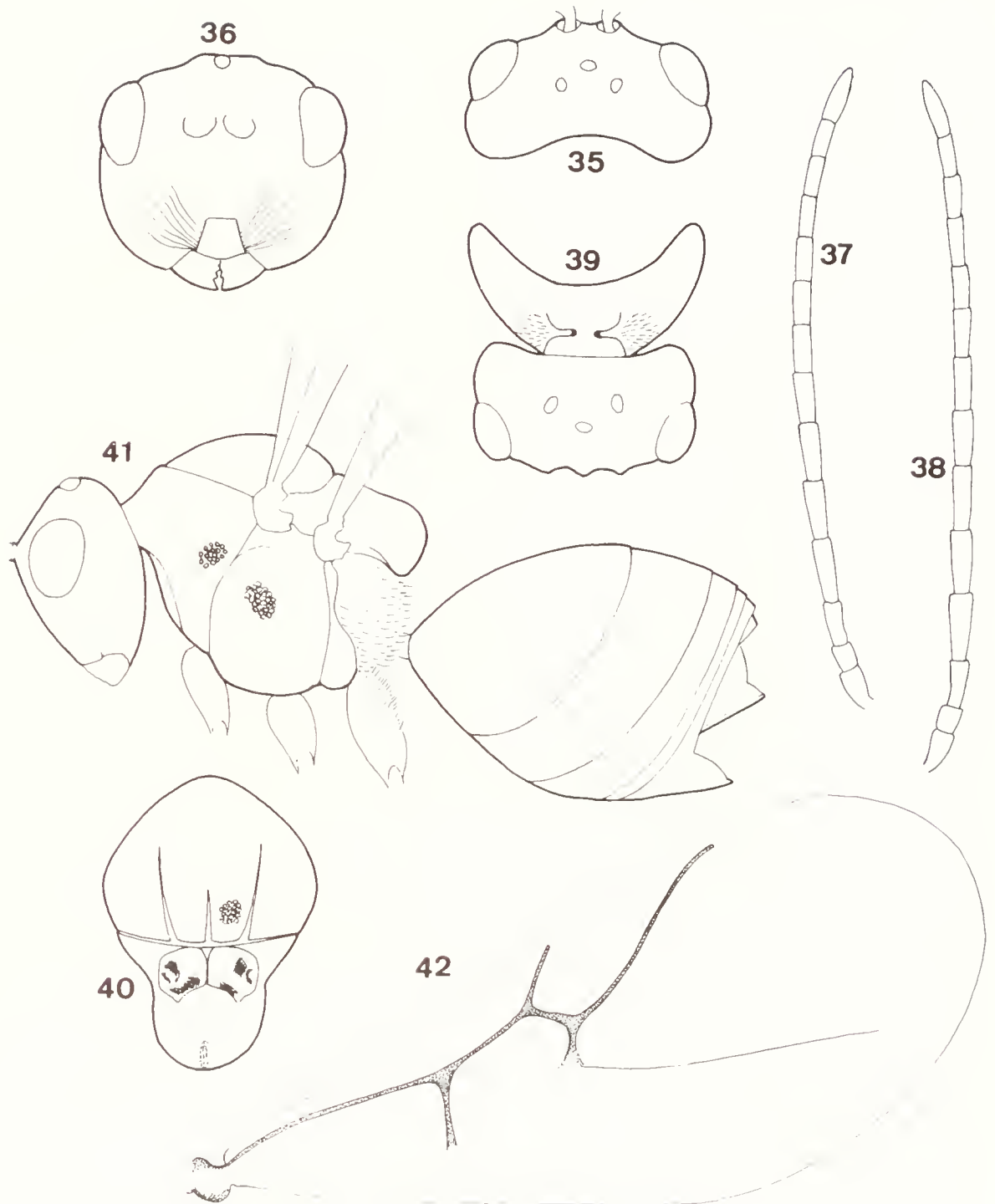
- AYLACINI Ashmead 1903 Host plant genus
- AULACIDEA* Ashmead, 1897
abdominalis (Thomson, 1877) ?
arnicae Hoffmeyer, 1930 *Arnica*
follioti Barbotin, 1972 *Sonchus*
hieracii (Bouché 1834) *Hieracium*
artemisiae (Thomson, 1877)
crassinervis (Thomson, 1877)
foveiger (Thomson, 1877)
kernerii (Wachtl, 1891) **comb. n.** *Nepeta*
kiefferi Cotte, 1915
laurae Nieves-Aldrey, 1992 ?
nibletti Quinlan, 1969 *Hieracium*
pilosellae (Kieffer, 1901) *Hieracium*
scorzonerae (Giraud, 1859) *Scorzonera*
subterminalis Niblett, 1946 *Hieracium*
tragopogonis (Thomson, 1877) *Tragopogon*
- AYLAX* Hartig, 1840
hypecoi Trotter, 1912 *Hypecoum*
minor Hartig, 1840 *Papaver*
papaveris (Perris, 1839) *Papaver*
artemisiae Weidner, 1968 **misident.**
- BARBOTINIA* gen. n.
oraniensis (Barbotin, 1964) **comb. n.** *Papaver*
- CECCONIA* Kieffer, 1902
WELDIELLA Ionescu and Roman, 1962 **syn. n.**
valerianellae (Thomson, 1877) *Valerianella*
aequalis (Ionescu and Roman, 1962) *Valerianella*
- DIASTROPHUS* Hartig, 1840
rubi (Bouché, 1834) *Rubus*
mayri Reinhart, 1876 *Potentilla*
- HEDICKIANA* gen. n.
levantina (Hedicke, 1928) **comb. n.** *Salvia*
- IRAELLA* gen. n.
luteipes (Thomson, 1877) *Papaver*
papaveris Kieffer in Goury and Gignon, 1905
- ISOCOLUS* Förster, 1869
fitchi (Kieffer, 1898) *Centaurea*
jaceae (Schenck, 1863) *Centaurea*
lichtensteini (Mayr, 1882) **comb. n.** *Centaurea*
- tavaresi* Nieves-Aldrey, 1984 **syn. n.**
scabiosae (Giraud, 1859) *Centaurea*
rogenhoferi Wachtl, 1880 **syn. n.**
serratulae (Mayr, 1882) **comb. n.** *Serratula*
- LIPOSTHENES* Förster
glechomae (Linnaeus, 1758) *Nepeta*
latreillei (Kieffer, 1898)
- NEAYLAX* gen. n.
salviae (Giraud, 1859) **comb. n.** *Salvia*
verbenacus (Nieves-Aldrey, 1988) **comb. n.** *Salvia*
versicolor (Nieves-Aldrey, 1985) **comb. n.** ?
- PANTELIELLA* Kieffer, 1902
ENDOCAULONIA Ionescu and Roman, 1960 **syn. n.**
fedtschenkoi (Rubsamen, 1896) *Phlomis*
bicolor (Ionescu and Roman, 1960) *Phlomis*
- PHANACIS* Förster, 1860
GILLETTEA Ashmead, 1897
caulicola (Hedicke, 1939) *Picris*
centaureae Förster, 1860 *Centaurea*
punctipleuris (Thomson, 1877)
hypochoeridis (Kieffer, 1887) *Hypochoeris*
taraxaci (Ashmead, 1897) *Taraxacum*
- RHODUS* Quinlan, 1968
oriundus Quinlan, 1968 *Phlomis*
- TIMASPIS* Mayr, 1881
AYLACOPSIS Heddicke, 1923 **syn. n.**
cichorii Kieffer, 1909 *Cichorium*
heraclei (Heddicke, 1923) **comb. n.** *Heracleum*
lampsanae Perris, 1873 *Lampsana*
lusitanica Tavares, 1904 *Crepis*
crepidos (Weidner, 1968) **syn. n.**
phoenixopodos Mayr, 1882 *Lactuca*
pilicornis (Thomson, 1877) ?
rufipes Ionescu and Roman, 1959 *Crepis*
sonchi (Steffani, 1900) *Sonchus*
urospermi Kieffer, 1901 *Urospermum*
- XESTOPHANES* Förster, 1869
brevitarsis (Thomson, 1877) *Potentilla*
potentillae (Retzius in Degeer, 1873) *Potentilla*
foveicollis (Thomson, 1877)
abreviatus (Thomson, 1877)



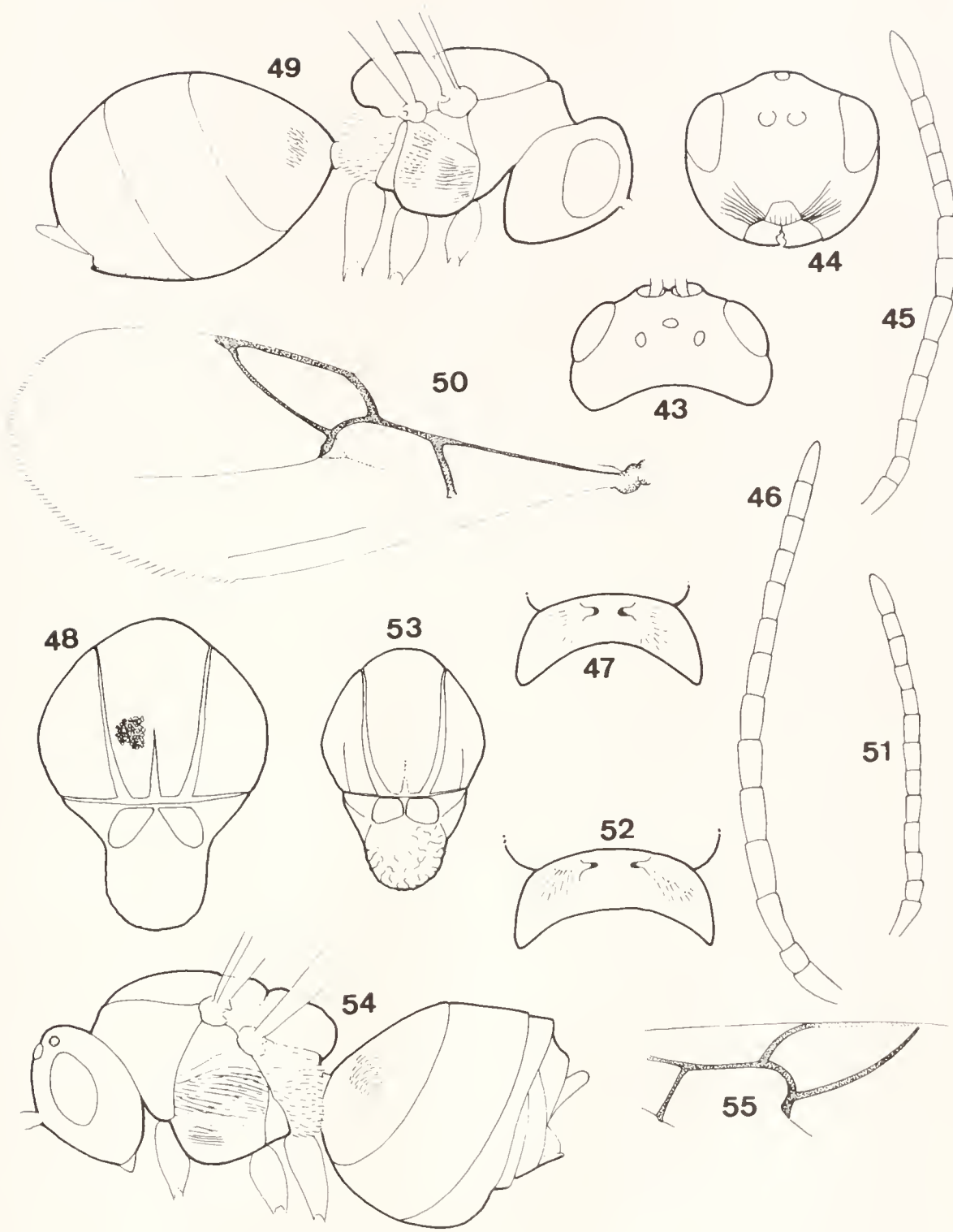
Figs. 1-15. Cynipidae. 1-3, Pronotum, dorsal view. 1, *Aylax papaveris*. 2, *Aulacidea hieraci*. 3, *Cynips divisa* ♀. 4, Scutellum, *Pediaspis aceris*. 5, Gula, *Perichistus brandtii*. 6-7, *Ceroptres*. 6, Gaster, lateral (♀). 7, Head, frontal view. 8, Gula, *Isocolus*. 9, Gaster, lateral, *Synergus thicinus* (♀). 10, Gaster, lateral, *Ceccoma valerianellae*. (♀). 11-13, *Eschatocerus*. 11, Mesoscutum and scutellum, dorsal view. 12, Forewing (hairs omitted) 13, Head, dorsal view. 14-15, *Diplolepis rosae*. 14, Mesopleuron. 15, Gaster, lateral (♀).



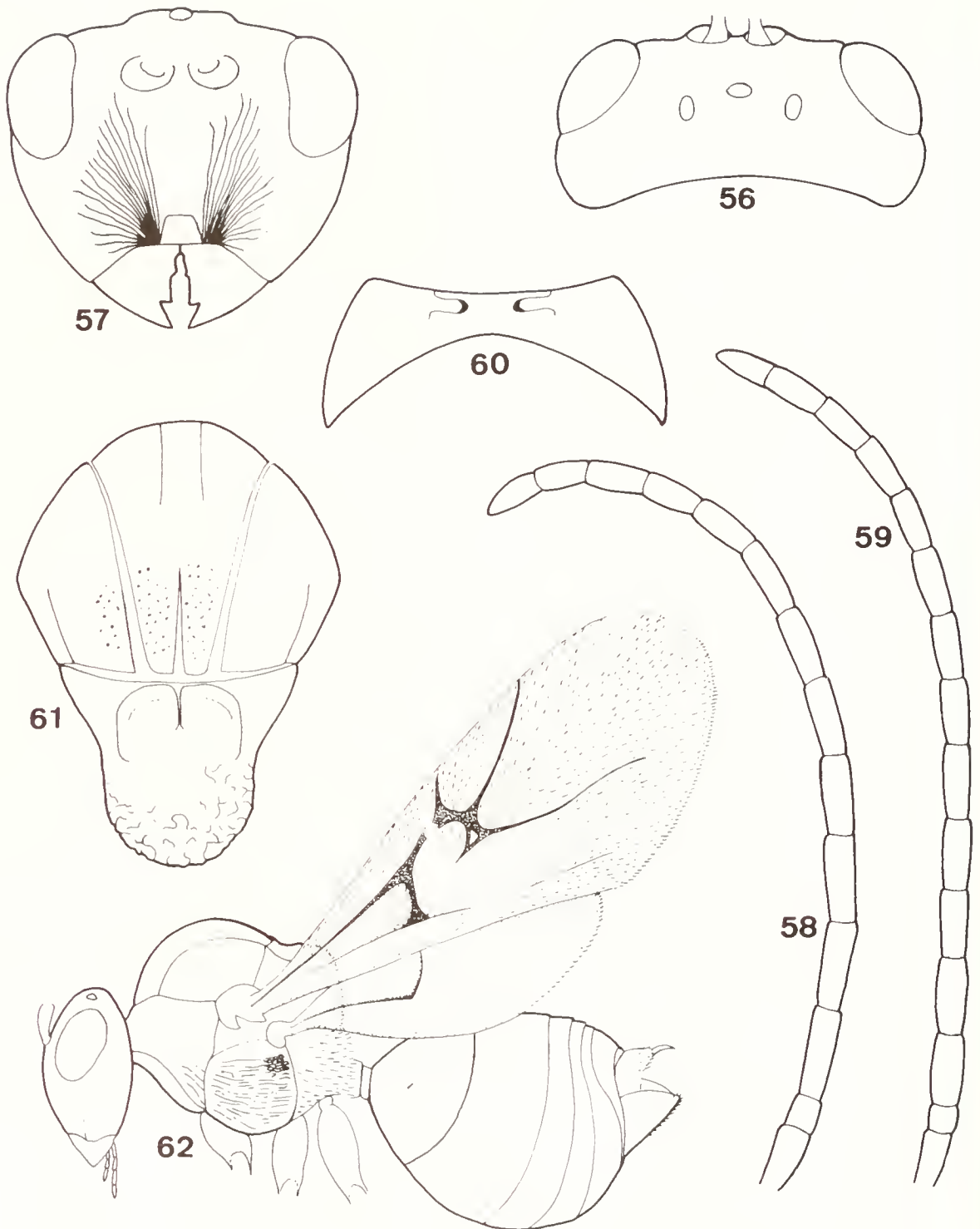
Figs. 16-34. Aylacini. 16-20, Tarsal claws. 16, *Diastrophus rubi* (lund). 17, *Xestophanes potentillae* (front). 18, *X. potentillae* (hind). 19, *Barbotinia oraniensis* (hind). 20, *Isocolus lichtensteini* (hind). 21, Forewing, *X. potentillae*. 22, Forewing, *D. rubi*. 23-27, *Iracella luteipes* (♀). 23, Pronotum. 24, Head and thorax, lateral. 25, Forewing. 26, Head, frontal view. 27, Antenna, first segments. 28, Mesopleuron, *Phanacis caulicola*. 29-30, *Cecconia valerianellae* ♂. 29, Head, frontal view. 30, Forewing. 31-33, *Liposthenus glechomae* ♀. 31, Head and thorax, lateral. 32, Mesoscutum and scutellum, dorsal view. 33, Antenna, first segments. 34, Forewing *Aylax papaveris* (♀).



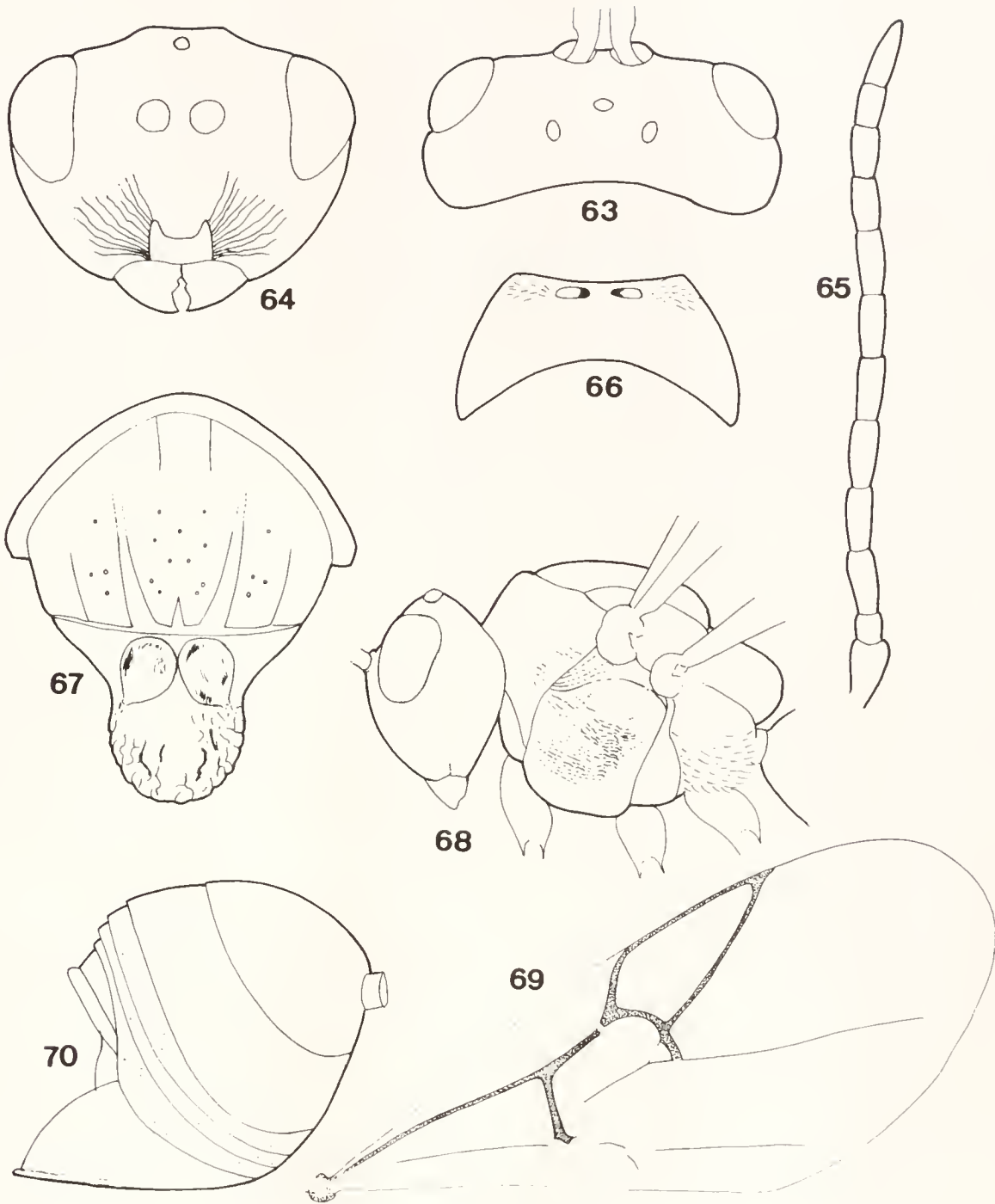
Figs. 35-42. *Antistrophus pisum*. 35, Head, dorsal view. 36, Head, frontal view. 37, Antenna (♀). 38, Antenna (♂). 39, Pronotum. 40, Mesoscutum and scutellum. 41, Body, lateral. 42, Forewing (hairs omitted).



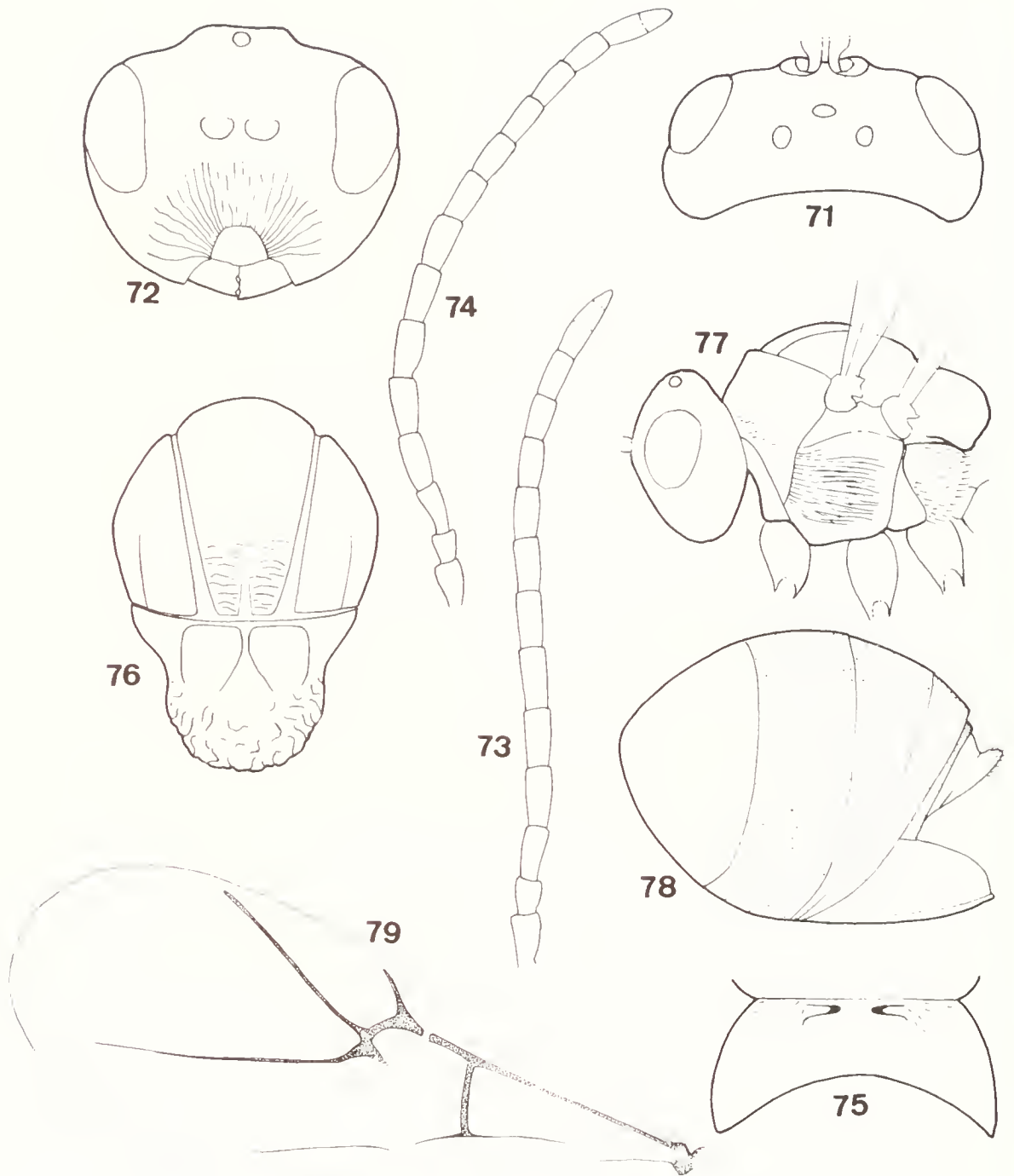
Figs. 43-55. *Aulacidea*. 43-50, *Aulacidea harringtoni*. 43, Head, dorsal view. 44, Head, frontal view. 45, Antenna (♀). 46, Antenna (♀). 47, Pronotum. 48, Mesoscutum and scutellum. 49, Body, lateral. 50, Forewing (hairs omitted). 51-55, *Aulacidea kernerii*. 51, Antenna (♀). 52, Pronotum, 53, Mesoscutum and scutellum. 54, Body, lateral. 55, Radial cell of forewing (hairs omitted).



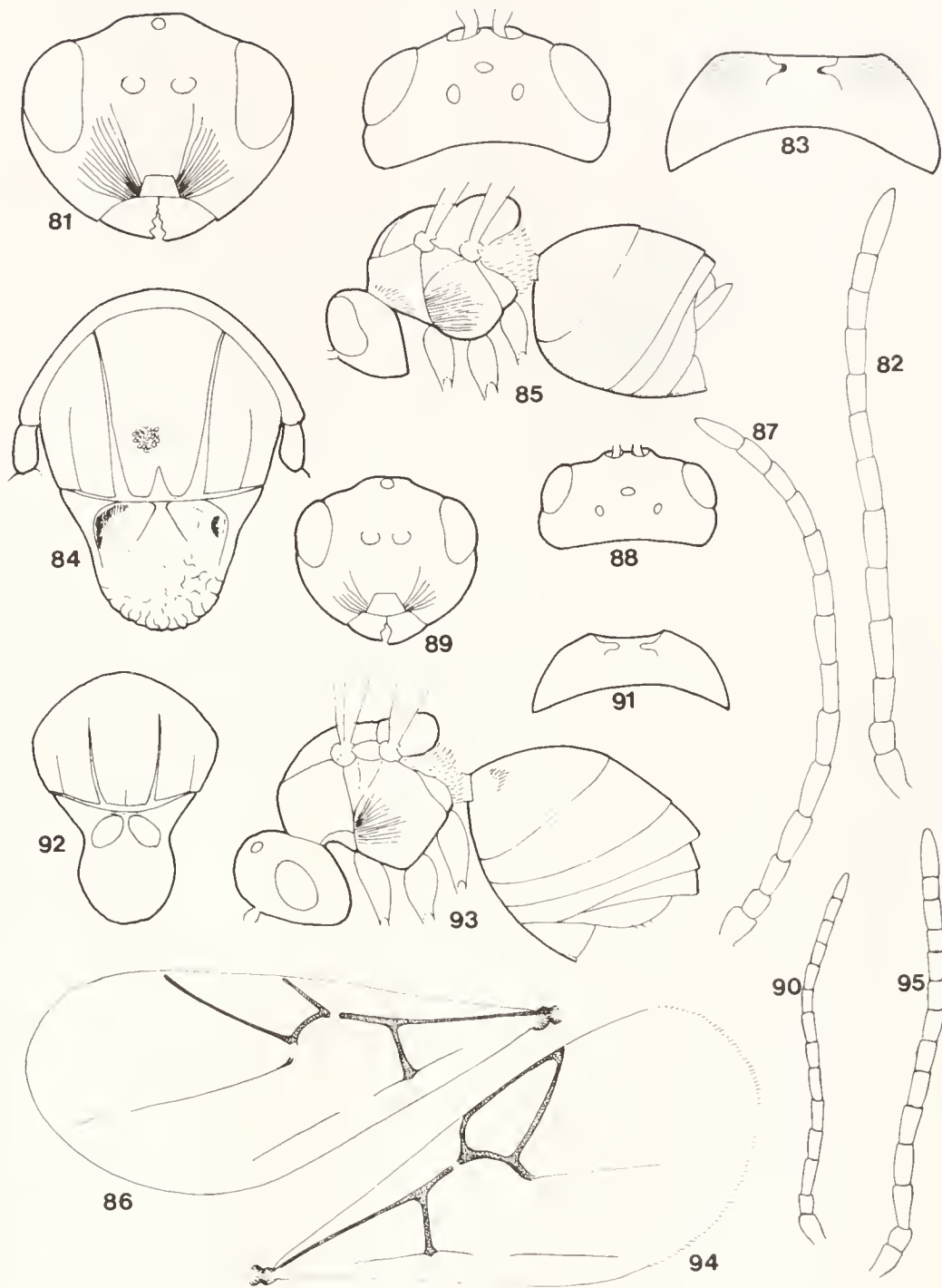
Figs. 56-62. *Barbotinia oraniensis*. 56, Head, dorsal view. 57, Head, frontal view. 58, Antenna (♀). 59, Antenna (♂). 60, Pronotum. 61, Mesoscutum and scutellum. 62, Body and wings.



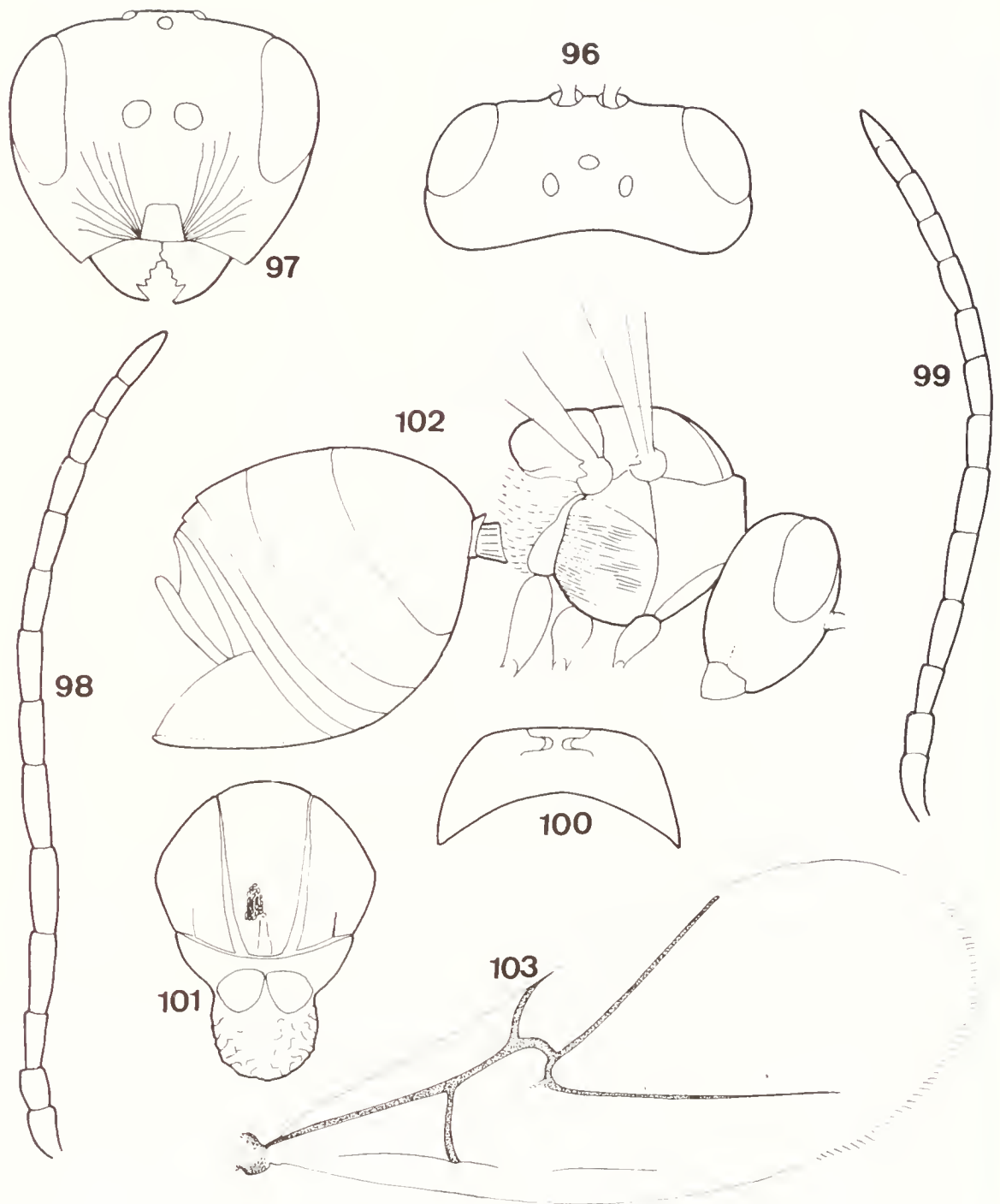
Figs. 63-70. *Hedickiana levantina*. 63, Head, dorsal view. 64, Head, frontal view. 65, Antenna (♀). 66, Pronotum. 67, Mesoscutum and Scutellum. 68, Mesopleuron. 69, Forewing (hairs omitted). 70, Gaster, lateral.



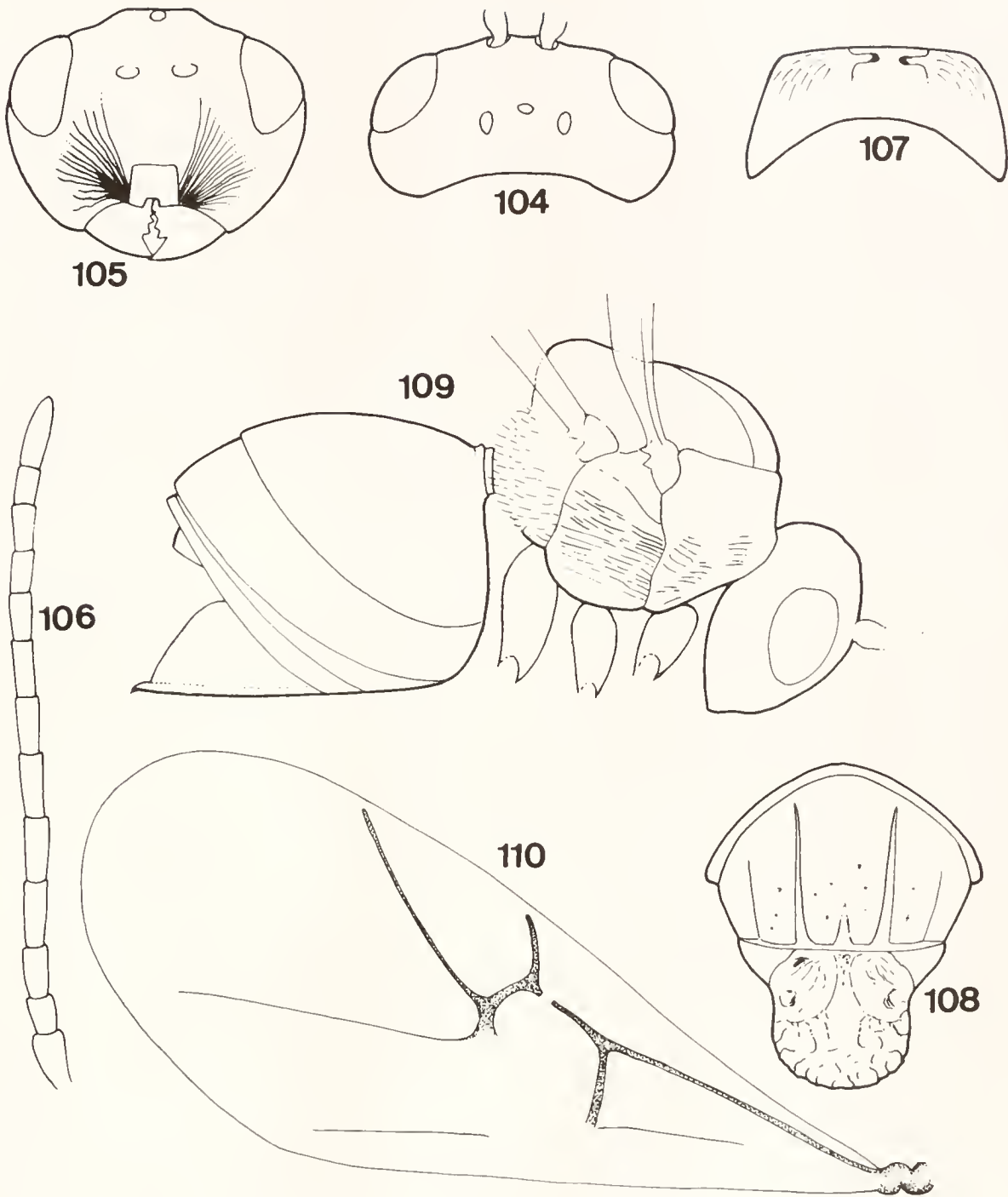
Figs 71-79. *Isocolus scabiosae*. 71, Head, dorsal view. 72, Head, frontal view. 73, Antenna (♀). 74, Antenna (♂). 75, Pronotum. 76, Mesoscutum and scutellum. 77, Mesopleuron. 78, Gaster, lateral. 79, Forewing (hairs omitted).



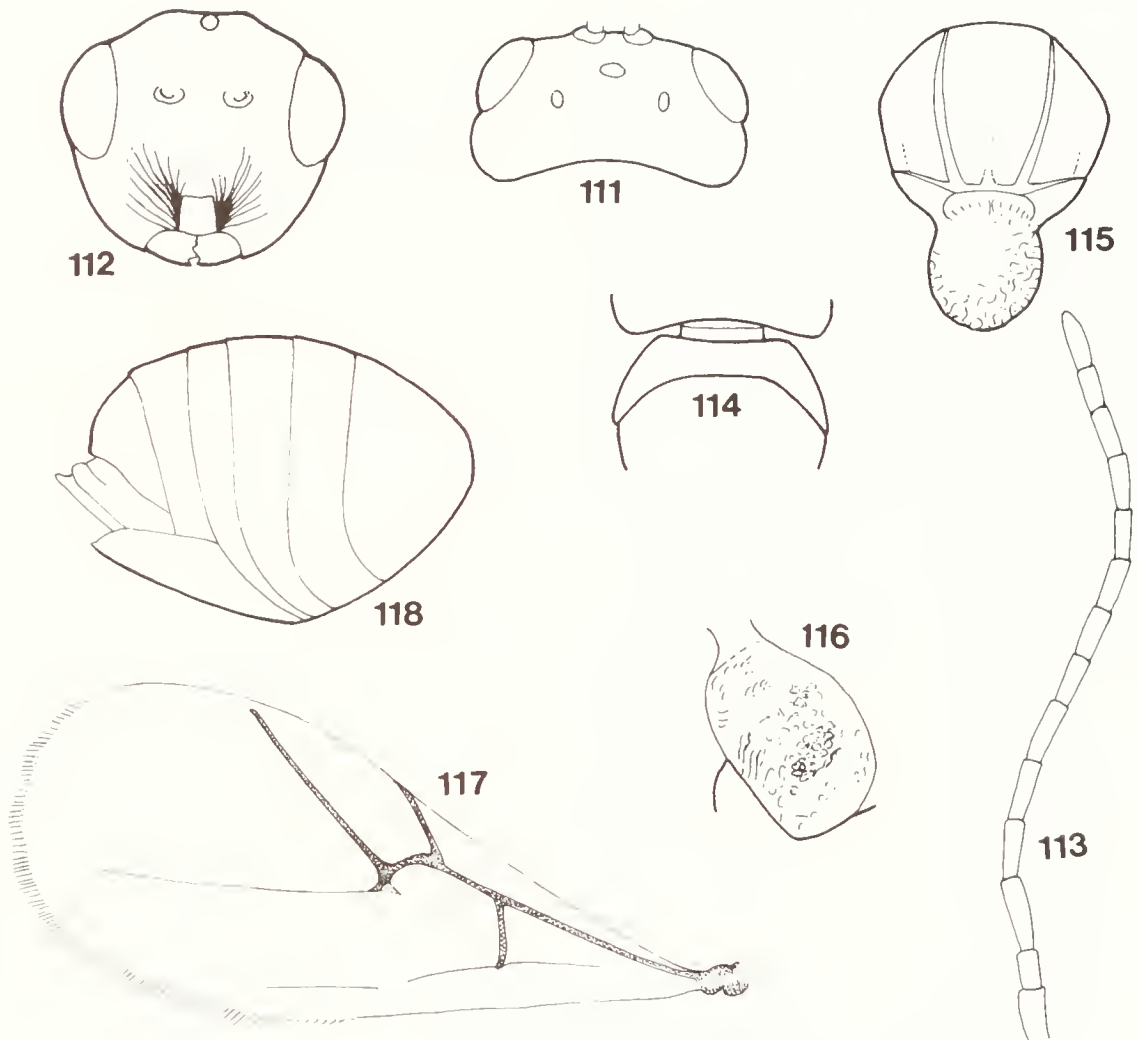
Figs. 80-95. *Isocolus* and *Aulacidea*. 80-87, *Isocolus serratulae*. 80, Head, dorsal view. 81, Head, frontal view. 82, Antenna (♀). 83, Pronotum. 84, Mesoscutum and scutellum. 85, Body, lateral. 86, Forewing (hairs omitted). 87, Antenna (♂). 88-95, *Aulacidea scorzonerae*. 88, Head, dorsal view. 89, Head, frontal view. 90, Antenna (♀). 91, Pronotum. 92, Mesoscutum and scutellum. 93, Body, lateral. 94, Forewing (hairs omitted). 95, Antenna (♂).



Figs. 96-103. *Neaylax salviae*. 96, Head, dorsal view. 97, Head, frontal view. 98, Antenna (♀). 99, Antenna (♀). 100, Pronotum. 101, Mesoscutum and scutellum. 102, Body, lateral. 103, Forewing (hairs omitted).



Figs. 104-110. *Rhodus oriundus*. 104, Head, dorsal view. 105, Head, frontal view. 106, Antenna (♀). 107, Pronotum. 108, Mesoscutum and scutellum. 109, Body, lateral. 110, Forewing (hairs omitted).



Figs. 111-118. *Timaspis heraclei*. 111, Head, dorsal view 112, Head, frontal view. 113, Antenna (♀). 114, Pronotum, 115, Mesoscutum and scutellum. 116, Mesopleuron. 117, Forewing (hairs omitted). 118, Gaster, lateral.

A Review of North American *Belomicrus* (Hymenoptera, Sphecidae, Crabroninae)

RICHARD M. BOHART

Department of Entomology, University of California, Davis, CA 95616

Abstract.—The North American *Belomicrus* are reorganized into five groups containing a total of 40 species. Of these, 14 are described as new: *californicus* (central Sierra of California), *costalis* (central California), *darwinii* (sw. U.S.); *desertus* (s. California); *inyo* (Inyo Co., California), *longiceps* (sw. U.S.), *melanus*, (central Sierra of California), *montanus* (central Sierra of California), *oraibi* (Arizona and s. Utah), *pallidus* (s. California), *powelli* (coast range mts. of California), *siccatus* (s. California), *sierrae* (central Sierra of California), *texensis* (Texas and Baja California Sur). Keys, illustrations, and distributions are given. New synonymy: *quemaya* Pate is raised to full species; and *jurumpa* Pate is synonymized under *quemaya*.

Belomicrus Costa (1871) is one of several crabronine genera in the tribe Oxybelini. Bohart and Menke (1976:359-370) gave an overview of present day knowledge of the tribe. They pointed out that the presence of metanotal projections (squamae) and a propodeal projection (mucro) in addition to a lateral carina on terga I-III, and sometimes IV-V, characterize *Belomicrus*. As far as known, distribution of the genus is holarctic and Ethiopian. Bohart and Menke listed 63 species of which 25 were North American. I now recognize 40 species in the latter region, of which 14 are new.

Among earlier writers the work of Pate (1940a,b) was outstanding. His overall assessment of *Belomicrus* and its relatives was brilliant, and his descriptions were meticulous. The only criticisms that can be made are that some of his phylogenetic discussions suffered from lack of material, and his descriptions contain much detail irrelevant at the species level.

Belomicrus are ground-nesting wasps, mostly in sandy areas. Prey of the *forbesii* group are nymphal Miridae (Bohart 1956, Evans 1969). The *franciscus* group provisions with adult dasytid beetles (Williams 1936, Bohart and Menke 1976). Prey of the other groups are unknown.

Members of the genus are few in most collections. Through museum visits and borrowings I have been able to examine about 600 specimens. The majority of these are in the University of

California at Riverside museum and were collected by P. H. Timberlake. Diligent work by Bohart Museum collectors at Davis has made some 3,000 more specimens available for study.

Principal cooperating museums and individuals are listed below. Museum designations are identified by their city locations in capital letters.

The manuscript was read by Dr. Arnold Menke and Dr. Eric Grissell. Their comments and corrections were quite helpful, and their assistance is gratefully acknowledged.

BERKELEY—J. Powell, P. D. Hurd (deceased), Essig Museum, University of California at Berkeley.

DAVIS—L. S. Kimsey, S. Heydon, Bohart Museum, University of California at Davis.

LOGAN—G. E. Bohart, Entomology Museum, Utah State University.

NEW YORK—J. Rozen, Entomology Museum, American Museum of Natural History.

OTTAWA—L. Masner, Biological Resources Division, Agriculture Canada.

PHILADELPHIA—S. Roback, Daniel Otte, D. Azuma, Academy of Natural Sciences.

RIVERSIDE—P. H. Timberlake (deceased), S. Frommer, Entomology, Museum, University of California at Riverside.

SAN FRANCISCO—W. J. Pulawski, P. Arnaud, Entomology Museum, California Academy of Sciences.

VIENNA—M. Fischer, Naturhistorische Museum, Vienna, Austria.

WASHINGTON—A. S. Menke, K. V. Krombein, U.S. National Museum.

Terms used in the species key and in descriptions which may need explanation are: epipleural "button", small raised area just behind pronotal lobe; T-I, T-II, etc. terga after propodeum; S-I, S-II, etc., sterna after propodeum; LID, least interocular distance; PD, puncture diameter; post-tegula, basal wing sclerite.

The generotype, *Belomicrus italicus* A. Costa (1871), has a palearctic distribution and is similar to species in the *forbesii* group. However, it should be placed in a different group because the clypeus has a considerable flattened area on the median lobe, and the more posteriorly blunt metanotal

projection is divided by a median carina.

The ten groups of North American *Belomicrus* which Pate (1940b) proposed are now reduced to five. Bohart and Menke (1976) considered only 2 groups, *forbesii* and *cladothericis*. With the discovery of additional species it now seems desirable to divide the *forbesii* group into four according to the following key.

The purpose of this and other keys in the paper is to give a quick means of making identifications. It is understood that the key user should have access to at least a representative named collection of *Belomicrus* for comparative purposes.

KEY TO THE SPECIES GROUPS OF NORTH AMERICAN *BELOMICRUS*

- 1 Metanotal projections (squamae) divided into two distinct lobes (Figs. 28-43), basally joined or separated but without an outer membranous area; body rarely more than 4mm long; postocular tubercles well defined; (Figs. 18-24) *cladothericis* group
- Metanotal projections joined to form a roughly triangular plate with a posterior notch and an outer partly membranous edge (Figs. 11-14), postocular tubercles various 2
- 2 Mandible of females and some males with an obtuse angle subapically on lower edge (Fig. 15), mesopleuron with an omaulus *vanyume* group
- Mandible with at most a slight inferior angle subapically, mesopleuron without omaulus 3
- 3 Clypeus with an anchorlike apical projection in female (Fig. 16), body about 2 mm long *apache* group
- Clypeus simply pointed or with a deflected apical bevel, body 3.5 mm long or more 4
- 4 Clypeus medially hoodlike, often somewhat wrinkled, not deflected apically but ending in a small point (Fig. 17) *forbesii* group
- Clypeus with an apicomedial polished triangle or deflected bevel (Figs. 3-7) *franciscus* group

Belomicrus forbesii group

The only previous key to the *forbesii* group is that given as part of a more extensive one by Pate (1940b:210). The *forbesii* part was based on about 65 specimens, of which some 43 were *forbesii* and *columbianus*, 10 were *cookii*, seven were *penuti* (as a subspecies of *forbesii*), 3 were *coloratus*, and two were *querecho*. I have studied about 1,500 specimens of the group.

Instead of the six now valid species recognized by Pate, this figure has been raised to 10, which includes four new species.

Members of the *forbesii* group have relatively few "structural" differences. However, the coloration and color patterns seem to be quite constant in long series. Therefore, I am treating *columbianus* as distinct from *forbesii*, *sierrae* as distinct from *penuti*, and *desertus* as distinct from *cookii*. Details on differences are given in the key, which follows:

KEY TO THE *BELOMICRUS FORBESII* SPECIES GROUP

- 1 T-I with basal slope all or mostly red 2
- T-I with basal slope dark reddish brown, dark brown, or black 5
- 2 Postocular tubercles weak and obtuse, tergal pale yellow bands usually well developed on T-I and often on T-II, weak or faint on T-III and following *montanus* R. Bohart
- Postocular tubercles well developed, tergal markings various 3
- 3 S-II and following with distinct, close, moderately fine punctures; S-II with a broad median depression *querecho* Pate
- S-II and following with indistinct, close, fine punctures or other microsculpture; S-II with at most a median flattened area 4
- 4 Terga without distinct pale yellow bands, these sometimes faintly visible; band across pronotum nearly always broken a little inside pronotal lobe, wing membrane stained *powelli* R. Bohart
- Terga with distinct pale yellow bands on most terga, band across pronotum complete to pronotal lobes, wing membrane nearly clear *desertus* R. Bohart
- 5 Epipleural "button" cup shaped, cup usually with a membranous outer edge, or pronotal collar all black 6
- Epipleural "button" not cup shaped, only slightly indented, pronotal collar nearly always maculate 7
- 6 Pronotal collar all black, T-I to IV all dark or with indistinct bands, epipleural "button" pocket without a lighter colored edge, postocular tubercles weak *sierrae* R. Bohart
- Pronotal collar maculate, terga with pale bands or lateral spots usually on T-I to V, epipleural "button" pocket deeper and with a lighter colored edge, postocular tubercles often well developed *penuti* Pate
- 7 Tergal markings weak, pale bands indistinct at least on T-III to V; pronotal collar black laterally and sometimes medially *columbianus* (Kohl)
- Tergal markings prominent; pronotal collar nearly always completely banded 8
- 8 T-I, II and sometimes III in female with dark ground color, following terga with red ground color; both sexes with small but sharp postocular tubercles *cookii* Baker
- T-I and most following terga in both sexes with reddish brown to black ground color; both sexes with at most weakly to moderately developed, but not sharp, postocular tubercles 9
- 9 Tergal coloration in front of yellow bands brownish red or reddish brown, postocular area without definite tubercles *coloratus* Baker
- Tergal coloration in front of yellow bands dark brown to nearly black, postocular area nearly always with low but definite tubercles *forbesii* Robertson

Belomicrus coloratus Baker

Belomicrus colorata Baker 1909:29. Holotype female, Ormsby Co., Nevada (DAVIS), examined.

I have studied 422 males and 140 females from Nevada and California. They were all taken in the months of June and July at elevations of 4,000 to 8,000 feet. Nevada county records include Ormsby, Douglas, and Eureka. California counties are Alpine, El Dorado, Inyo, Lassen, Mono, Nevada, Placer, Sierra, and Tuolumne. A single Oregon record is 5 mi e. Bly, Klamath Co.

The principle diagnostic features, especially the tergal markings, are given in the key.

Belomicrus columbianus (Kohl)

Oxybelus columbianus Kohl 1892:208. Lectotype female (examined and here designated), Revelstoke, British Columbia (VIENNA). Treated as a subspecies of *forbesii* by Bohart and Menke (1976). New status.

Oxybelus larimerensis Rohwer 1908:417. Holotype female, Larimer Co., Colorado (WASHINGTON), examined. Treated as a synonym of *forbesii* by Bohart and Menke (1976). Revised synonymy.

In all, 54 males and 69 females have been studied. These were taken during the months of May (rarely), June, July, and August, mostly at elevations above 4,000 feet. Western state records include British Columbia, Alberta, Colorado, Idaho, Montana, Nevada, Oregon, Utah, and Washington. California records are: Bell Echo Camp,

Dorris, and Rattlesnake Meadow, Siskiyou Co.; Morrison Meadow and Snowslide Park, Trinity Co.

The new status of *columbianus* and its synonym, *larimerensis* is indicated by the difference in markings from *forbesii* as outlined in the key.

Belomicrus cookii Baker

Belomicrus cookii Baker 1909:29. Lectotype male, Claremont, Los Angeles Co., California (WASHINGTON). Lectotype designated by Pate (1940a).

This species is known from a few southern California localities. I have seen 8 males and 11 females from Los Angeles Co. (Claremont, Newhall) and Riverside Co. (Riverside, Gavilan), all taken during the months of April and May at low elevations in foothill locations.

Belomicrus desertus R. Bohart, new species

Female holotype.—Length 5 mm. Black, red are: clypeal apex, foretarsus partly, tegula dully, terga mostly, sterna except for dark median blotches on T-I to T-III; whitish yellow are: mandible basally, scape partly, flagellum beneath, apical spots on femora, tibiae outwardly, squamal triangle, apical bands on T-I to III, weak on IV-V; wings nearly clear. Pubescence moderate, silvery and appressed on clypeus, lateral frontal band enlarged above, short supraclypeal spot, postocular, mesopleural, and lateral tergal areas moderately silvered. Punctuation fine and close, a little shiny across frons below ocelli; pygidial plate with coarse, separated punctures. Postocular tubercles well developed, epipleural "button" weakly indented.

Male.—Length 4-5 mm. Whitish yellow are: mandible mostly, clypeus across apex, basal tarsal segment, apical bands on T-I to VII (usually).

Holotype female (DAVIS), 3 mi s. Kramer Junction, San Bernardino Co., California, IV-6-66 (R.M. Bohart). Paratypes, 123 males, 31 females topotypical, collected in April of various years by R.M. Bohart, E.I. Schlinger, M.E. Irwin, D.S. Horning, J.C. Hall, F.D. Parker. Other paratypes from San Bernardino Co., California: 3 males, 5 females, Joshua Tree National Monument, (H.K. Court); 13 males, 4 females, Adelanto (E.I. Schlinger, *et al.*); 6 males, 2 females, Apple Valley (W. R. Mason, P. D. Hurd). Other specimens (not

paratypes) were from California counties: San Bernardino (Victorville, Morongo Valley, Red Mountain), Imperial (Palo Verde), Los Angeles (Llano, near Lovejoy Buttes), Ventura (Chuchupate Ranger Sta., Frazier Mt.), Kern (Dove Well), *inyo* (Panamint Mts., 8 mi w. Brown). Paratypes in cooperating museums.

This species is similar to *powelli* which also has well developed postocular tubercles, the basal slope of T-I red, and the epipleural "button" scarcely indented. However, *desertus* usually has extensive whitish yellow tergal markings. Sometimes, these may be on T-I only. See also *powelli*.

Etymology.—specific name derived from Latin adjective, *desertus* = abandoned.

Belomicrus forbesii (Robertson)

Figs. 12, 17

Oxybelus forbesii Robertson 1889:85. Holotype male, Colorado (PHILADELPHIA), examined.

I have studied 118 males and 122 females, collected from May to August at elevations of 4,000 to 10,000 feet in the following states and counties: California (Alpine, Lassen, Modoc, Mono, Nevada, Sierra, Siskiyou, Trinity), Colorado (Larimer, Denver), Montana (Missoula), Nevada (Elko, Pine, Washoe), Utah (Box Elder, Kane, Summit), and Wyoming (Sublette, Teton, Uinta). Female face (Fig. 17).

Diagnostic characters, particularly the abundant tergal markings, are given in the key.

Belomicrus montanus R. Bohart, new species

Female holotype.—Length 5 mm. Black, red are: clypeal apex, terga and sterna mostly except for dark blotches on S-I-II; whitish are: mandible basally, scape apically, flagellum beneath, pronotal collar and lobe, apical spot on forefemur, tibiae outwardly, squamal triangle, T-I apex faintly; wings lightly stained. Pubescence light, silvery and appressed on clypeus, lateral frontal area, short supraclypeal spot, postocular and mesopleural areas moderately. Punctuation fine and close, not shiny across frons below ocelli; pygidial plate with coarse, separated punctures. Postocular tubercles quite weak, epipleural "button" slightly indented.

Male.—Length 4-4.5 mm. Foretarsus partly

off-white, T-I whitish apically.

Holotype female (DAVIS), White Mts., Mono Co., California, 10,000 ft., VII-10-68 (R.M. Bohart). Paratypes, 14 males, 13 females, topotypical but collected from June 22 to July 23 by J.W. MacSwain, J. Powell, and G.I. Stage. Other California paratypes: 1 pair, Benton, Mono Co., V-23-86 (R.M. Bohart); 3 males, Westgard Pass, Inyo Co., V-VI-37 (G.A. Hamsher, C.D. Michener); 2 females, Deep Springs, Inyo Co., V-13, V-14 (L.D. French, N.J. Smith). Paratypes in cooperating museums as far as possible.

There is some similarity to *querecho*, *powelli*, and *desertus*, since the basal slope of T-I is mainly red, and the epipleural "button" is scarcely indented. From all three of these the weakly indicated postocular tubercles of *montanus* are differentiating. Also, it may be separated from *querecho* by the distinct sternal punctation of the latter, as well as its broad depression on S-II.

Etymology.—specific name derived from Latin adjective, *montanus* = dwelling on mountains.

Belomicrus penuti Pate

Belomicrus forbesii penuti Pate 1940:27. Holotype male, Yosemite Valley, Mariposa Co., California (PHILADELPHIA). Raised to species status by Bohart and Menke (1976).

The 1,115 males and 51 females I have studied were collected during April to September in California and neighboring Nevada at elevations mostly above 5,000 feet. California counties are: Alpine, El Dorado, Fresno, Lassen, Mariposa, Mono, Nevada, Placer, Calaveras, Sierra, Tulare, Amador, and Tuolumne. Nevada records are Incline Village and Little Valley, Washoe Co. Also, Pate (1940a:28) recorded *penuti* from southern Oregon: Crater Lake and Lake of the Woods, Klamath Co. I have not studied these specimens.

The relationships to *columbianus* and *forbesii* are outlined in the key.

Belomicrus powelli R. Bohart, new species

Female holotype.—Length 5 mm. Black, red are: clypeal apex, terga and sterna mostly except for dark blotches on S-II-III; whitish are: mandible basally, flagellum beneath, pronotal collar medially, pronotal lobe, apical spot on femora, tibiae

outwardly, foretarsus dully, squamal triangle; wings moderately stained. Pubescence silvery appressed on clypeus, lateral frontal area, stout supraclypeal triangle, postocular and mesopleural areas (weakly). Punctation fine and close, not shiny across frons below ocelli, somewhat shiny on terga; pygidial plate with coarse, separated punctures. Postocular tubercles well developed, epipleural "button" slightly indented.

Male.—Length 4-4.5 mm. Characters about as in female. Scape whitish at apex.

Holotype female (SAN FRANCISCO), La Panza, 12 mi ne. Pozo, San Luis Obispo Co., California, IV-29-62 (J. Powell). Paratypes, 5 males, 16 females (all from California collected in April and May): Monterey Co.: 1 male, 5 females, Hastings Reserve (D.L. Linsdale); 1 pair, Arroyo Seco (D. Burdick, P. Torchio); female, 12 mi n. Cholame (D.H. Janzen); San Luis Obispo Co.: 2 pair, topotypical (J. Powell, R.W. Thorp); female, 5 mi ne. Santa Margarita (R.W. Thorp); Fresno Co.: 12 mi w. Coalinga (J.W. MacSwain); Ventura Co.: 3 males, 8 females, Chuchupate Ranger Sta., Frazier Mt. (J. Powell, P.D. Hurd). Paratypes in SAN FRANCISCO, DAVIS.

The well developed postocular tubercles are also found in *desertus*, which see. The all red terga and broken yellow pronotal band of *powelli* are distinguishing. Although primarily a coastal form, *powelli* occurs with *desertus* on Frazier Mt., Ventura Co., at Chuchupate Ranger Station. In fairly long series the differences given in the key seem to hold. The species is named for my friend, Jerry Powell, a lepidopterist who has also worked with wasps.

Belomicrus querecho Pate

Belomicrus querecho Pate 1940:36. Holotype male, Alamogordo, Otero Co., New Mexico (PHILADELPHIA), examined.

This southwestern species is largely restricted to the Chihuahuan Life Zone. I have studied 3 males and 20 females, collected in April, May, and June in the following states: Arizona (near Apache and Willcox, Cochise Co.; Tubac, Santa Cruz Co.; Oak Creek Valley Road, Yavapai Co.; 10 mi w. Jacob Lake, Coconino Co.). Utah (25 mi s. Moab, Grand Co.). New Mexico (Skeleton Canyon, Peloncillo Mts., and Rodeo, Hidalgo Co.;

Alamogordo, Otero Co.; 5 mi e. Las Cruces and Leasburg Dam, Dona Ana Co.). Nevada (4 mi s. Warm Springs, Nye Co.) and Texas (Rankin, Upton Co.).

***Belomicrus sierrae* R. Bohart, new species**

Female holotype.—Length 5 mm. Black or dark brown, red are: flagellum beneath dully, foretarsus dully, apical half of pygidial plate; whitish yellow are: mandible basally, femorotibial joints, tibiae outwardly, apicomedial spot on squamal triangle (all yellow in some paratypes); wings moderately stained. Pubescence silvery appressed on clypeus laterally, narrowly on lateral frontal area, short supra-clypeal spot, weakly on postocular and mesopleural areas. Punctuation fine, close, dull; clypeus wrinkled, with a pair of coarse punctures above polished apex, pygidial plate with coarse, separated punctures. Postocular tubercles present but weak, epipleural "button" deeply indented but not covered with a thin membrane; lateral propodeal carina flattened, somewhat bent inward.

Male.—Length 4.5-5 mm. About as in female. Pronotal lobe sometimes dully pale.

Holotype female (DAVIS), Sagehen Creek, Nevada Co., California, 6,500 feet, VI-25-68 (R.M. Bohart). Paratypes, 118 males, 97 females, topotypical, V-29 to VII-25 (R.M. Bohart, J.A. Skinner, L.S. Kimsey, M.E. Irwin, D.S. Horning, J.E. Slansky, J. Powell, B. Villegas). Also paratypes, 10 males, 19 females, Grass Lake, El Dorado Co., California, 8,000 ft., VII-5-62 and VII-16-62 (R.M. Bohart *et al.*). Other specimens (not paratypes) have been studied from other California counties at 6,000 ft. or above: Alpine, Calaveras, Plumas, Lassen, Placer, and Trinity. Paratypes in all cooperating museums.

The dark basal slope of T-I and the deeply indented epipleural "button" ally *sierrae* with *penuti*. However, the "button" is not as thinly lidded above as in *penuti*. Furthermore, the latter seems always to have at least several of the terga with whitish bands. The dark abdomen of *sierrae* is similar to that of *columbianus*, and conceivably the two species might occur together in California near the Oregon border. In addition to the epipleural "button" difference, *columbianus* has the lateral propodeal carina simple, whereas in *sierrae* it is not sharp but flattened and bent inward.

Etymology.—the specific name refers to the California Sierra.

Belomicrus apache group

The *apache* group contains only the single known species, *apache* Pate. It was described in detail from a single female by Pate (1940a) and placed in a key by Pate (1940b). This is one of the smallest known *Belomicrus*, approximately 2 mm in length. The female has a peculiar anchoriform terminal process figured by Pate (1940a) and herein (Fig. 16). The male clypeus is more ordinary. Features of the group are characterized in the key. A brief description of the species, including the previously unknown male, and additional locality records follow:

***Belomicrus apache* Pate**

Figs. 13, 16

Belomicrus apache Pate 1940a:15. Holotype female, Las Cruces, Doña Ana Co., New Mexico (PHILADELPHIA), examined

Female.—Length 2 mm. Black with red unbanded abdomen; legs partly whitish yellow, frons at narrowest point about equal to eye breadth, clypeus with an apical anchoriform projection (Fig. 16), no postocular tubercles or omaulus, squamal triangle translucent laterally, deeply incised posteriorly (Fig. 13).

Male.—Length 2 mm. Much as in female but LID slightly greater and clypeal bevel triangular rather than anchoriform.

I have seen three males and seven females from the following western states: New Mexico (Las Cruces, Doña Ana Co.; Rodeo, Hidalgo Co.), Arizona (Aztec, and 7 mi s. Quartzite, Yuma Co.; Quijotoa and Sells, Pima Co.; Willcox, Cochise Co. on *Euphorbia* mat), California (Cathedral City, Riverside Co. on *Euphorbia polycarpa*). Collections were made from August to October.

Belomicrus vanyume group

The *vanyume* group consists of three species of which one is described below as new. Pate (1940a, b) placed *vanyume* in a monotypic group of its own. The *vanyume* group, as I consider it, is unified by the distinct omaulus running vertically along the widest point of the mesopleuron, and ending

in a tooth or angle. This is followed halfway to the midcoxa by another tooth. Females have the forefemur right-angled subbasally. Except for *vanyume*, males also have this feature. Further, females have the mandible broadened before the apex (Fig. 15).

KEY TO SPECIES OF THE *BELOMICRUS VANYUME* GROUP

- 1 Postocular area a little swollen but not tuberculate, clypeus broadly rounded, scape light yellow, squamal unit with windowlike clear areas *vanyume* Pate
 — Postocular area with prominent tubercles, clypeus with a longitudinal raised area medially, scape dark, squamal unit various 2
 2 Pronotum all dark, mesopleuron completely punctate and dull, clypeus (as seen in side view) not dentate above bevel, T-II to V or III to V black *texensis* R. Bohart
 — Pronotum usually partly whitish, pronotal lobe white, clypeus ending above bevel in a forward-directed tooth (Fig. 15), T-I to V usually red, especially in females *maricopa* Pate
-

***Belomicrus maricopa* Pate**
 Figs. 14, 15

Belomicrus maricopa Pate 1947:54. Holotype female, Higley, Maricopa Co., Arizona (WASHINGTON), examined.
Belomicrus mariposa Pate 1947:55. In error.

I have seen 44 males and 58 females from Arizona (Higley, Willcox, 28 mi s. Quartzite, Picacho Canyon), New Mexico (5 mi e. Las Cruces, 9 mi n. Cotton City), California (18 mi w. Blythe, Palo Verde), and Sonora, Mexico (Guaymas).

This species is similar to *texensis*, described below and differences enumerated. The undescribed male is much like the female but is a little smaller and the mandible is somewhat less expanded. Also, the last few terga are darker. The principal differences between the two species are the shinier mesopleuron and apically toothed clypeus of *maricopa* (Fig. 15).

***Belomicrus texensis* R. Bohart, new species**

Female holotype.—Length 5 mm. Black, light yellow are basal two-thirds of mandible, foretibia outwardly; brownish are: legs partly; reddish are: forefemur at base, T-I to III; wings clear, veins mostly orange. Silvery appressed pubescence on clypeus mostly, broad patch along eye margin reaching up as far as an imaginary line drawn across beneath midocellus, short but large

supraclypeal patch. Punctuation of mesonotum and interocellar area coarse and separated by 1-2 PD of microsculpture, mesopleuron similar but rugose below, tergal punctuation moderate and a little shiny, coarse on pygidial plate. LID about 1.7x scape length, clypeus with median raised area bearing longitudinal depression, clypeal bevel transverse and nearly linear, frontal groove well impressed, postocular tubercles well developed, gena in side view bent outward at middle below, mandible strongly expanded at distal one-third, front dorsal margin of pronotum obtusely cornered, squamal unit as in Fig. 14, forefemur rightangled near base, pygidial plate narrowly triangular.

Male.—Length 4 mm. Legs mostly brownish red, forewing veins dark, clypeal bevel broadly triangular, T-I-II red, III a little red laterally and posteriorly, VII dully red.

Female holotype (DAVIS), Kingsville, South Pasture, Kleberg Co., Texas, VI-16-68 (J. E. Gillaspay). Paratypes, 4 females (DAVIS, NEW YORK), same data as holotype but V-6-67 and V-6-68; on *Ratibida columnaris*; paratype male (SAN FRANCISCO), Mexico: Baja California Sur, e. edge of Sierra Placeres, III-24-84 (W. J. Pulawski).

The large size (for *Belomicrus*!), large postocular tubercles, expanded mandible subapically and all dark antenna are also found in *maricopa*. However, *texensis* has many differences: pronotum all dark,

punctuation of mesopleuron and mesonotum much closer and not shiny, female clypeus with a longitudinal flattened and shallowly grooved median ridge, clypeus also without a forward-pointing apical tooth, wing veins of female mostly orange instead of black, marginal cell of forewing somewhat shorter, and T-III to V mostly or all black.

Etymology.—the specific name indicates "of or from" Texas.

Belomicrus vanyume Pate

Belomicrus vanyume Pate 1940a:17. Holotype female, Victorville, San Bernardino Co., California (PHILADELPHIA), examined.

In addition to the type I have seen five males and three females, all from California counties: Riverside (Box Canyon, Thousand Palms), San Bernardino (Apple Valley, Kramer Hills, Adelanto, 11 mi w. Ludlow), Imperial (Fish Creek Mts.), Inyo

(Darwin Falls). These were all taken in April, May, and June. The previously undescribed male is much like the female but the last two terga may be dark.

Belomicrus franciscus group

The absence of an omaulus, triangular median squamal complex (Fig. 11), mandible not angled beneath toward apex, and clypeus with an apical deflected bevel or polished triangle, when taken together distinguish the group. I have identified eight species, of which three are herein described as new.

Species characters are the extent of tergal yellow markings, flagellar coloration, pronotal maculation, punctuation of the postmandibular area of males, development of the mandibular midtooth, and form of the clypeal apex. Since females may be difficult to distinguish, the following key is based on males.

KEY TO MALES OF THE *BELOMICRUS FRANCISCUS* GROUP

- | | | |
|---|--|-------------------------------|
| 1 | Ventral area of head just posterior to mandibular insertion nearly all polished, flagellum relatively short, flagellomeres hardly longer than broad (Fig. 2) | 2 |
| — | Ventral area of head just posterior to mandibular insertion distinctly but not closely punctate, flagellum various | 4 |
| 2 | Clypeal apex arched (Fig. 5), T-I usually with a subapical yellow band or spot (central California below 3,000 feet) | <i>costalis</i> R. Bohart |
| — | Clypeal apex not much, if any, arched; terga usually all red or with only a narrow streak of yellow on T-I | 3 |
| 3 | Flagellum pale yellow beneath on I-IX or X; mandible tooth on inner margin well developed (Fig. 9); punctures of interocellar area close but not contiguous, area a little shiny (central Sierra of California at 4,000 to 5,000 feet) | <i>californicus</i> R. Bohart |
| — | Flagellum orange beneath before apex; mandible tooth on inner margin small (Fig. 8), punctuation of interocellar area contiguous and dull (low elevations in California from San Luis Obispo Co. to San Diego Co.) | <i>serrano</i> Pate |
| 4 | Ground color on T-I to T-VI black, tergal markings whitish (central Sierra of California above 5,000 feet) | <i>melanus</i> R. Bohart |
| — | Ground color on T-I to T-III, at least, red; tergal markings pale yellow | 5 |
| 5 | Clypeal bevel produced downward laterally (Fig. 4), terga maculate | 6 |
| — | Clypeal bevel narrowed laterally, maculation various | 7 |
| 6 | Flagellum unusually long, mostly orange, many flagellomeres longer than broad as viewed laterally (Fig. 1); clypeal bevel often with a small median point (Fig. 4); terga often with yellow spots but rarely with complete yellow bands (desert areas from Inyo Co., California and Clark Co., Nevada south to Sonora, Mexico) | <i>quemaya</i> Pate |
| — | Flagellum rather stout, dark above (Fig. 2), flagellomeres about as broad as long in lateral view; clypeal bevel without a median denticle; terga with complete yellow banding (San Francisco) | <i>franciscus</i> Pate |
| 7 | Clypeal apex convex overall, bevel simple below, femora often extensively red (southern California) | <i>cahuilla</i> Pate |
| — | Clypeal apex more nearly flat, bevel margined below by a slight inflection, femora black with a small amount of pale yellow (central Sierra of California at 5,000-7,000 feet) | <i>mono</i> Pate |

Belomicrus cahuilla Pate

Belomicrus cahuilla Pate 1940:39. Holotype male, Andreas Canyon, Riverside Co., California (PHILADELPHIA), examined.

The male differs from that of *mono* by the simple and convex clypeal bevel. In the female the bevel is more indented than that in *mono* or *quemaya*. Both sexes have dark median areas on the terga, which may extend all across on T-III and following. Only a single female has been identified, so variation cannot be assessed. The type series of four males came from Andreas Canyon (Palm Springs). I have also seen five males from close by (Taquiz Canyon, F. D. Parker and L. A. Stange). Other southern California records are: male, female, near Cajon Junction, San Bernardino Co. (J. C. Hall, E. I. Schlinger); males, Walker Pass and West Wofford Heights, Kern Co. (J. Powell); male, 2 mi e. Banner, Riverside Co. (H. C. Dickson). Dates of capture ranged from April 16 to June 7 (males), and July 4 (female).

Belomicrus californicus R. Bohart, new species
Figs. 7, 9

Belomicrus franciscus Pate of Bohart, in Bohart and Menke 1976:363. Misidentification.

Male holotype.—length 4.5 mm. Black, whitish are: mandible mostly, scape in front, flagellum beneath except at apex, pronotal collar medially, lobe, squamal unit, tip of mucro, femora distally, tibiae outwardly, foremetatarsus dully; red are: clypeal bevel mostly, abdomen except for median dark blotches on T-III to VI; wings weakly stained. Silvery appressed pubescence along inner eye margin, stout supraclypeal spot, weak pubescence on postocular area, mesopleuron, and terga. Punctuation sparse on mostly polished postmandibular area of head venter, fine and close on dorsum of body, a little shiny on interocellar area. Clypeal bevel quite thin (Fig. 7), distinctly darkened laterally; mandibular inner tooth well developed.

Female.—Length 5 mm. Clypeal bevel slightly margined below, mandible (Fig. 9).

Holotype male (DAVIS), Baxter, Placer Co., California, elev. 5,000 ft., VI-16-56 (R. M. Bohart). Paratypes: 18 males, 21 associated females, all from the California Sierra at 4,000 to 5,000 ft. elevation during May to July, in the following

counties: Placer (Dutch Flat, Baxter, Colfax), Tuolumne (Strawberry), El Dorado (Pyramid Ranger Station and near Icehouse Road). Collectors were J. G. Rozen, J. W. MacSwain, R. M. Bohart, W. J. Pulawski, and H. M. Kimball Court. Paratypes are deposited in museums listed in acknowledgements.

This species is close to *serrano*. Both have the male postmandibular area practically impunctate, but in *californicus* the mandible tooth is well developed, and punctuation of the interocellar area is a little less dense.

J. MacSwain and I observed a large nesting area in 1956 near Pyramid Ranger Station north of Placerville, California. Females were provisioning ground nests with dasytine beetles, *Amecocerus cervicalis* Blaisdell (Melyridae).

Etymology.—the specific name indicates "of or from" California.

Belomicrus costalis R. Bohart, new species
Fig. 5

Male holotype.—Length 4.5 mm. Black marked with whitish yellow: scape and mandible mostly, flagellum beneath, pronotum all across, posttegula, squamal unit, large forefemoral spot, small distal midfemoral spot, tibiae and metatarsi outwardly, subapical band on T-I, attenuate laterad; red are: clypeal bevel, T-I to III mostly, T-IV to VI except for median dark blotches, T-VII, wings weakly stained. Silvery appressed pubescence in strip along inner eye margin, a little expanded above, supraclypeal spot, postocular area and mesopleuron moderately, terga lightly. Punctuation sparse on mostly polished postmandibular area of head venter, fine and close on dorsum of body, somewhat reflective on interocellar area. Clypeal bevel somewhat arched (Fig. 5).

Female.—Length 5 mm. Terga all red, scape pale in front only, flagellum reddish yellow beneath. Clypeal bevel flat, not margined below; mandibular inner tooth well developed.

Holotype male (DAVIS), Cache Creek Canyon, Yolo Co., California, IV-30-54 (R. M. Bohart). Paratypes (all from California at low to moderate elevations): male (DAVIS), 4 mi nw. Lake Berryessa, Napa Co., V-12-61 (F. D. Parker); 2 males (DAVIS, WASHINGTON), Sacramento, Sacramento Co., V-19-61 (R. M. Bohart); male (BERKELEY), Alpine Lake, Marin Co., VI-6-57 (J. Powell); 2 males

(DAVIS), Midlake, Lake Co., V-10-56 (E. I. Schlinger); male (BERKELEY), near Quincy, Plumas Co., VI-22-49 (J. W. MacSwain); 2 males (NEW YORK), Tuolumne City, Tuolumne Co., V-30-53 (J. G. Rozen); male (DAVIS), Boca, Nevada Co., VI-19-62 (R. M. Bohart); male (DAVIS), Kyburz Flat, Sierra Co., VII-15-76 (R. M. Bohart); male (DAVIS), Daffodill Hill, Amador Co., VI-5-63 (R. M. Bohart). Also, 6 presumed and associated females from localities listed above: Cache Creek Canyon, Boca, Daffodill Hill, Sacramento.

The band on the pronotal collar is sometimes broken in both sexes. The arched clypeal apex (Fig. 5) differentiates males from *serrano* and *californicus* which agree with *costalis* in having the postmandibular area polished. Females are best distinguished by association with males.

Etymology.—specific name derived from Latin noun, *costa* = side. The species occurs especially on the western side of California.

Belomicrus franciscus Pate

Figs. 2, 3, 11

Belomicrus franciscus Pate 1331:77. Holotype male, Lone Mountain, San Francisco, San Francisco Co., California (PHILADELPHIA), examined.

I have studied several of the type series. The rather stout male flagellum (Fig. 2), extensively yellow-banded terga, and partly punctate male postmandibular area distinguish this species. Female face (Fig. 3). The type series was collected by F. X. Williams (1936) in sandhills of San Francisco. Williams found a colony of the species in late April and early May of 1930. Females were provisioning with *Trichochrous antennatus* Mots. (Melyridae). In all probability the type locality has been taken over by a housing development.

Belomicrus melanus R. Bohart, new species

Fig. 6

Male holotype.—Length 4.5 mm. Black or brown, whitish are: scape in front, mandible mostly, flagellum beneath, pronotum medially, pronotal lobe, post-tegula, squamal unit, tip of mucro, outer distal spots on fore and midfemora, tibiae and foremetatarsus outwardly, subapical band on T-I, weak subapical bands on T-II to VI, apex of VII; dark red: clypeal bevel; wings weakly stained.

Silvery appressed pubescence in strip along inner eye margin nearly to level of midocellus, stout supra-clypeal spot, postocular area, mesopleuron moderately, terga lightly. Punctuation moderate on postmandibular area of head venter, fine and close on dorsum of body, slightly reflective on interocellar area. Clypeal bevel thin all across (Fig. 6).

Female.—Length 5 mm. Whitish bands on T-I-V sometimes better developed in paratypes, pronotum sometimes white all across, pygidial plate partly red. Postmandibular area and rest of head venter polished. Mandibular inner tooth well developed, clypeal bevel thin but impressed over its entire breadth.

Holotype male (DAVIS), Sonora Pass, Tuolumne Co., California, elev. 9,624 ft., VII-6-61 (R. M. Bohart). Paratypes (all from California Sierra at elevations above 5,000 ft.): female, same data as holotype; 3 females, Hope Valley, Alpine Co., VII, 1948, 1978 (R. M. Bohart); male, Fred's Place, El Dorado Co., VII-10-67 (R. M. Bohart); male, Gold Lake, Sierra Co., VII-8-54 (R. M. Bohart). Paratypes all in DAVIS museum.

This species belongs to the subgroup in which males have the postmandibular area somewhat punctate. It differs from other members of the subgroup by the extensively black (rather than red) ground color of the terga. In *caluilla* the terga may be partly black but the male clypeal bevel is not rimmed above, and the terga are not spotted with whitish yellow.

Etymology.—specific name derived from the Greek *melanos* = black.

Belomicrus mono Pate

Belomicrus serrano mono Pate 1940:46. Holotype female, 5 mi n Round Valley, Mono Co. California (PHILADELPHIA), examined

Belomicrus mono Pate, of Bohart and Menke 1976:363.

The male belongs to the subgroup with punctate postmandibular area on the head venter. The characters given in the key separate it. Females are best identified by association with males.

I have seen 83 males and 65 associated females from 5,000 to 7,000 feet, in the California Sierra of the following counties: Mono (Round Valley holotype), Placer (Lake Tahoe), Sierra (Yuba Pass, Sierra Valley, Independence Lake, Sattley), Nevada

(Sagehen Creek), Glenn (Plaskett Meadows). The Sagehen Creek locality is represented by a long series. Collection dates are mostly in June and July.

Belomicrus quemaya Pate

Figs. 1, 4, 10

Belomicrus quemaya Pate 1940:47. Holotype male, Palm Springs, Riverside Co., California (PHILADELPHIA), examined.

Belomicrus jurumpa Pate 1940:53. Holotype male, Gavilan, Riverside Co., California (PHILADELPHIA), examined. New synonymy.

Belomicrus franciscus quemaya Pate, of Bohart and Menke 1976:363.

The punctate postmandibular area of the head venter in the male places *quemaya* in its subgroup. The unusually long and lightly colored flagellum of both sexes and the distinctive clypeal bevel of the male (Figs. 1, 4) are distinguishing. Wings are nearly clear in both sexes. Females are best identified by association with males. *B. jurumpa* appears to be a simple synonym based on an examination of the holotypes.

I have studied 60 males and 30 associated females collected from March to May. California county records are: Riverside (Whitewater Canyon, Gavilan, Thousand Palms, 18 mi w. Blythe, Palm Springs), San Bernardino (Kramer Jct., Adelanto), Kern (Short Canyon, Iron Canyon), Imperial (Kane Springs, Fish Creek Mts., Palo Verde), Inyo (Mazourka Canyon, Lone Pine), San Diego (Borrego). Other records are Clark Co., Nevada (Searchlight, Jean), and Sonora, Mexico (9 mi e. Kino).

Belomicrus serrano Pate

Fig. 8

Belomicrus serrano serrano Pate 1940:42. Holotype male, Tujunga Wash, San Gabriel Mts., Los Angeles Co., California (PHILADELPHIA), examined.

The polished postmandibular area of the male places the species in the same subgroup as *costalis* and *californicus*. The dull interocellar area and weak mandible tooth (Fig. 8) separate *serrano*. Also, the relatively simple male clypeal bevel, and the indented one of the female are additional characters.

I have seen 46 males and 27 females in addition to the type series. The species is widespread in

southern California. The range includes low elevation localities in the following counties: Los Angeles, Riverside, San Bernardino, San Diego, Kern, Ventura, and San Luis Obispo. Collection dates are from March 27 to May 7.

Belomicrus cladothericis group

The deeply divided squamal lobes of the metanotum (Figs. 28-43), and short body length, characterize the group. With the exception of *cladothericis* Cockerell (1895), all previously known species were described by Pate (1940a, 1947). The group appears to be largely confined to western United States, only a few species occurring east of the 100th meridian or in Sonora and the Baja Californian peninsula of Mexico. Considering a small amount of synonymy and the 6 new species described herein, the total number of known species in the group is now 18. In most of these the squamal lobes are separated at the base by dark integument. In some species, however, the pale color and setal texture may be continuous basally, at least in females. These are *cladothericis*, *erigoni*, and *sechi*.

Species characters of the tiny forms in this group are squamal structure, scutal and interocellar punctation, frons breadth, clypeal bevel details, and the somewhat variable coloration. In one species, *sechi*, the unusual amount of silvery pubescence, and shape of the male scape are distinguishing.

Although little is known about the life history of these species, they are all presumably ground nesting (personal observation of *erigoni* at Antioch, California), and they are most frequently collected on the flowers of *Eriogonum*. Other flower hosts reported are *Chilopsidis*, *Lepidospartum*, *Euphorbia*, *Cladotherix*, *Cleomella*, *Rhamnus*, *Chrysothamnus*, *Solidago*, *Cercidium*, *Prosopis*, *Sphaeralcea*, *Asclepias*, *Baeria*, and *Salsola*. Because of the small size of species in the *cladothericis* group (2-4 mm long), it can be surmised that they, like many other diminutive sphecids, provision with thrips.

A great deal of descriptive matter on the group was given by Pate (1940a, b, 1947). However, he had a limited amount of material to work with and many of his new species were based on one or two specimens, often of a single sex. His remarks on geographical range must not be taken too literally. For instance, on *timberlakei* he said (1940a:93), "Known at present only from the two specimens

recorded above from Riverside, *timberlakei* will in all probability eventually be found rather widespread throughout the southern piedmont of the

Transverse Ranges district of southern California". As I have shown later in this paper, Pate's conclusion was far off the mark.

KEY TO SPECIES OF THE CLADOTHRICIS GROUP

- 1 Scutum partly polished, punctures widely spaced 2
- Scutum with rather close punctation 3
- 2 Forewing veins normally dark, squamae separated by less than 3x mucro width (Fig. 34) *mescalero* Pate
- Forewing veins practically all white, squamae separated by about 4x mucro width (Fig. 33) *pallidus* R. Bohart
- 3 Pronotum all dark including lobe 4
- Pronotum partly whitish, at least on pronotal lobe 6
- 4 Distance between squamal apices about half length of scutellum (Fig. 35), area between squamae not pointing posteriorly *timberlakei* Pate
- Distance between squamal apices at least two-thirds length of scutellum (Figs. 41, 42), area between squamae various 5
- 5 Area between squamae pointed posteriorly (Fig. 43), scutal punctures moderate and close, terga brown to black *bridwelli* Pate
- Area between squame truncate (Fig. 41), scutal punctation quite coarse, T-I or T-I-III with some red *potawatomi* Pate
- 6 Squamae relatively long and angled inward so that apices are not or hardly farther apart than width of mucro (Figs. 37, 39, 40), LID 1.3x to 1.6x length of scape 7
- Squamal apices not unusually long or angled inward, apices farther apart than width of mucro, LID various 9
- 7 Scutal punctation fine and close, not reflective, interocellar area likewise, T-I not yellow spotted or banded, LID 1.4-1.5x length of scape *pachappa* Pate
- Scutal punctation a little uneven, some punctures medium fine; surface reflective, interocellar area likewise, tergal markings and LID various 8
- 8 Scutal and interocellar punctation a little more coarse and distinct, terga without yellow markings *tuktum* Pate
- Scutal and interocellar punctation a little finer and less distinct, T-I or T-I-II often with yellow markings *istam* Pate
- 9 Abdomen black; squamae slender, crescent shaped (Fig. 22), scutal punctation medium coarse with polished interspaces of 1 PD or more; scape whitish, flagellum partly pale beneath; pronotal collar whitish all across; tibiae and tarsi whitish *vierecki* Pate
- Abdomen with some pale markings or at least with T-I usually somewhat reddish, squamae not so crescent shaped, scutal punctation with microsculptured interspaces, antenna and pronotal collar various, tibiae and tarsi various 10
- 10 Head unusually long and narrow (Figs. 21, 24), inner eye margins nearly parallel below ocelli, postocular tubercles prominent and sharp, female genal area depressed and densely silvery below (genal carina undeveloped), frontal groove extending below broadly rounded brow, hindtibia and hindmetatarsus all whitish outwardly 11
- Head not unusually long and narrow (Figs. 18, 20), inner eye margins more strongly curved, female genal area not depressed, frontal groove and leg markings various 12
- 11 Flagellum extensively pale beneath, forewing veins mostly pale, T-I to III (male) or T-I to VI (female) with prominent whitish bands, squamae somewhat curved but shorter than their interapical distance (Fig. 36) *oraibi* R. Bohart

- Flagellum dark beneath, forewing veins mostly brown, T-I-VI unbanded, squamae strongly curved within and longer than their interapical distance (Fig. 38) *longiceps* R. Bohart
12. Body with exceptional amounts of silvery pubescence (Fig. 30), interocellar area and vertex silvery setose, propodeum usually extensively red, male scape strongly swollen distally (Fig. 27) *sechi* Pate
- Body with moderate amounts of silvery pubescence, interocellar area and vertex not silvery, propodeum black, male scape not swollen 13
13. Flagellum at least partly lighter colored toward base 14
- Flagellum practically all dark 16
14. Flagellum mostly light orange with some dark spots laterally, squamae moderately stout (Fig. 32) *darwini* R. Bohart
- Flagellum somewhat lighter toward base beneath; squamae short and stout 15
15. Interocellar area, vertex, and scutum dull; terga red, at least toward base; female frons length below midocellus 1.6x LID (Fig. 22) *eriogoni* Pate
- Interocellar area, vertex, and scutum somewhat shiny; T-I or II often pale marked, female frons length below midocellus 1.9x LID (Fig. 18) *cladothricis* Cockerell
16. Frons length below midocellus 1.2-1.3x LID (Fig. 19), wing veins often mostly orange (female) or light brown (male) rather than dark brown to black *siccatus* R. Bohart
- Frons length below midocellus 1.7-1.9x LID (Fig. 20), wing veins mostly dark brown to black 17
17. Mid and hindmetatarsi brown or brownish red (Fig. 26) postocular tubercles small as seen laterally or dorsally, LID in female usually nearly equal to scape length, female scape whitish in front *inyo* R. Bohart
- Mid and hindmetatarsi white (Fig. 25), female only known, postocular tubercles large, LID a little broader, scape all whitish *cucamonga* Pate

Belomicrus bridwelli Pate
Fig. 43

Belomicrus bridwelli Pate 1940a:93. Male holotype, Clifton, Fairfax Co., Virginia (PHILADELPHIA), examined.

In addition to the holotype and four topotype paratypes, I have also studied the following: male, Branford, Suwannee Co., Florida, VII-31-30; 2 males, female, Fort Bragg, Cumberland Co., North Carolina; female, Dayton, Rhea Co., Tennessee, VI-20-54; male, 15 mi nw. Big Spring, Howard Co., Texas, VI-13-63. According to these meager records, *bridwelli* occurs east of 102° latitude in May, June, and July. Female squamae and mucro (Fig. 43).

Belomicrus cladothricis (Cockerell)
Fig. 18

Oxybelus cladothricis Cockerell 1895:309. Female lectotype, Las Cruces, New Mexico (PHILADELPHIA), examined. Lectotype designated by Cresson (1928).

Belomicrus cladothricis prosopidis Pate 1940a:72. Male holotype, Palm Springs, Riverside Co., California (PHILADELPHIA), examined.

Belomicrus minidoka Pate 1940a:79. Male holotype, Hagerman, Gooding Co. Idaho (WASHINGTON), examined.

This rather wide-ranging and relatively abundant species is represented in the DAVIS collection by 450 males and 198 females taken at 51 localities during March to October. All of the captures were made south of 41.5° longitude and west of 100° latitude. Outlying states in the range are Nebraska, Texas, Utah, Idaho, and California. Elevations were moderate to low and many were in strictly desert areas. As might be expected of such a common and widespread species, there is a considerable amount of variation. The short and rather broad squamae are a consistent feature. Also, the narrow LID of females (Fig. 18) helps identification. Many western examples have yellow spots on basal terga. Punctuation of the scutum and interocellar area is close but allows some shininess not found in several related species such as *eriogoni*. The legs are usually extensively reddish but this occurs in some other species. T-I-II are often reddish in males but II may be all dark brown as in the type of *prosopidis*, or I-II brown as in the type of *minidoka*.

Belomicrus cucamonga Pate

Fig. 25, 31

Belomicrus cucamonga Pate 1940a:76. Female holotype, Camp Baldy, San Gabriel Mts., San Bernardino Co., California (PHILADELPHIA), examined.

In addition to the holotype I have seen three females from Big Pine, Inyo Co., California, VII-10-61 (R. M. Bohart); and a female from Batchelder Springs, Inyo Co., VI-10 (H. K. Court). The more abundant whitish of the scape and tarsi (Fig. 25), as well as the larger postocular tubercles and broader frons, distinguish *cucamonga* from *inyo*. Female squamae and mucro (Fig. 31).

Belomicrus darwini R. Bohart, new species

Fig. 32

Female holotype.—Length 3 mm. Black or dark brown, white are: mandible mostly, scape in front, pronotal lobe, squama, mucro distally; reddish are: clypeal bevel, flagellum (pale orange, spotted laterally), tibia and tarsi mostly (brownish red), hindtibia lighter in basal ring, dull apical bands on T-I to III; wings clear, veins black. Silvery appressed pubescence extending upward along two-thirds of inner eye margin, short supraclypeal patch, weak on genal and mesopleural areas. Punctures of scutum and interocellar area medium fine, slightly separated by microsculpture. LID about 1.4x scape length, frontal suture relatively deep halfway from midocellus to clypeus, clypeal bevel margined and triangular, postocular tubercle small, squamae short and slightly curved (Fig. 32).

Male.—Length 2.5 mm. Scape mostly brownish, flagellum a little spotted laterally as viewed in front.

Holotype female (DAVIS), Darwin Falls, Inyo Co., California, May 17, 1970 (R. M. Bohart). Paratypes, 2 males, 2 females, same data as holotype but collected by E. E. Grissell and R. M. Bohart. Other paratypes, female (DAVIS), Wikiup, Mohave Co., Arizona, IV-11-57 (T. R. Haig); female (RIVERSIDE), Kyle Canyon, Clark Co., Nevada, V-4-41 (P. H. Timberlake); female (DAVIS), near Boron, Clark Co., Nevada, VI-7-41 (P. H. Timberlake).

As indicated in the key, the rather close punctation, moderate LID, brownish legs and terga, short squamae, light orange flagellum, and long

frontal suture characterize the species. The flagellum is a little longer and more slender than in other species.

Etymology.—named for Dr. Darwin French, who discovered Darwin Falls in 1860.

Belomicrus eriogoni Pate

Fig. 22

Belomicrus cladothricis eriogoni Pate 1940a:70. Male holotype, San Lucas, Monterey Co., California (PHILADELPHIA), examined.

Belomicrus eriogoni Pate of Bohart and Menke (1976).

I have studied 240 males and 165 females in the DAVIS collection. These were taken during May to September in California, Arizona, New Mexico, Nevada, and Utah. California records are from Mono Co., Lassen Co., Sacramento Co., and Contra Costa Co., south to the Mexican border. Mexican records are from Baja California. At times the species is abundant, especially on the flowers of *Eriogonum fasciculatum*. Female facial proportions (Fig. 22).

Belomicrus inyo R. Bohart, new species

Fig. 20, 26, 28

Female holotype.—Length 2.5 mm. Black, white are: mandible mostly, scape in front, pronotal lobe, squama, foretibia outwardly, mid and hindtibiae on basal one-third; reddish are: clypeal bevel, abdomen (more brownish on T-II to VI); wings clear, veins black. Silvery appressed pubescence is narrow along lower half of inner eye margin, supraclypeal patch conical, moderate on gena and mesopleuron. Punctures of scutum and interocellar area medium fine, slightly separated by microsculpture. LID about equal to scape length (Fig. 20); frontal suture not deep; faintly visible halfway from midocellus to clypeus; clypeal bevel triangular, postocular tubercles small; squamae curved, well separated distally (Fig. 28).

Male.—Length 2.5 mm. Hindtibia mostly orange with dirty white basal area, mid and hindmetatarsi orange or reddish brown. LID about 1.7x scape length.

Holotype female (DAVIS), Antelope Springs, Inyo Co. California, V-10-61 (R. M. Bohart). Paratypes, 2 males, 1 female (DAVIS, BERKELEY), topotypes, VI-29-61, VII-1-61, VIII-24-60, on

Solidago (P. D. Hurd, G. I. Stage).

The orange to brown metatarsi (Fig. 26), dark flagellum, narrow female LID (Fig. 20), basally banded mid and hindtibiae (Fig. 26), close and dull punctation, and well separated squamae (Fig. 28) characterize the species.

Etymology.—specific name is an acronymic noun inspired by Inyo Co., where all of the type series was collected.

***Belomicrus istam* Pate**

Fig. 37

Belomicrus istam Pate 1940a:81. Male holotype, 4.5 mi nw. Edom, Riverside Co., California (PHILADELPHIA), examined.

I have seen a total of 37 males and 62 females collected from March to June in sandy areas of 11 localities. These range in California from Sacramento to Borrego Valley, and in Nevada from Nixon to Stillwater. I collected a long series of both sexes lighting on a sandy slope in Sand Canyon, Kern Co., California, on April 14, 1962. Female squamae and mucro (Fig. 37).

***Belomicrus longiceps* R. Bohart, new species**

Figs. 24, 38

Female holotype.—Length 2 mm. Black, white are: mandible mostly, pedicel partly, pronotal lobe, post-tegula, squama, mucro, tibiae outwardly, tarsi; reddish are: clypeal bevel, abdomen; wings clear, veins brown. Silvery appressed pubescence present along lower half of eye margin, short supraclypeal patch, dense on genal area and mesopleuron. Punctation on scutum and interocellar area fine and close but a little irregular, somewhat shiny. Head unusually long and narrow (Fig. 24), inner eye margins nearly straight (Fig. 24), frontal carina distinct one-third of distance from midocellus to clypeus, LID 1.7x length of scape, clypeal bevel broader than high, postocular tubercle prominent and sharp, genal area flattened to a little concave inside row of erect hairs, squamae short but curved and well separated (Fig. 38).

Male.—length 1.8 mm. T-I-II partly black, T-III-VII black.

Holotype female (DAVIS), 6 mi nw. Adelanto, San Bernardino Co. California, V-11-79, on

Sphaeralcea (R. M. Bohart). Paratypes collected April to August, 4 males, female (DAVIS, WASHINGTON), 18 mi w. Blythe, Riverside Co., California (M. E. Irwin, F. D. Parker, R. M. Bohart, R. W. Brooks); male (DAVIS), 15 mi w. Baker, San Bernardino Co., California (N. J. Smith); female (BERKELEY), Surprise Canyon, Inyo Co., California (P. D. Hurd); male (DAVIS), Patrick, Washoe Co., Nevada (E. E. Grissell); female (NEW YORK), 2 mi n. Rodeo, Hidalgo Co., Nevada (J. G. Ehrenfeld).

Characteristic are the long head (Fig. 24), dark antenna, sharp postocular tubercles, extensively silvery female gena and mesopleuron, brown wing veins, and unbanded abdomen. The only other species with a rather long head (compare Figs. 21, 24) is the much more abundantly marked *oraibi*, which see.

***Belomicrus mescalero* Pate**

Fig. 34

Belomicrus mescalero Pate 1940a:87. Female holotype, Alamogordo, Otero Co., New Mexico (PHILADELPHIA), examined.

This species is known to occur in April and May. In addition to the three female types, one of which came from Needles, California, I have studied the following: male, female, 3 mi sw. Rodeo, Hidalgo Co., New Mexico, IV-30-65 (J. G. Rozen). The partly polished scutum, together with the dark wing veins, mostly red terga, and whitish-yellow spotted T-I are distinguishing. The male is in general agreement with the female description given by Pate, but T-VI-VII are reddish. Female squamae and mucro are shown in Fig. 34.

***Belomicrus oraibi* R. Bohart, new species**

Figs. 21, 36

Female holotype.—Length 3 mm. Black, white are: mandible mostly, scape in front, pronotal lobe, tegula, post-tegula, metanotum, mucro distally, tibiae and tarsi outwardly (a little reddish), T-I to VI mostly; reddish are: scape partly, flagellum beneath, clypeal bevel, femora distally, tibiae partly, terga basally; wings clear, most veins light orange. Silvery appressed pubescence along lower three-fourths of eye margin, short supraclypeal patch, dense on genal area and mesopleuron. Punctation fine, close and dull on scutum, a little reflec-

tive on interocellar area. Head longer than usual (Fig. 21), inner eye margins nearly straight, frontal carina distinct, LID 1.7x length of scape, clypeal bevel broader than high, postocular tubercles prominent and sharp, genal area slightly concave inside row of erect hairs; squamae short, curved, well separated (Fig. 36).

Male.—Length 2.5 mm. About as in female but T-IV-VI black. Genal area not concave.

Holotype female (DAVIS), Oraibi, Navajo Co., Arizona, VIII-30-76, on *Chrysothamnus* (R. M. Bohart). Paratype female (WASHINGTON), Dinnebito Wash, 5 mi nw. Hotevilla, Navajo Co., Arizona, VIII-31-86 (A. S. Menke); paratype male (DAVIS), 23 mi nw. Page, Kane Co., Utah, VI-22-70 (N. J. Smith); paratype male (SAN FRANCISCO), Green River, 5 mi ne. Jensen, Uinta Co., Utah, VI-26-82 (W. J. Pulawski).

Although generally similar to *longiceps*, which also has an unusually long head, *oraibi* differs by its pale wing veins and extensively white terga. The concavity of the lower gena of the female is even more pronounced. The presumed males from Utah agree with the female in punctation and wing vein color. However, they have T-IV to VI dark. The presently known range includes northern Arizona and southern Utah.

Etymology.—the name is an acronymic noun inspired by the Oraibi indians of Navajo Co., Arizona.

***Belomicrus pachappa* Pate**

Fig. 40

Belomicrus pachappa Pate 1940a:73. Female holotype, Riverside, Riverside Co., California (PHILADELPHIA), examined.

I have studied 11 males and 30 females collected from April to August at 4 localities in California: Weed, Siskiyou Co. (J. Powell); Sand Canyon, Kern Co. (R. M. Bohart); Chuchupate Ranger Station, Ventura Co. (J. Powell, P. D. Hurd); Riverside, Riverside Co. (P. H. Timberlake). Nevada records are from Washoe Co.: Wadsworth (R. M. Bohart, G. I. Stage); Patrick (R. M. Bohart). The 3 species, *pachappa*, *tuktum*, and *istam*, have the squamae elongate and nearly touching distally. The close and dull punctation of *pachappa* separates it. The female has T-I-VI red, but the male has the abdomen dark following T-I or T-II. Female squamae and mucro (Fig. 40).

***Belomicrus pallidus* R. Bohart, new species**

Fig. 23, 33

Male holotype.—Length 2 mm. Black, white are: mandible mostly, antenna mostly but dark distally in front, pronotum all across, tegula and post-tegula, wing veins, squamae and mucro, legs beyond basal two-thirds of femora; reddish are: legs basad of white markings, abdomen; wings clear. Silvery appressed pubescence on face below midocellus except for a median bare spot (Fig. 23), genal and mesopleural areas densely silver, scutum with scattered silvery setae. Punctuation fine and sparse on extensively polished mesonotum, a little less so on interocellar area. LID (just above antennal insertion) 1.4x scape length, inner eye margin weakly curved below midocellus (Fig. 23); frontal groove and clypeal bevel (if any) obscured by silvery pubescence; postocular tubercle prominent, sharp; squamae short, curved, pubescent, well separated (Fig. 33).

Female.—Unknown.

Male holotype (SAN FRANCISCO), Borrego, San Diego Co., California IV-25-54 (P. D. Hurd). Paratype male (DAVIS), Blythe, Riverside Co., California, on *Asclepias*, VII-8-56 (M. Wasbauer).

The rather extensive silvery pubescence is reminiscent of *sechi*, but there are many points of difference, one of which is the simple scape in *pallidus* male. General features characterizing *pallidus* are the considerably polished mesonotum, whitish wing veins, and red and white legs.

Etymology.—specific name based on the Latin adjective *pallidus* = pale.

***Belomicrus potawatomi* Pate**

Fig. 41

Belomicrus potawatomi Pate 1947:57. Female holotype, Sioux City, Woodbury Co., Iowa (WASHINGTON), examined.

The holotype was collected July 12, 1935 by C. N. Ainslee. The only other record of which I am aware is: female, Regnier, Cimarron Co., Oklahoma, June 9 (NEW YORK). This species is similar to *bridwelli* which also has the squamae far apart. However, the metanotum is posteriorly pointed (compare Figs. 41, 43) in *bridwelli* and its scutal punctation is less coarse.

Belomicrus sechi Pate

Figs. 27, 30

Belomicrus sechi Pate 1940a:60. Male holotype, 6 mi n. Palm Springs, Riverside Co. California (PHILADELPHIA), examined.

I have seen 17 males and five females of this extensively silvery pubescent species. They were taken from May to August in the following desert localities of southern California: Palm Springs, Magnesia Canyon, and Rancho Mirage, all Riverside Co.; 11 mi w. Ludlow, San Bernardino Co.; and Borrego Valley, San Diego Co.; a male (SAN FRANCISCO) comes from Arizona: Roper Lake State Park, Graham Co., V-26-83 (W. J. Pulawski). The male has a unique, distally swollen scape (Fig. 27). Otherwise, the female agrees with the description given by Pate. The female squamae and mucro are shown in Fig. 30.

Belomicrus siccatus R. Bohart, new species

Figs. 19, 29

Female holotype.—Length 2.5 mm. Black, white are: mandible basally, pronotal tubercle, squamae, mucro distally; light dull orange are: wing veins, tibiae and tarsi; dark red are: T-I-II, pygidium; wing membrane clear. Silvery appressed pubescence in a broad patch reaching up along two-thirds of inner eye margin, supraclypeal patch undeveloped, postocular and mesopleural patches moderate. Punctuation of scutum and interocellar area fine and a little separated, somewhat shiny. LID 2x scape length, inner eye margin gently curved (Fig. 19), postocular tubercles present but not sharp, squamae nearly straight (Fig. 29).

Holotype female (DAVIS), Thousand Palms Canyon, Riverside Co., California, IV-9-64 (R. M. Bohart). Paratypes, from Riverside Co.: 2 males (DAVIS), Whitewater, IV-17-87 (N. J. Smith); 7 males (DAVIS), SAN FRANCISCO, WASHINGTON, same data as holotype; 2 male topotypes (DAVIS), III-29-77 (R. M. Bohart, N. J. Smith); 2 male topotypes (DAVIS), III-31-63 (F. D. Parker); female topotype (DAVIS), IV-11-70 (R. M. Bohart). Also a paratype female (RIVERSIDE), Apple Valley, San Bernardino Co., California, V-20-41 (P. H. Timberlake).

The combination of unusually broad frons (Fig. 19) black flagellum, nearly straight squamae (Fig. 29) orange (female) to brownish (male) wing

veins, and orange-tinted leg markings characterize the species.

Etymology.—specific name derived from the Latin adjective *siccus* = dry.

Belomicrus timberlakei Pate

Fig. 35

Belomicrus timberlakei Pate 1940a:91. Male holotype, Riverside, Riverside Co., California (PHILADELPHIA), examined.

This species has been collected from April to September. I have studied 41 males and 11 females from California, Nevada, Utah, Arizona, and New Mexico. In California 13 localities range from Siskiyou Co. to Riverside Co., mostly in the Transition Life Zone. One record is at 8,000 ft. on Carson Pass, Alpine Co. Non-California records are: Cochise Co., Arizona (Willcox, Apache, Santa Rita Mts.); Eureka Co., Nevada (Eureka); Churchill Co. Nevada (Frenchman); Grant Co., Utah (Moab); Emery Co. Utah (Greenriver); Hidalgo Co., New Mexico (Rodeo); Baja California, Mexico (10 mi e. San Quintin).

Of the 3 species with all dark pronotum (*tiberlakei*, *potawatomi* and *bridwelli*) only *tiberlakei* has the squamae only moderately separated (Fig. 35). The female resembles the male in nearly all respects but its LID equals 2x the scape length instead of 1.7.

Belomicrus tuktum Pate

Fig. 39

Belomicrus tuktum Pate 1940a:84. Male holotype 5 mi e. Edom, Riverside Co., California (PHILADELPHIA), examined.

In addition to the holotype I have studied 24 males and 25 females collected from March to May. The 13 localities represented include the following California counties: Inyo (Darwin Falls, Little Lake, Surprise Canyon), Kern (Sand Canyon), Ventura (Quatal Canyon), Riverside (Thousand Palms, Deep Canyon, 18 mi w. Blythe, Whitewater Canyon), San Bernardino (5 mi n. Barstow), Imperial (Glamis), and San Diego (Borrego Valley). This species is quite similar to *istam*. Females have the abdomen essentially all dark red, but males usually have T-I dark red, the rest brown. Female squamae and mucro are shown in Fig. 39.

Belomicrus vierecki Pate

Fig. 42

Belomicrus vierecki Pate 1940a:56. Male holotype, Alamogordo, Otero Co., New Mexico (PHILADELPHIA), examined.

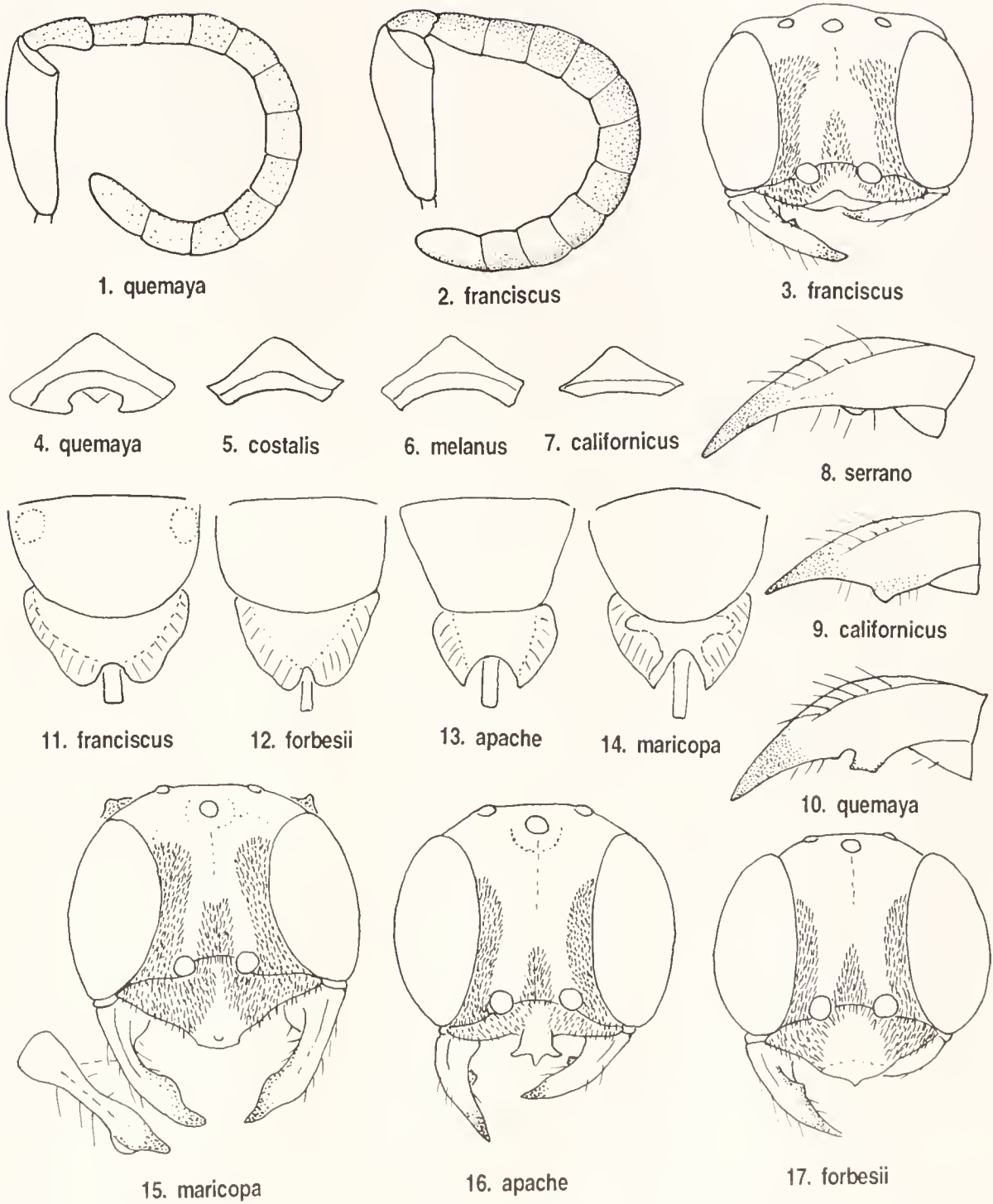
This is a relatively abundant and widespread species. I have seen 272 males and 47 females collected from March to July. I swept a long series from flowers of *Chilopsis linearis* at 15 mi w. Baker, San Bernardino Co., California in May. Other preferred hosts are *Cercidium* and *Prosopis*. The 15 localities for California are all sandy situations at

low elevations south of 38.6 longitude. Arizona records are from Wickenburg, Tucson, and Santa Rita Mts. New Mexico records are Alamogordo, Las Cruces, and near Laguna, Valencia Co. Mexican material has been seen from Sonora (Alamos), Puebla (Petlalcingo), Durango (Nombre de Dios), and Baja California Sur (La Ribera). The most eastern record in the United States is Presidio, Texas at about 104.5° latitude.

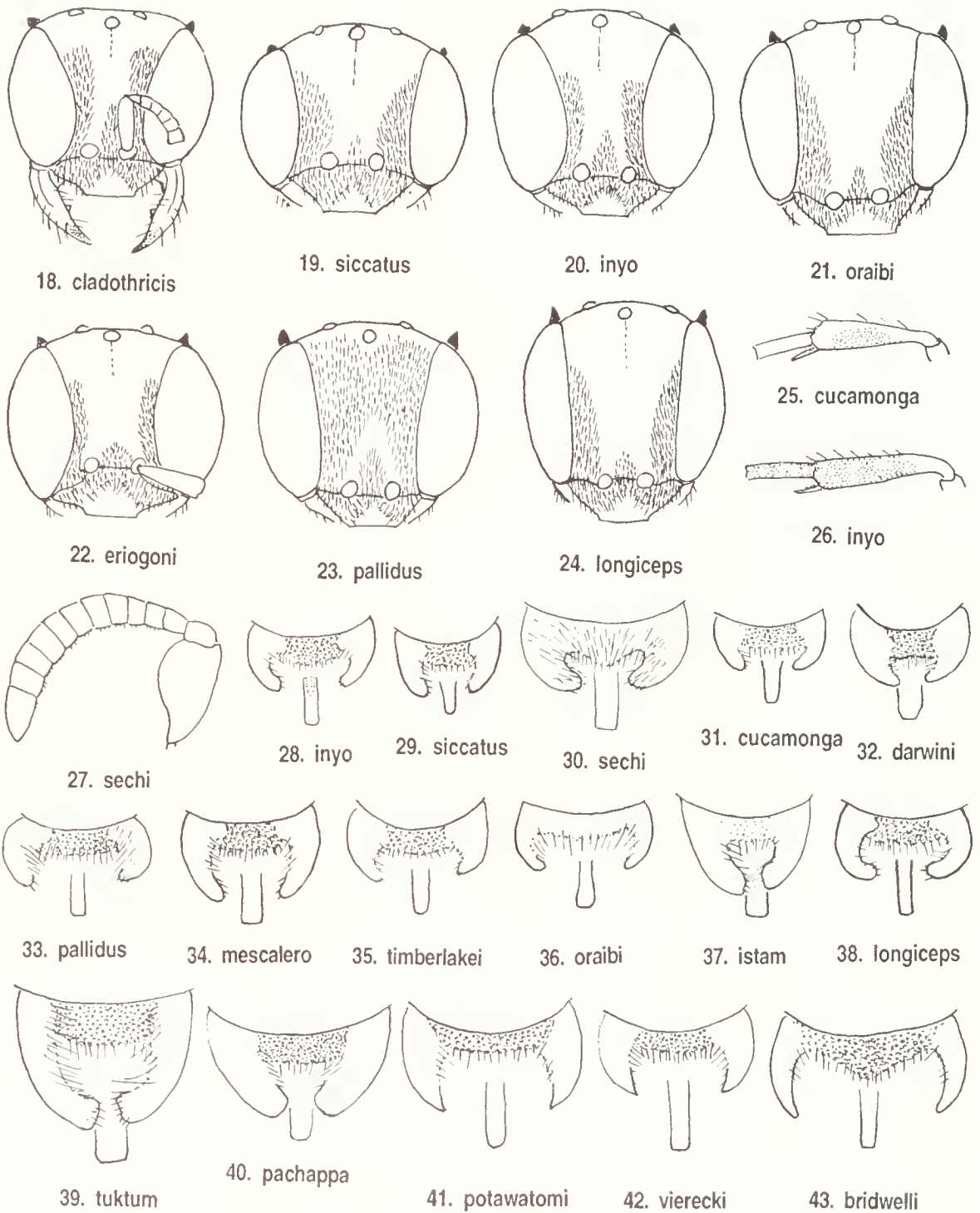
The dark brown abdomen, white tibiae and tarsi, extensively polished interocellar area, narrow LID, and well separated crescentic squamae (Fig. 42), make identification relatively simple.

REFERENCES

- Baker, C. F. 1909. Studies in Oxybelidae I. *Pomona Journal of Entomology* 1:27-30.
- Bohart, R. M. 1956. Prey captures of *Belomicrus penuti* and *B. coloratus*. In Bohart and Menke 1976: 363. Ibid
- Bohart, R. M. and A. S. Menke. 1976. *Sphexid Wasps of the World A Generic Revision* ix + 695 pp. Univ. California Press, Berkeley.
- Cockerell, T. D. A. 1895. The second *Anacrabro* and the smallest American *Oxybelus*. *Canadian Entomologist* 27: 308-309.
- Costa, A. 1871. Prospetto sistematico degli Immenotterologia Italiana. *Ann. Mus. Zool. Univ. Napoli* 6: 28-83.
- Cresson, E. T. 1928. The types of Hymenoptera in the Academy of Natural Sciences of Philadelphia other than those of Ezra T. Cresson. *Memoirs of American Entomological Society* 5: 1-90.
- Evans, H. E. 1969. Notes on the nesting behaviour of *Pisonopsis clypeata* and *Belomicrus forbesi*. *Journal of the Kansas Entomological Society* 42: 117-125.
- Kohl, F. F. 1892. Neue Hymenopterenformen. *Ann. Nat. Hist. Hofmus. Vienna* 7: 197-234.
- Pate, V. S. L. 1931. A new *Belomicrus* from the West. *Ent. News* 42: 77-78.
- Pate, V. S. L. 1940a. The taxonomy of the Oxybeline wasps I. A review of the genera *Belomicroides*, *Brimocelus* and *Belomicrus* with particular reference to the nearctic species. *Transactions of the American Entomological Society* 66: 1-99.
- Pate, V. S. L. 1940b. The taxonomy of the Oxybeline wasps II. The classification of the genera *Belomicrus* and *Enchemicrum*. *Transactions of the American Entomological Society* 66: 209-264.
- Pate, V. S. L. 1947. New North American *Belomicrus*. *Proceedings of the Entomological Society of Washington* 49: 54-57.
- Robertson, C. 1889. Synopsis of North American species of *Oxybelus*. *Transactions of the American Entomological Society* 56: 77-85.
- Rohwer, S. A. 1908. Four new Hymenoptera. *Entomological News* 19:417-420.
- Williams, F. X. 1936. Notes on two oxybelid wasps in San Francisco. *Pan-Pacific Entomologist* 12: 1-8.



Figs. 1-17. 1, 2, male antenna x100; 3, female face; 4-7, male clypeus, anterior view x100; 8-10, female mandible x75; 11-14, female scutellum, squamae, and mucro, not to scale; 15-17, female face, not to scale.



Figs. 18-24, female face $\times 50$; 25-26, female hindtibia and metatarsus $\times 50$; 27, male antenna $\times 100$; 28-43, female squamae and mucro, dorsal $\times 100$. Silvery scales on face and squamae shown as dark setal areas.

Myosomatoides Gen. Nov., (Hymenoptera: Braconidae), A Neotropical Larval Parasitoid of Stem-borer Pests, *Diatraea* (Lepidoptera: Pyralidae)

DONALD L. J. QUICKE

Department of Biology, Imperial College at Silwood Park, Ascot, Berks SL5 7PY, England

Abstract. - A new genus, *Myosomatoides* Quicke (type species: *Myosoma pennipes* Westwood 1882), from South America is described and illustrated. *Ipobracon pennipes* Myers 1931 (non Westwood), originally recorded as a parasitoid of an unspecified *Diatraea* species from British Guiana and subsequently reared from *D. angustella* Dyar, is congeneric with *Myosomatoides pennipes* (Westwood) comb. nov. and is therefore a junior subjective homonym of the former. A new name, *Myosomatoides myersi* is proposed for Myers's species and a key is provided to enable its separation from *M. pennipes* (Westwood) comb. nov.

INTRODUCTION

Diatraea, a large genus of New World pyralid moths, whose larvae bore in the stems of graminaceous plants, includes several species of considerable economic importance in both the temperate and particularly the tropical regions where they attack sugarcane, corn and sorghum (Elias 1970, Chippendale 1979, Agnew et al. 1988, Pashley et al. 1990). Several genera of parasitic wasps of the braconid subfamily Braconinae have been recorded as attacking species of *Diatraea*, viz. *Bracon* Fabricius (Muesebeck 1925, Shenefelt 1978), *Digonogastra* Viereck (Wharton et al. 1989), *Myosoma* Brullé (Quicke 1989) and *Palabracon* Quicke (Quicke 1988a). All of these are believed to be ectoparasitoids attacking relatively late instar host larvae. In addition to these, Myers (1931) described and illustrated three species of Braconinae reared from *Diatraea* spp. in British Guiana, all of which he placed in *Ipobracon* Thomson, though he recognized that one of his new species, *I. pennipes* Myers (non Westwood), was an "isolated species". *Ipobracon* was subsequently shown to be a junior synonym of *Cyanopterus* Haliday (Quicke 1985, 1987) and the limits of that genus were restricted such that the great majority of New World species described under both *Ipobracon* and *Iphiaulax* Foerster, and including the other two species described by Myers, actually belong to a distinct, though related genus,

Digonogastra Viereck (Quicke 1988b, Wharton et al. 1989). As Myers implied; however, *I. pennipes* does not belong to *Digonogastra*, and in fact, it is a member of a new genus near *Myosoma* Brullé which is described below.

By coincidence, Westwood (1882) had earlier described another species belonging to the same new genus under the name of *Myosoma pennipes*, which therefore becomes a senior, subjective homonym of *pennipes* Myers. In addition to the type specimens of *Myosomatoides pennipes* (Westwood) comb. nov. (Hope Entomological Collections, Oxford) and *M. myersi* comb. et nom. nov. (Natural History Museum, London: type no. 3^c 418) the author has seen seven other specimens belonging to the new genus from Argentina, Brazil, Colombia, British Guiana, Ecuador, Paraguay, and Peru, though none of these has any associated host data. Both *M. myersi* and *M. pennipes* appear to be widespread in South America.

Available material suggests that there are only two species of *Myosomatoides* in South America, viz. *M. pennipes* and *M. myersi* nom. nov. A key is provided to enable their separation. Some variation is apparent for both species. In particular, specimens of *M. pennipes* vary in the extent of the black coloration on the body, the wing coloration, the extent and length of setosity, the degree of compression of the hind leg, the shape of the head, the relative lengths of hindwing veins 1r-m and SC+RI, and the relative length of the ovipositor.

Because no two specimens examined were found to be entirely similar, I consider it most likely that they represent a single rather variable species rather than a diverse polyspecific complex though the latter possibility cannot be completely excluded.

Myers (1931) provided a fairly complete description of *M. myersi* (= *pennipes* Myers non Westwood), in which he illustrated the rather distinctive metasoma. Following Myers' original record, the species was recorded as a parasitoid of *Diatraea*, on several further occasions (Myers 1932, Thomson 1953) and, in particular, of *D. angustella* Dyar in Argentina (Parker et al. 1953, De Santis & Esquivel 1966). Members of the related genus *Myosoma* are similarly idiobiont ectoparasitoids of stem-boring pyralid moth larvae, including *Diatraea* and *Chilo* species (Quicke 1989, Quicke & Wharton 1989). At least one species of *Myosoma* is gregarious.

Myosomatoides is being described here to make the name available to biocontrol workers in South and Central America and for a forthcoming manual to the New World genera of Braconidae (Marsh & Wharton, in preparation).

Terminology follows that of Achterberg (1979, 1988).

MYOSOMATOIDES Quicke gen. nov.

Type species: *Myosoma pennipes* Westwood, 1882.

Diagnosis.—Superficially similar to *Myosoma* except that the 2nd metasomal tergite is strongly pinched-up in the middle to form a mid-longitudinal ridge (Fig. 4). In addition, the hind femur and tibia are extremely broad and laterally compressed and have very long, dense setosity (Fig. 3). In Quicke & Sharkey's (1989) key to the North American genera of Braconinae, *Myosomatoides* will key to *Bracon* Fabricius, from which it can be distinguished by its extremely compressed hind femur and tibia.

Description.—Head. Antenna with approximately 50 flagellomeres. Terminal flagellomere acuminate. Medial flagellomeres wider than long. Scapus small, shorter ventrally than dorsally in lateral aspect, emarginate apico-laterally, not emarginate apicomediaally. Clypeus very shallow; without a transverse carina separating reflexed ventral part from dorsal part; dorsal part punctate. Clypeus

separated from face by weak groove. Malar area weakly impressed, punctate. Face densely setose except for smooth, shiny, glabrous supraclypeal triangular area. Antennal sockets approximately level with middle of eye. Frons very weakly impressed with indistinct midlongitudinal sulcus; with moderately dense short setosity.

Mesosoma. Mesosoma smooth, shiny. Notauli indicated only by weak depressions at anterior of mesoscutum. Scutellar sulcus narrow, smooth. Propodeum simple, without carinae.

Forewing. Veins 1-M and 1-SR+M straight, vein cu-a interstitial (or virtually so), the 2nd submarginal cell rather long (i.e. vein 3-SR 0.67-0.95 times SR1), vein m-cu less than or equal to 0.5 times length of 2-SR.

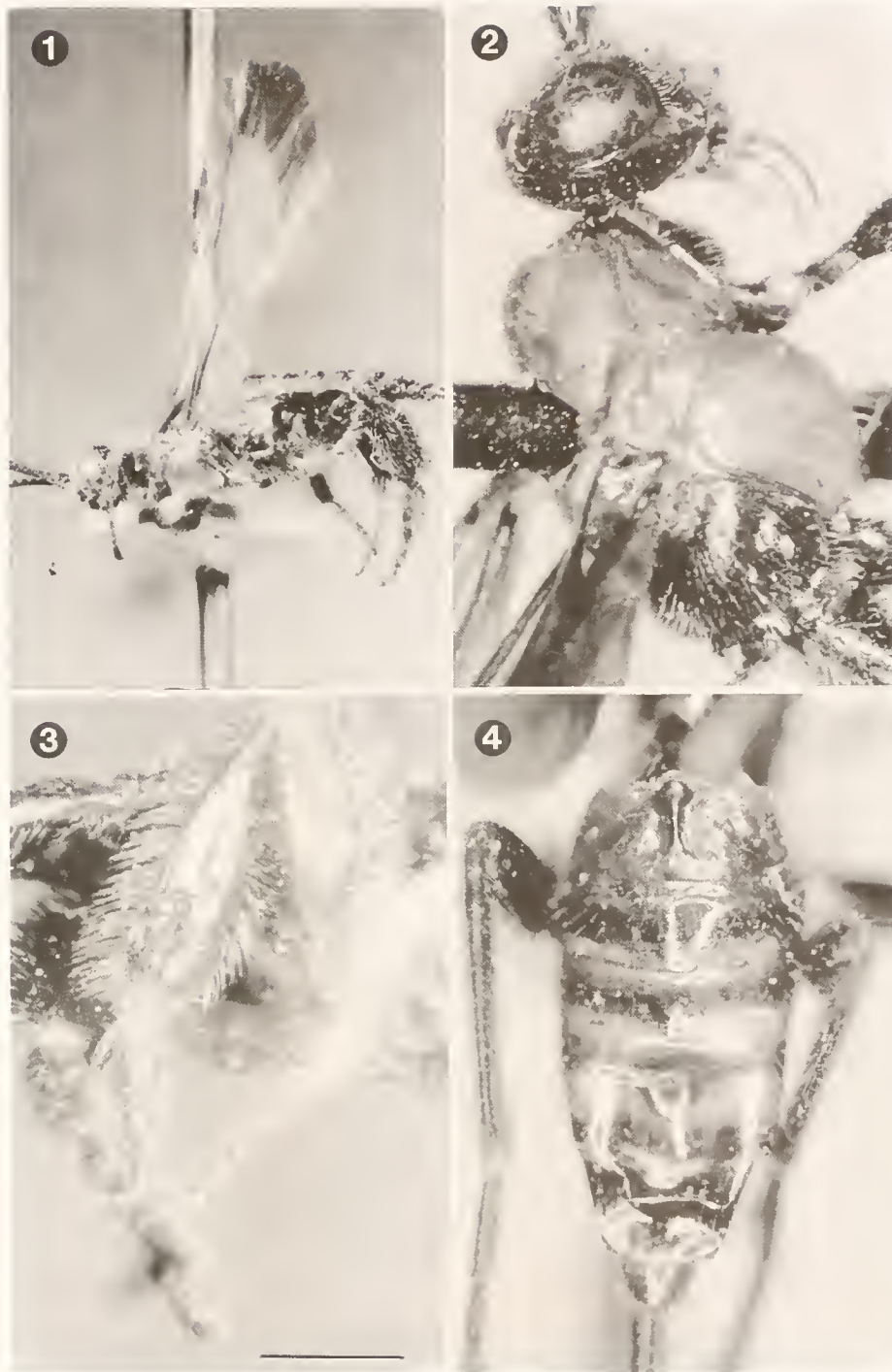
Hindwing. Vein lr-m more or less straight, slightly shorter than, to slightly longer than, vein SC+RI. Apex of vein C+SC+R with one especially thickened bristle. Base of wing evenly and densely setose. Vein 2-IA absent.

Legs. Claws with large, acutely pointed, basal lobes. Telotarsi swollen in dorsal aspect compared to basal tarsal articles. Hind leg and often mid-leg (though less so) extremely laterally compressed, tibia markedly expanded in lateral aspect (Figs. 1,2,4).

Metasoma. Smooth, shiny, sparsely setose. First metasomal tergite rather long, approximately 1.5-2.0 times longer than wide, and without carinae. Second tergite transverse, with midlongitudinal carina. Third to seventh tergites without transverse grooves subbasally or subposteriorly, without anterolateral areas, and membranous posteriorly. Hypopygium not extending beyond apex of metasoma, pointed in lateral aspect. Ovipositor (part exerted beyond apex of metasoma) approximately two-thirds length of metasoma, with a pre-apical dorsal nodus and apicoventral serrations.

Male genitalia. Digitus with two rather small, well separated apical teeth. Parameres not extending beyond base of digitus; setation restricted to a fairly narrow band at apex. Volsellae virtually glabrous. Basal ring moderately produced medioanteriorly, approximately as long as wide.

Internal anatomy. Rectum small with four circular rectal pads. Male with a pair of weak, pouch-shaped, intertergal gland reservoirs between abdominal tergites 7 and 8, and with similar but weaker intertergal glands between tergites 6



Figs 1-4. *Myosomatoides pennipes* (Westwood) gen. et comb. nov., Light photomicrographs of male from Brazil. 1. Habitus, lateral aspect. 2. Detail of hind leg. 3. Head and mesosoma lateral aspect. 4. Metasoma and hind legs, dorsal aspect. Scale lines: 1=2 mm; 2=0.6 mm; 3=0.7 mm, 4=0.8 mm.

and 7; abdominal tergum 8 without obvious glands.

Etymology.—Name based on the existing generic name *Myosoma* and the Greek suffix -oides indicating close affinity; gender masculine.

Distribution.—*M. myersi*: Argentina, Brazil, British Guiana, Colombia, Ecuador, and Paraguay; *M. pennipes*: Brazil (Amazonia) and Peru.

Biology.—*M. myersi* nom. nov. is a larval parasitoid of members of the pyralid borer genus *Diatraea*. Nothing is known of the biology of *M. pennipes* (Westwood).

KEY TO THE SPECIES OF *MYOSOMATOIDES*

- 1 Wings uniformly brown
 *M. myersi* nom. nov.
- Wings largely hyaline with the apical third of the forewing brown (Fig. 1)
 *M. pennipes* (Westwood)
-

DISCUSSION

Myosomatoides gen. nov. most closely resembles and is probably closely related to the small and widespread, but principally New World genus *Myosoma* Brullé. Individuals of both genera have the hind femur rather strongly laterally compressed and densely clothed with setae (Mason 1978): *Myosomatoides* differs from *Myosoma* in having an even more strongly laterally compressed hind femur and tibia (apomorphous) (Figs. 1, 2, 4), and in having the 2nd metasomal tergite 'pinched-up' in the middle so as to form a more or less complete midlongitudinal ridge (apomorphous) (Fig. 4). In *Myosoma*, the 2nd tergite totally lacks carinae, the 1st metasomal tergite is longer and narrower than in *Myosomatoides* (apomorphous) and has the flattened lateral areas absent or nearly so (apomorphous) (Mason 1978, Quicke & Wharton 1989), and often the anterolateral part of the 2nd metasomal tergite is only weakly sclerotized (apomorphous). *Myosomatoides* also resembles *Myosoma* in its complement of intertergal glands (Quicke 1990) and in the form of the male genitalia (Quicke 1988c), though in *Myosoma* there is only one tooth on the digitus (apomorphous). *Myosoma* and *Myosomatoides* appear therefore to be sister groups though at present the possibility that the

flattened hind tibiae and general habitus simply represent convergence cannot be totally excluded. As with *Myosomatoides*, members of the genus *Myosoma* are parasitoids of lepidopterous grass-stem borers including Pyralidae and Sesiidae (Maetô 1992).

ACKNOWLEDGMENTS

I would like to thank Tom Huddleston (The Natural History Museum, London), Paul Marsh (USNM), Chris O'Toole (Hope Entomological Collections, Oxford), L. Stange (Florida State Collection of Arthropods) and David Wahl (American Entomological Institute, Gainesville) for allowing me access to specimens in their care. This work was partly supported by the American Entomological Institute, a scientific exchange visit to Budapest funded by the Royal Society, and by a research grant jointly to DLJQ and Mike Fitton (BMNH) from the NERC.

LITERATURE CITED

- Achterberg, C. van, 1979. A revision of the subfamily Zelinae auct. (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* 122: 241-479.
- Achterberg, C. van, 1988. Revision of the subfamily Blacinae Foerster (Hymenoptera, Braconidae). *Zoologische Verhandlungen, Leiden* 249: 1-324.
- Agnew, C.W., Rodriguez-del-Bosque, L. A., Smith, J. W. Jr. 1988. Misidentification of Mexican stalkborers in the subfamily Crambinae (Lepidoptera: Pyralidae). *Folia Entomologica Mexicana* 75: 63-75.
- Chippendale, G.M. 1979. The southwestern corn borer, *Diatraea grandiosella*: case history of an invading insect. *Bulletin of the Missouri Agricultural Experiment Station*, no. 1031, 1-52.
- De Santis, L., Esquivel, L. 1966. Tercera lista de himenopteros parasiticos y predadores de los insectos de la Republica Argentina. *Revista del Museo de La Plata (Sección Zoología N.S.)* 9: 47-215.
- Elias, L.A. 1970. *Maize resistance to stalk borers in Zeadiatraea Box and Diatraea Guilding at five localities in Mexico*. 172 pp. Ph.D. dissertation, Kansas State University (Univ. Microfilms no. 70-16 627).
- Maetô, K. 1992. Japanese species of the *Myosoma* group (Hymenoptera? Braconidae). *Japanese Journal of Entomology* 60: 714.
- Mason, W. R. M. 1978. A synopsis of the Nearctic Braconini, with revisions of Nearctic species of *Coeloides* and *Myosoma* (Hymenoptera, Braconidae). *Canadian Entomologist* 110: 721-768.
- Muesebeck, C. F. W. 1925. A revision of the parasitic wasps of the genus *Microbracon* occurring in America north of Mexico. *Proceedings of the United States National Museum* 67: no. 2580: 1-85.
- Myers, J. G. 1931. Descriptions and records of parasitic Hymenoptera from British Guiana and the West Indies. *Bulletin of Entomological Research* 22: 267-277.

- Myers, J. G. 1932. Biological observations on some Neotropical parasitic Hymenoptera. *Transactions of the Royal Entomological Society of London* 80: 121-136.
- Parker, H. L., Berry P. A. Silveira Guido A. 1953. Host-parasite and parasite-host lists of insects reared in the South American Parasite Laboratory during the period 1940-1946. *Revista de la Asociacion de Ingeniera Agronomica, Montevideo*, no. 92: 1-101.
- Pashley, D. P., Hardy T., Hammond A. M., Mihm J. A. 1990. Genetic evidence for sibling species within the Sugarcane Borer (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 83: 1048-1053.
- Quicke, D. L. J. 1985. Two new genera of Braconinae (Insecta, Hymenoptera) from the Afrotropical Region. *Zoologica Scripta* 14: 117-122.
- Quicke, D.L.J. 1987. The Old World genera of braconine wasps (Hymenoptera: Braconidae). *Journal of Natural History* 21: 43-157.
- Quicke, D. L. J. 1988a. A new genus and species of Braconinae (Hymenoptera: Braconidae) parasitic on *Diatraea* (Lepidoptera: Pyralidae) in Ecuador. *Bulletin of Entomological Research* 78: 15-18.
- Quicke, D. L. J. 1988b. *Digonogastra*: the correct name for Nearctic *Iphiaulax* of Authors. *Proceedings of the Entomological Society of Washington* 90: 196-200.
- Quicke, D. L. J. 1988c. Inter-generic variation in the male genitalia of the Braconinae (Insecta, Hymenoptera, Braconidae). *Zoologica Scripta* 17: 399-409.
- Quicke, D. L. J. 1989. Further new host records for genera and species of Braconinae (Hym., Braconidae). *Entomologist's Monthly Magazine* 125: 199-205.
- Quicke, D. L. J. 1990. Tergal and inter-tergal metasomal glands of male braconine wasps (Insecta, Hymenoptera, Braconidae). *Zoologica Scripta* 19: 413-423.
- Quicke, D. L. J. Sharkey M. J. 1989. A key to and notes on the genera of Braconinae Hymenoptera: Braconidae) from America north of Mexico with descriptions of two new genera and three new species. *Canadian Entomologist* 121: 337-361.
- Quicke, D. L. J., Wharton R. A. 1989. *Myosoma nyanzaensis* sp.n. (Hymenoptera: Braconidae) parasitic on the stem-borer pest *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in Kenya. *Bulletin of Entomological Research* 79: 1-5.
- Shenefelt, R. D. 1978. *Hymenopterorum Catalogus* (nov. ed.). Part 15. Braconidae, vol. 10. The Hague, Junk, pp. 1425-1865.
- Thomson, W. R. 1953. *A catalogue of the parasites and predators of insect pests*. Section 2, host parasite catalogue. Part 2, hosts of the Hymenoptera (Agaonidae to Braconidae). Commonwealth Institute of Biological Control, Ottawa, 190 pp.
- Westwood, J. O. 1882. Descriptions of new or imperfectly known -Ichneumonones adsciti. *Tijdschrift voor Entomologie* 25: 17-48.
- Wharton, R.A., Smith J. W. Jr, Quicke D. L. J., Browning H. W. 1989. Two new species of *Digonogastra* Viereck (Hymenoptera: Braconidae) parasitic on Neotropical pyralid borers (Lepidoptera) in maize, sorghum and sugarcane. *Bulletin of Entomological Research* 79: 401 -410.
-

**Immature Stages of *Aganaspis pelleranoi* (Brèthes)
(Hymenoptera: Cynipoidea: Eucoilidae),
a Parasitoid of *Ceratitis capitata* (Wied.)
and *Anastrepha* Spp. (Diptera: Tephritidae).**

SERGIO M. OVRUSKI

Centro de Investigaciones para la Regulación de Poblaciones de Organismos Nocivos (CIRPON), Pasaje Caseros 1050,
C.C.C. 90, S. M. de Tucumán (4.000), Argentina.

Abstract.—The embryological-larval development of *Aganaspis pelleranoi* (Brèthes), a larval parasitoid of *Ceratitis capitata* (Wied.) and *Anastrepha* spp. is described and illustrated. *A. pelleranoi* possesses a stalked egg, eucoiliform first- and second-instar larvae, and hymenopteriform third- and fourth-instar larvae, followed by a prepupal and pupal stage. The duration of each stage at 25-26°C was as follows: egg, 3-4 days; first-, second-, and third-instar larvae, 2-3 days each; fourth-instar larva, 3-4 days; prepupa, 1-2 days; pupa, 9-14 days.

Aganaspis pelleranoi (Brèthes) is a parasitoid of *Ceratitis capitata* (Wied.) and several *Anastrepha* species (Diptera: Tephritidae) in Argentina (De Santis 1965), that attacks the final larval instar of these fruit flies (Turica and Mallo 1961). *Aganaspis pelleranoi* has also been reported from Lonchaea spp. (Diptera: Lonchaeidae) in Brazil (De Santis 1980).

From 1941 to 1945, *A. pelleranoi* was released as a control agent of fruit flies in Tucumán province, Argentina (Nasca 1973). In 1942 this species was introduced and reared in Perú for the control of *A. fraterculus* (Wied.) (Clausen 1978).

Ovruski (in press) carried out studies on host detection behaviour in this fruit fly parasitoid. Otherwise little is known of the biology of *A. pelleranoi*, and descriptions of the immature stages of this species have not been published. In fact very little at all is published on the development of eucoilid parasitoids of fruit flies, except that Clausen et al. (1965) briefly described the immature stages of *A. daci* (Weld) (= *Trybliographa daci* Weld), a parasitoid of *Dacus dorsalis* Hendel, the oriental fruit fly.

In this paper, studies on the life cycle and pre-imaginal development of *A. pelleranoi* are presented.

MATERIALS AND METHODS

Aganaspis pelleranoi was reared on last instar larvae of *C. capitata* in the laboratory as described by Ovruski (in press). The host larvae were reared on carrot/corn meal/yeast medium as described by Nasca (1977).

The life cycle and immature stages of *A. pelleranoi* were studied by exposing 20 to 30 *C. capitata* larvae to individual parasitoid females. The rearings and experimentation were conducted at 25-26°C, 70-80% RH, and 12:12 LD photoperiod. Host larvae and host puparia were removed at intervals of 24 h after parasitism and dissected in Insect Ringer's solution on depression slides. The parasitoid larvae were removed from each host puparium and preserved in 70% ethanol for later examination by light microscopy. Eight fourth-instar larvae were refixed in 4% glutaraldehyde and 0.2 M phosphate buffer, and dehydrated in 35-50-70-90-100% ethanol. Thereafter they were placed in 100% acetone. These specimens were critical point dried before examination by scanning electron microscopy (SEM). Descriptions are based on several specimens. Thirty-four eggs in different stages of development were mounted on slides and examined by light microscopy. Six first-, five

second-, and five third-instar larvae were mounted and examined by light microscopy. Eight fourth-instar larvae were observed with SEM and fifteen fourth-instar larvae were examined by light microscopy. Six females of *A. pelleranoi* of different ages were dissected in Insect Ringer's solution to observe the ovarian mature eggs. The terms used for morphological structure follow Kopelman and Chabora (1984) and Evans (1987). The drawings were made with a camera lucida. Data are presented as range and/or mean. Specimens, in ethanol and mounted, are deposited in the Miguel Lillo Institute Foundation, S. M. de Tucumán Argentina.

LIFE CYCLE

Females of *A. pelleranoi* deposited a single egg in the body cavity of the host larva and one parasitoid adult emerged from each host puparium.

Under laboratory conditions, the period from oviposition in the host larva to the emergence of a parasitoid adult varied from 25 to 27 days in males and from 26 to 30 days in females. Thus, males tended to emerge somewhat earlier than females. The egg stage inside the host larva lasted about 3-4 days. Observations of the postembryological development showed the presence of four larval instars. The first, second, and third instar each lasted about 2-3 days and the fourth instar 3-4 days (9-13 days in total). The prepupal stage lasted 1-2 days, and the pupal stage from 9 to 14 days.

EMBRYOLOGICAL DEVELOPMENT

The newly laid egg is 0.32 mm–0.56 mm long and 0.06 mm - 0.10 mm wide; the stalk is 0.42 mm - 0.73 mm long and the embryo is not yet distinguishable (Fig. 1).

24 h after oviposition inside the host larva, the parasitoid egg is 0.26 mm–0.48 mm long and 0.08 mm - 0.15 mm wide. The stalk is reduced in length, and the embryo, vitelline membrane and the chorion are well discernible (Fig. 2).

By 48 h after oviposition, the egg has lengthened and swelled (0.52 mm–0.66 mm long and 0.24 mm - 0.26 mm wide), and the stalk has decreased still more (Fig. 3). The embryo shows signs of body segmentation, a caudal portion and thoracic appendages.

After 72 h the parasitoid larva is completely

formed. The stalk disappears (Fig. 4) and the size of the egg is similar to the 48 h old egg. Eclosion of the first-instar larva occurs after 78-80 h. The chorion is broken through anteriorly by the mandibles and posteriorly by movements of the tail (Fig. 5).

LARVAL DEVELOPMENT

After hatching, the first-instar larva actively feeds on the internal tissues of the host. For this purpose, the mandibles are protruded from the oral cavity, although it was not possible to verify their use in feeding by direct observation. During this stage, the tail becomes less prominent and the head wider.

The second-instar larva appears on the fifth to sixth day after oviposition, when the host puparium is formed. The larva continues to feed inside the host pupa.

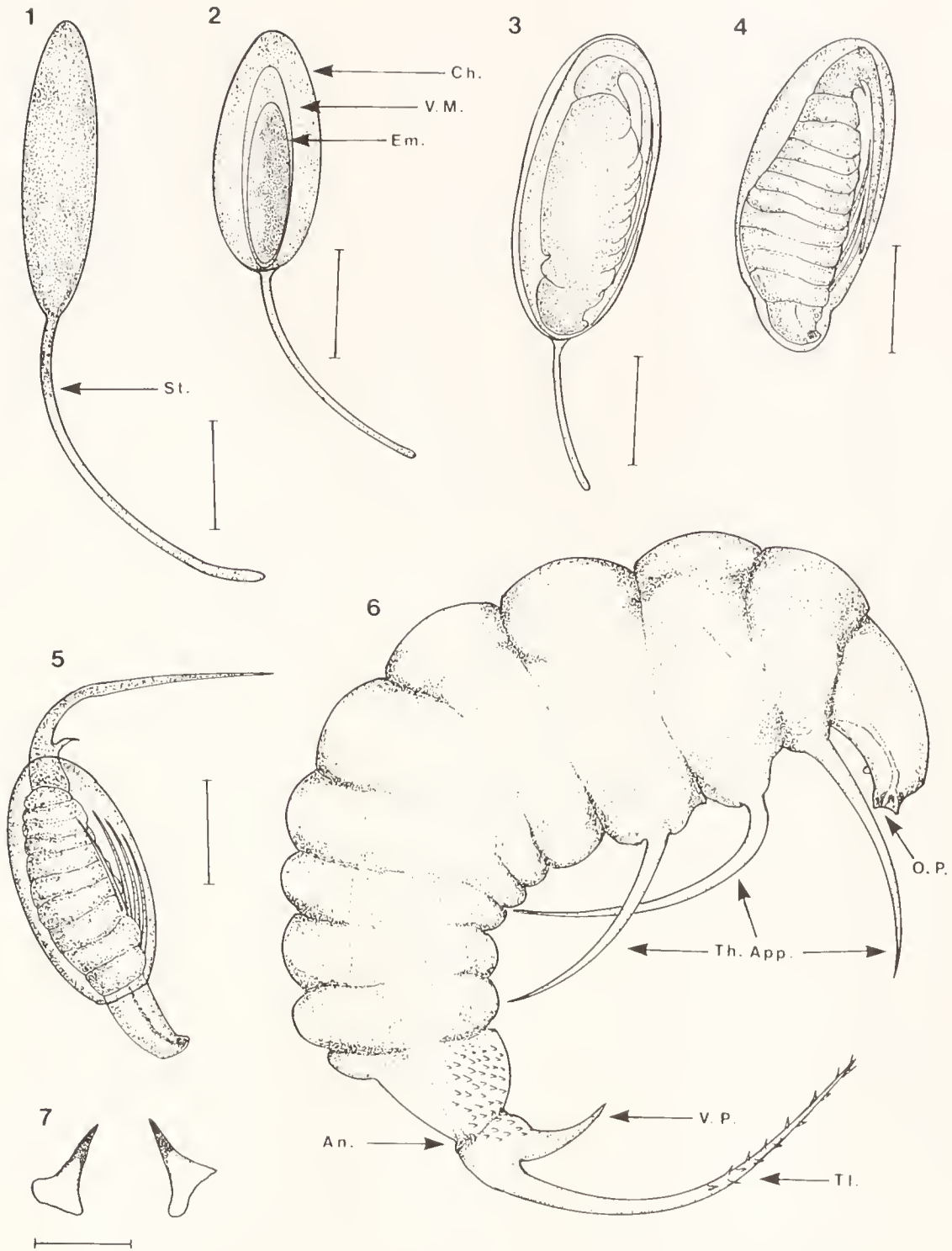
The third-instar larva appears on the eighth to ninth day after oviposition. In this stage the parasitoid larva partially emerges from the host pupa near the middle region, and it then feeds externally within the host puparium. The parasitoid larva occupies both internal and external positions in the host pupa and develops two respiratory mechanisms: cuticular respiration through submerged posterior parts of the body and tracheal respiration through prothoracic spiracles.

In the fourth-instar larva, which appears on approximately the tenth day after oviposition, feeding continues externally on what remains of the host pupa. The parasitoid larva is very sluggish and occupies 3/4 of the host puparium. After feeding is completed, the meconium is released. It appears as a dark crust in the posterior apex of the puparium (Fig. 14).

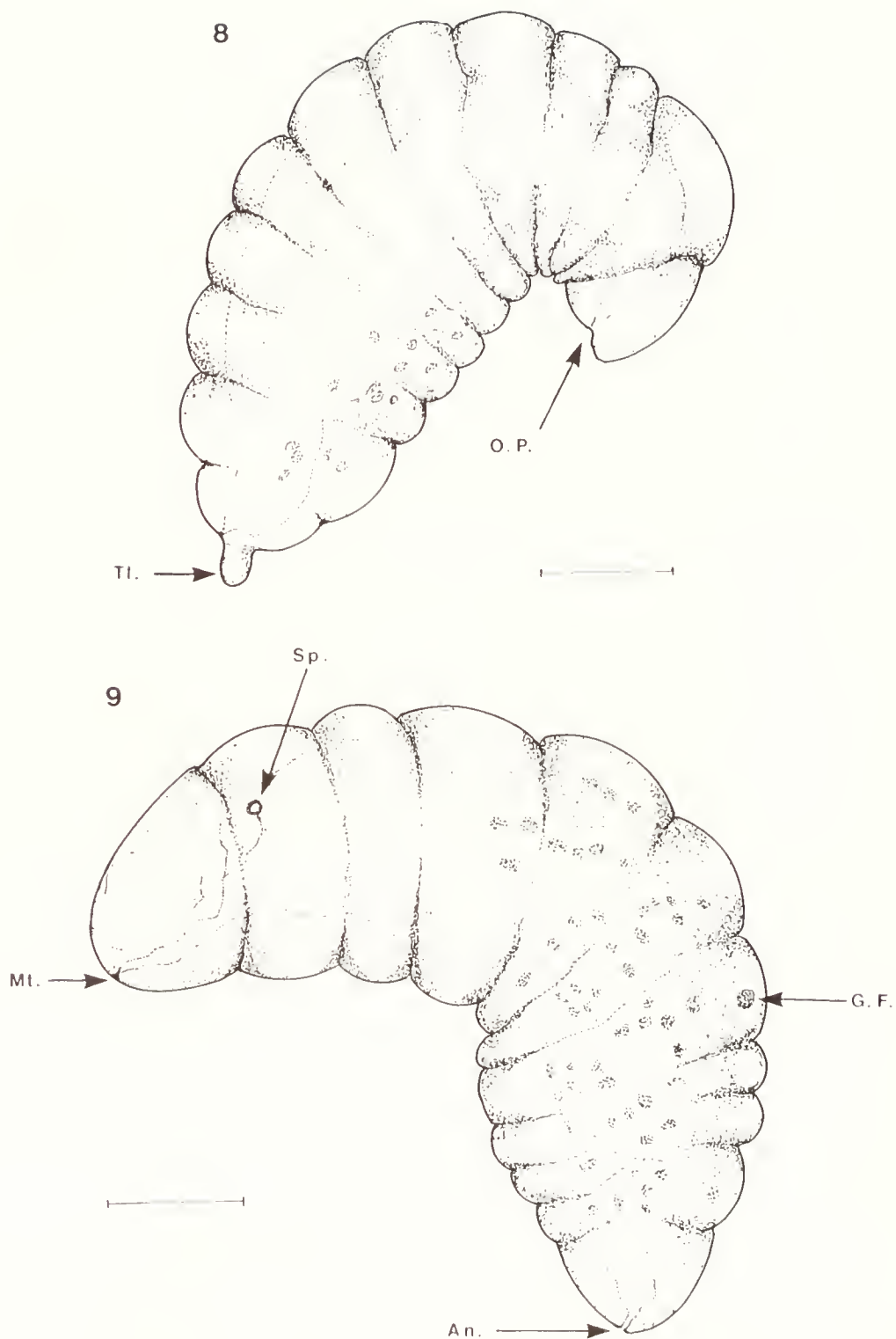
DESCRIPTIONS OF IMMATURE STAGES

Mature ovarian egg.— (Fig. 1.) Stalked; total length on average 0.60 mm; stalk 1.2 X longer than egg body, the latter portion 3.5 X longer than wide; chorion translucent and smooth.

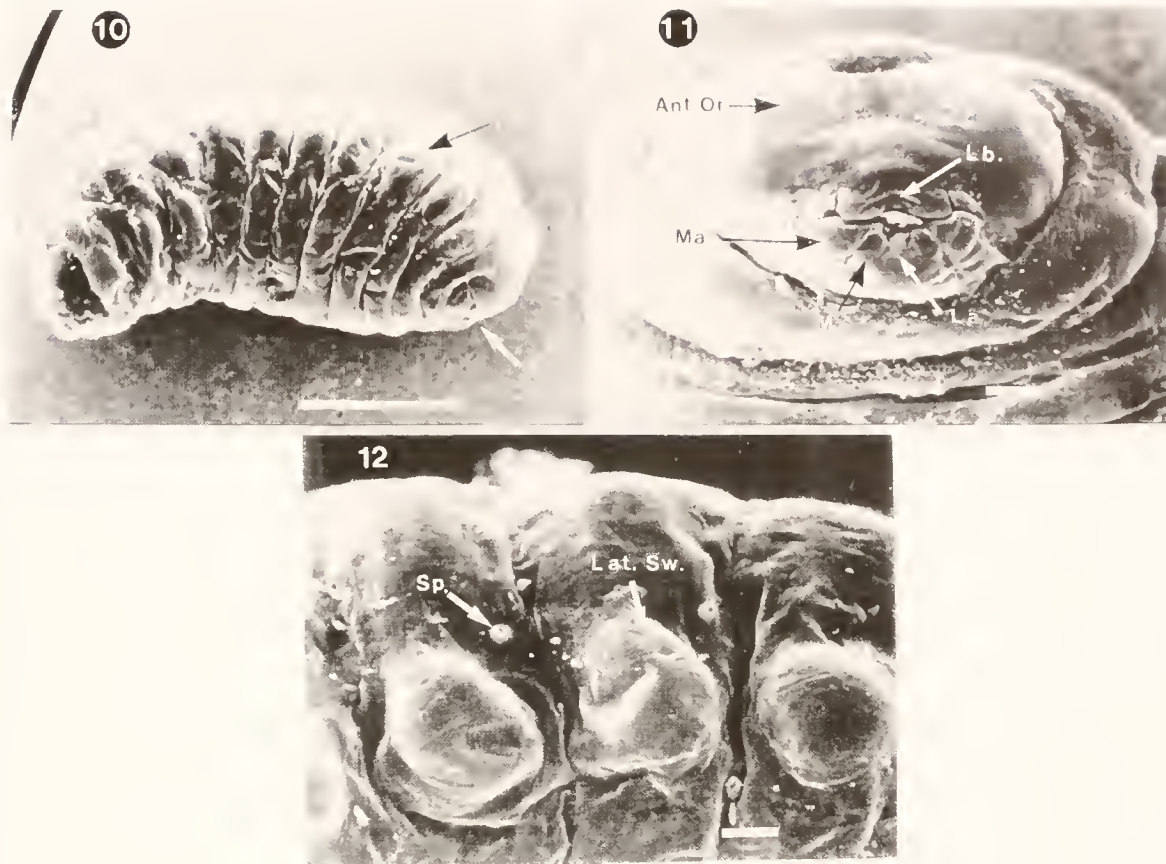
First-instar larva.— (Fig. 6, 7). Length 0.93 mm - 1.39 mm; 2.2 X longer than wide; eucoiliform; translucent; subcylindrical in shape with elongate distinct head; mouth surrounded by several oral papillae, inside with a pair of unidentate



Figs. 1-7. *Aganaspis pelleranoi*. 1, ovarian egg. *st.*, stalk. Scale bar = 0,12 mm. 2, egg at 24 h. after oviposition. *ch.*, chorion; *V.M.*, vitelline membrane; *Em.*, embryo. Scale bar = 0,12 mm. 3, egg at 48 h. after oviposition. Scale bar = 0,12 mm. 4, egg at 72 h. after oviposition. Scale bar = 0,12 mm. 5, egg at 80 h. after oviposition. Scale bar = 0,12 mm. 6, first-instar larva. *O.P.*, oral papillae; *Th. App.*, thoracic appendages; *V.P.*, ventral process; *Tl.*, tail; *An.*, anus. Scale bar = 0,12 mm. 7, mandibles of first-instar larva. Scale bar = 0,02 mm.



Figs. 8-9. *Aganaspis pelleranoi*. 8, second-instar larva. O.P., oral papillae; Tl., tail. Scale bar = 0,25 mm. 9, third-instar larva. Sp., spiracle; Mt., mouth; G.F., globular fat; An., anus. Scale bar = 0,32 mm.



Figs. 10-12. *Aganaspis pelleranoi*. 10, fourth-instar larva. *Lat. Sw.*, lateral swelling; *An.*, anus. Scale bar = 1,0 mm. 11, anterior view of head, fourth-instar larva. *Ant. Or.*, antennal orbit; *Ma.*, mandible; *Mx.*, maxilla; *La.*, labium; *Lb.*, labrum. Scale bar = 0,10 mm. 12, lateral view of body segment 6-8, fourth-instar larva. *Sp.*, spiracle; *Lat. Sw.*, lateral swelling. Scale bar = 0,10 mm.

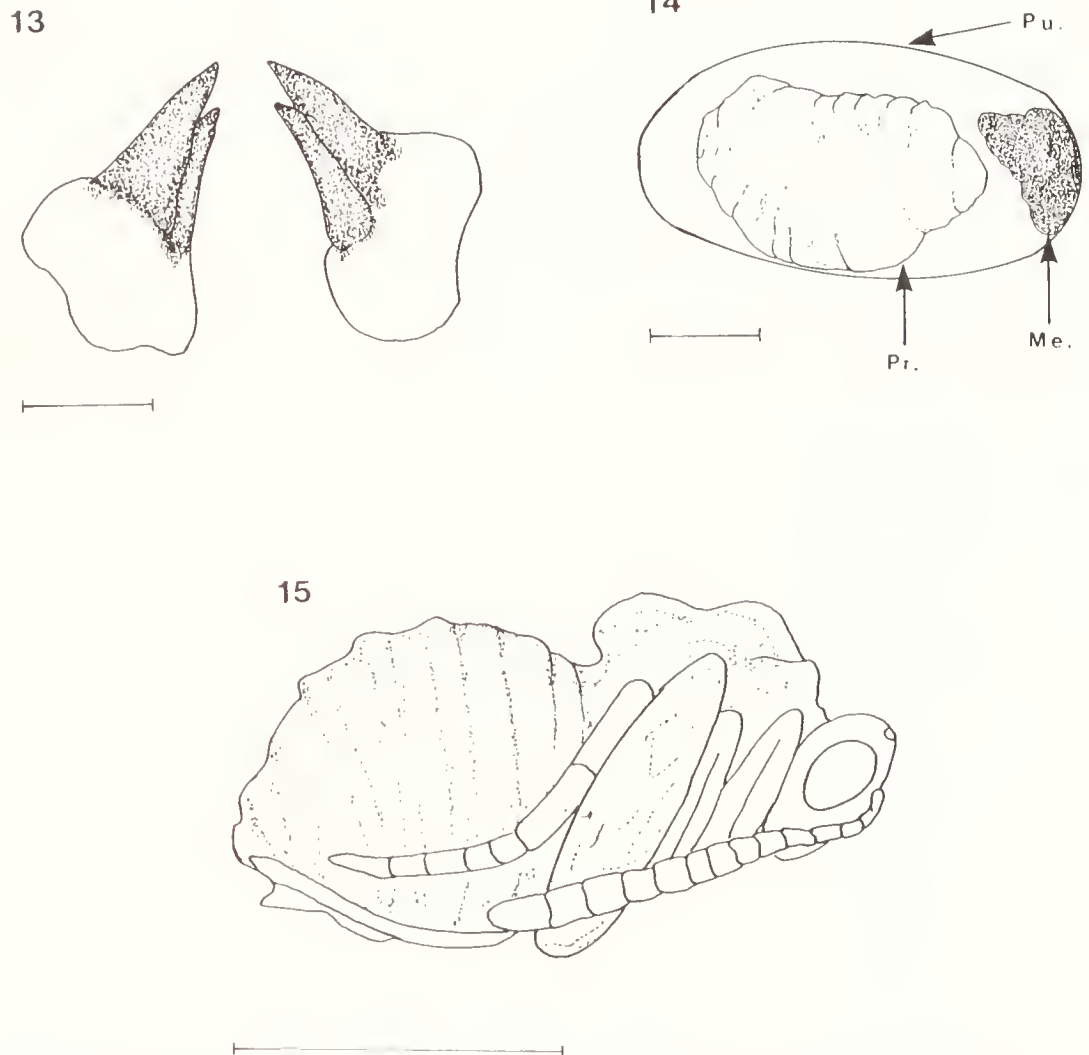
subtriangular mandibles (Fig. 7); ventral surface of head with a prominent tubular projection; gut easily discernible; each thoracic segment with a pair of long slender ventral appendages; seven well-defined abdominal segments; caudal segment with a long tail and short ventral process; tail bearing several small setae apically; ventral margin of 7th abdominal segment and basal end of caudal segment with scalelike ornamentation; tail 6 X longer than ventral process; anus opening dorsally.

Second-instar larva.—(Fig. 8). Length 1.53 mm - 2.31 mm; 2 X longer than wide; modified eucoiliform; whitish yellow with some white globular fat particles; cylindrical in shape with short and fleshy head; mouth with external oral papillae; unidentate mandibles; gut well discernible; without thoracic appendages; caudal seg-

ment with very short tail and without ventral process; anus opening dorsally.

Third-instar larva.—Fig. 9. Length 2.78 mm–3.45 mm; 3 X longer than wide; more typically hymenopteriform; yellowish with several white globular fat particles in thorax and abdomen; cylindrical in shape with slender posterior portion; broad head; small unidentate mandibles, difficult to discern; prothoracic segment with a single pair of spiracles; ten distinguishable body segments; brain and gut easily discernible; without tail and ventral process; anus opening ventrally.

Fourth-instar larva.—Figs. 10, 11, 12, 13). Length 3.48 mm–4.13 mm; 2 X longer than wide; hymenopteriform; whitish yellow with many small white globular fat particles dispersed throughout dorsolateral parts of thorax and abdomen; head



Figs. 13-15. *Aganaspis pelleranoi*. 13, mandibles of fourth-instar larva. Scale bar = 0,04 mm. 14, prepupa inside the host puparium. Pu., puparium; Pr., prepupa; Me., meconium. Scale bar = 1,0 mm. 15, pupa. Scale bar = 1,6 mm.

relatively large, subcircular in front view, without setae; antennal orbits large; prominent bidentate mandibles, 1.2 X broader than long basally, very dark apically (figs. 11 and 13); labrum 3.2X broader than long, with rounded lateral sides and median depression on apical margin; maxillae circular in shape and joined to labium; body very swollen; only eleven body segments discernible; except prothoracic and terminal abdominal segment, all segments with a pair of spiracles; each body segment provided with lateral voluminous swellings behind spiracles (Fig. 12); integument smooth and without setae; anus opening ventrally.

Prepupa.— (Fig. 14). Length 2.55 mm - 2.98 mm; width 1.18 mm - 1.56 mm; similar to fourth-

instar larva; body curved and reduced in size; occupying 2/3 of the host puparium.

Pupa.— (Fig. 15). Length 2.68 mm - 2.99 mm, initially white, later becoming dark; antennae 1,7 mm - 2.1 mm in length, extending to first abdominal segment.

DISCUSSION

Aganaspis pelleranoi produces a stalked egg, typical of the Eucoilidae. The transition from endoparasitic to ectoparasitic life has also been reported for other species of Eucoilidae (Jenni 1951; Wishart and Monteith 1954; Sychevskaya 1974; Kopelman and Chabora 1984). The embryological

and larval development is similar to other eucoilid parasitoids: *Trybliographa rapae* (Westwood) (James 1928; Wishart and Monteith 1954); *Hexacola* sp. (Simmonds 1952); *Hexacola* sp. near *Websteri* (Crawford) (Eskafi and Legner 1974); *Leptopilina boulandi* (Barbotin et al.) (Kopelman and Chabora 1984); *Eucoila trichopsila* (Hartig) (Sychevskaya 1974) and *Kleidotoma japonica* Huz. (Huzimatu 1940).

Clausen et al. (1965) reported three larval instars in *A. daci*. This study proves the presence of four larval instars in *A. pelleranoi*. The first-, second-, and fourth-instar larvae described here are similar to the first-, second-, and supposed third-instar larvae of *A. daci* respectively. The third-instar larvae of *A. pelleranoi* is a transition between the eucoiliform type and the hymenopteriform type. This stage is distinguished by a single pair of open spiracles, in the prothoracic segment, as in the supposed third stage of *T. rapae* (Wishart and Monteith 1954), the supposed fourth stage of *E. trichopsila* (Sychevskaya 1974) and the supposed fourth stage of *L. boulandi* (Kopelman and Chabora 1984). Further comparative work would be needed to confirm these apparent differences between species, as intermediate instars of apocritan larvae are notoriously easy to overlook.

Furthermore Clausen et al. (1965) stated that the first-instar larva of *A. daci* does not possess discernible mandibles, but the first-instar larvae of *A. pelleranoi* has a pair of well developed unidentate mandibles with their ends projecting from the oral cavity, similar to the first-instar larvae of *E. trichopsila* (Sychevskaya 1974).

Prominent bidentate mandibles in last instar larvae have also been reported for *A. daci* (Clausen et al. 1965), *Trybliographa Förster* and *Hexacola Förster* (Evans 1987).

ACKNOWLEDGMENTS

I am especially grateful to Dr. Patricio Fidalgo (CIRPON, Argentina), Dr. Abraham Willink (CONICET-UNT, Argentina), and Dr. Göran Nordlander (Swedish University of Agricultural Sciences, Uppsala, Sweden) for suggestions and critical reviews of the manuscript.

LITERATURE CITED

- Clausen, C. P. 1978. Tephritidae, pp. 320-334. In Clausen, C. P., ed. Introduced Parasites and Predators of arthropod pests and weeds: a World Review. *U.S. Agriculture Hand Book*, N° 480. 545 pp.
- Clausen, C. P., D. W. Clancy and Q. C. Chock. 1965. Biological control of the oriental fruit fly (*Dacus dorsalis* Hendel) and the other fruit flies in Hawaii. *Technical Bulletin United States Department of Agriculture*, N° 1322. 102 pp.
- De Santis, L. 1965. Nota sobre un parásito de la mosca sudamericana de la fruta (Hymenoptera: Cynipidae). *Revista de la Sociedad Entomológica Argentina* 27 (1-4): 73-74.
- De Santis, L. 1980. Catálogo de los himenópteros brasileños de la Serie Parasítica, incluyendo Bethyloidea. *Universidad Federal do Paraná, Curitiba*. 395 pp.
- Eskafi, F. M. and E. F. Legner. 1974. Descriptions of immature stages of the cynipid *Hexacola* sp. near *Websteri* (Eucoilinae: Hymenoptera), a larval-pupal parasite of *Hippelates* eye gnats (Diptera: Chloropidae). *The Canadian Entomologist* 106: 1043-1048.
- Evans, H. E. 1987. Cynipoidea, gall wasp and others, pp. 665-66. In Stehr, F. W., ed. *Immature insects*. Kendall Hunt, Dubuque, Iowa. 754 pp.
- Huzimatu, K. 1940. The life history of a new cynipid fly, *Kleidotoma japonica*, n. sp. *Science Report, Toboku Imperial University, Sendai* 15: 457-480.
- James, H. C. 1928. On the life histories and economic status of certain parasites of dipterous larvae, with descriptions of some new larval forms. *Annals of Applied Biology* 15: 287-316.
- Jenni, W. 1951. Beitrag zur Morphologie und Biologie der Cynipide *Pseudeucoila bochei* Weld, eines larvenparasiten von *Drosophila melanogaster* Meig. *Acta Zoologica* 32: 177-254.
- Kopelman, A. H. and P. C. Chabora. 1984. Immature stages of *Leptopilina boulandi* (Hymenoptera: Eucoilidae), a protylean parasite of *Drosophila* spp. (Diptera: Drosophilidae). *Annals of the Entomological Society of America* 77(3): 264-269.
- Nasca, J. A. 1973. Parásitos de "moscas de los frutos" establecidos en algunas zonas de Tucumán. *Revista Agrícola del Noroeste Argentino* 10 (1-2): 31-43.
- Nasca, J. A. 1977. Estudios relacionados con las posibilidades del Control Integrado de las moscas de las frutas. *Universidad Nacional de Tucumán, Informe CAFPTA*, N° 529. 61 pp.
- Ovruski, S. M. In press. Comportamiento en la detección del huésped en *Aganaspis pelleranoi* (Brèthes) (Hymenoptera: Cynipoidea, Eucoilidae) parasitoide de larvas de *Ceratitis capitata* (Wied) (Diptera: Tephritidae). *Revista de la Sociedad Entomológica Argentina* 53.
- Simmonds, F. J. 1952. Parasites of the frit-fly, *Oscinella frit* (L.), in eastern North America. *Bulletin Entomological Research* 43: 503-542.
- Sychevskaya, V. L. 1974. The biology of *Eucoila trichopsila* Hartig (Hymenoptera, Cynipoidea), a parasite of the larvae of synanthropic flies of the family Sarcophagidae (Diptera). *Entomological Review* 53: 36-44.
- Turica, A. and R. G. Mallo. 1961. Observaciones sobre la población de las "Tephritidae" y sus endoparasitoides en algunas regiones citricolas argentinas. *IDIA* 6: 145-161.
- Wishart, G. and E. Monteith. 1954. *Trybliographa rapae* (Westw.) (Hymenoptera: Cynipidae), a parasite of *Hylemya* spp. (Diptera: Anthomyiidae). *The Canadian Entomologist* 86: 145-154.

Phylogenetic Implications of the Mesofurca and Mesopostnotum in Hymenoptera

JOHN M. HERATY, JAMES B. WOOLLEY AND D. CHRISTOPHER DARLING

(JM) Biological Resources division, CLBRR, Agriculture Canada, C.E.F., Ottawa, Ontario, Canada K1A 0C6
(present address: Department of Entomology, University of California, Riverside, California, USA 92521);
(JBW) Department of Entomology, Texas A&M University, College Station, Texas, USA 77843;
(DCD) Department of Entomology, Royal Ontario Museum, Toronto, Ontario, Canada M5S 2C6

Abstract.—The skeleto-musculature of the mesofurca and the mesopostnotum is examined in Hymenoptera. Character systems based on internal structure of the mesothorax support recent hypotheses that suggest sawflies are paraphyletic with respect to Apocrita. Unique character states for Hymenoptera include the presence of two mesofurcal-laterophragmal muscles, a mesofurcal-third basalare muscle, and a scutellar-metanotal muscle. Other possible apomorphies include the medial emargination of the mesopostnotum and the formation of anterior furcal arms. The arrangement of mesofurcal muscles that attach to the profurca and the laterophragma are described and interpreted in light of recent phylogenetic hypotheses. Changes in attachment sites, fusion or loss of the anterior arms of the mesofurca and features of the laterophragma provide characters that are consistent with the monophyly of Tenthredinoidea + (Cephoidea + (Siricoidea (including Anaxyelidae) + (Xiphidriidae + Orussoidea + Apocrita))). Groundplan states for the Apocrita are proposed that include retention of a mesofurcal bridge, retention of an anterior process on the bridge that supports the interfurcal muscles, reduction of the mesofurcal-laterophragmal muscles from two to one, retention of the mesotergal-laterophragmal muscle, loss of the mesofurcal-third basalare muscle, and loss of the metafurcal-spina muscle. Within Apocrita the distribution of character state changes is less informative than in Symphyta, but provide evidence for relationships of some taxa. The mesofurcal bridge is lost convergently in Ceraphronoidea, Pelecinidae, Platygastroidea, Mymarommatoidea, Mymaridae and some Chalcidoidea. The tergal-laterophragmal muscle and associated posterior lobe of the laterophragma are postulated to have been lost independently in nine lineages of Apocrita. The development of the laterophragma into an axillary lever is a synapomorphy for Vespoidea and Apoidea, and in Apiformes the lever is an independent sclerite. The distribution of states for 12 characters is discussed for 62 families of Hymenoptera. Parsimony analysis of these data result in trees that generally agree with the current hypotheses for Symphyta but not for Apocrita.

INTRODUCTION

"Students of these [hymenopteran] parasites discover that the thorax presents valuable characters for the determination and classification of species, but they are handicapped by the lack of reliable studies on the structure of the thorax"

Snodgrass, 1910 p. 37

Since Snodgrass (1910) first attempted to expand our knowledge of the structure of the hymenopteran thorax, additional studies have described the skeleto-musculature of single species or single families (Weber 1925, 1927, Tulloch 1935, Maki 1938, Duncan 1939, Michener 1944, Bucher 1948, Alam 1951, Saini et al. 1982, Daly 1964, Gibson 1986, 1993). Fewer studies have compared thoracic structures among families of Hymenoptera (Snodgrass 1942, Daly 1963, Rasnitsyn

1969, 1980, Matsuda 1970, Shcherbakov 1980, 1981, Gibson 1985, Johnson 1988, Whitfield et al. 1989). The determination of homologous structures and polarity of characters in Hymenoptera are crucial for understanding phylogenetic relationships, a topic recently addressed by various authors (Rasnitsyn 1969, 1980, 1988, Brothers 1975, Königsmann 1977, 1978a 1978b, Carpenter 1986, Brothers and Carpenter 1993).

The mesofurca is an invagination of the sternum into the thorax that forms a central point of attachment for the ventral longitudinal muscles, the sterno-pleural muscles, the coxal and trochantal muscles, and the mesopostnotal muscles (Kelsey 1957, Matsuda 1970). The mesofurca is comprised of a basal plate (discriminal lamella) that rises vertically from the discrimen, slopes posteriorly to the furcal base, and divides dorsally

into two lateral arms, termed the sternal apophyses (Snodgrass 1927, Chapman 1992, Lawrence et al. 1992). The mesopostnotum is one of the primary dorsal sclerites involved in flight through the posterior inflection of the antecosta (second phragma) which forms the posterior attachment of the longitudinal flight muscles. Recent studies involving skeleto-musculature of the hymenopteran thorax have focused on the pleural attachments (Shcherbakov 1980, 1981, Gibson 1985, 1993), the extrinsic musculature of the mesocoxa (Johnson 1988), and the development of the metapostnotum (Whitfield et al. 1992). Rasnitsyn (1969, figs. 187-194) was the first person to compare the different skeletal structures for the mesofurca of 8 families of Symphyta. His illustrations show the transformation series for Symphyta that are discussed in this paper. Rasnitsyn (1988) refers to the furca for features supporting Tenthredinoidea and for Cephioidea + Siricoidea + Apocrita. Similarly, Snodgrass (1942) presented a pictorial evolutionary history for development of the axillary lever of Apoidea. This work expands upon these initial studies and extends the comparative aspects of these works to include most families of Apocrita.

This study of the mesofurca and mesopostnotum began as an attempt to understand the polarity and homology of mesofurcal structures and muscles of Aphelinidae (Chalcidoidea) and the phylogenetic implications of these attributes within the Chalcidoidea. Eventually the entire Hymenoptera needed to be surveyed to resolve what we initially thought were relatively simple questions. In this study, all muscles attaching to the mesofurca and mesopostnotum are identified and compared to homologous muscle groups in Neuropterida and Mecopterida (*sensu* Kristensen 1992), as they are considered to be phylogenetically close to Hymenoptera (Kristensen 1992), and have a mesothorax which is structured similar to the Symphyta. Within Hymenoptera, we have concentrated our analysis on the skeletal structure of the mesofurca and mesopostnotum, and on the muscles attaching between the thoracic furcae and the laterophragma of the mesopostnotum. The evidence provided by the mesofurca and mesopostnotum for relationships within the Chalcidoidea will be discussed in a subsequent paper.

MATERIALS AND METHODS

Terms for structures and muscles generally follow Snodgrass (1910, 1942), Daly (1963), Gibson (1985, 1986, 1993) and Ronquist and Nordlander (1989). Muscles were identified using the systems proposed by Kelsey (1957) and Daly (1963) (Table 1). Figures 1 and 2 are used to place the skeleto-musculature within the context of the mesosoma. Muscles and structures are extensively labeled in Figs. 3 and 4. The Kelsey system uses a fixed set of numbers and is useful for comparisons across the Endopterygota. Daly's system is preferred for clarity because the insertion-origin of attachment sites are readily identified and new muscles can be added to the system; for example, the new muscle fu_2-ba_3 was given the abbreviation $fb1$ for the Kelsey system as it could not be assigned a numeric value that would signify its relative position to other muscles in the mesothorax. Terms proposed by Matsuda (1970) are comprehensive and may be referenced across orders of insects; however his abbreviated system is difficult to use and is not followed here.

Several new classifications of families within Hymenoptera have been proposed recently that differ largely in placement of certain families as separate superfamilies, families, or subfamilies. We follow the classification of Huber and Goulet (1993), as it represents the most current synthesis of information across the order.

Dissections were based on specimens preserved in 70% ethanol or initially fixed in Dietrich's or Kahle's solution and then transferred to ethanol. All specimens were critical point-dried prior to dissection. The mesosoma of *Monomachus* (Monomachidae) was rehydrated using Barber's solution, transferred through increasing concentrations of ethanol to 98% and then critical point-dried. For each dissection, the mesosoma was anchored onto a standard SEM stub using chloroform-based silver paint. Dissections were made using hooked minuten pins or fragments of razor blades. Dried haemolymph and extraneous tissues were removed from dissections using small amounts of glue obtained by dragging a hooked minuten pin across clear sticky tape (Gibson 1985).

Exemplar taxa were chosen to represent the maximum variation within taxa. In some groups (e.g. Apoidea), there was virtually no variation; whereas within some taxa (e.g. Diapriidae) both

structure and presence of muscles varied and more genera were dissected to characterize this variation. Our primary concern was for establishing groundplan states for higher taxa, although autapomorphies are discussed. The taxa examined for internal characters are listed in Table 2. Numerous Chalcidoidea were also dissected as part of a comprehensive study of the mesofurca in that superfamily. Representative dissections are housed at the Canadian National Collection (CNCI), Royal Ontario Museum (ROM) and Texas A&M University (TAMU). When possible, conspecific adults of the dissected specimens are deposited as voucher specimens in the above collections. The majority of specimens were obtained from the CNCI alcohol collection.

The mesofurcal-mesopostnotal complex was broken up into 12 characters with a total of 36 character states. Seventy hymenopteran taxa were scored (Appendix 2) based on the examination of internal characters for 119 species (Table 2). A single outgroup taxon was scored based on dissections of 5 families of Neuropterida and 3 families of Mecopterida. Characters 1, 3 and 9 are postulated as unique characters for Hymenoptera; in each of these cases, the outgroup is coded as a unique character state (state 0). The state value "?" was used to denote uncertain homology, not missing data.

Illustrations were made with a camera lucida. Outlines of muscles present but not illustrated are represented by dashed lines. Some muscles not central to this study were not consistently figured (e.g. muscle 180 for Symphyta) and caution should be exercised in deriving additional interpretation from the illustrations. Abbreviations referring to muscles are circled in all figures, skeletal characters are not. The mesofurcal-mesopostnotal complex is abbreviated as MF-MPN complex.

RESULTS AND DISCUSSION

Character Analysis

Character 1. Mesofurcal bridge

The most significant modification of the mesofurca in Hymenoptera is the fusion of the elongate anterior arms (af) into a mesofurcal bridge (fb) that characterizes virtually all Apocrita. In basal groups of Symphyta (excluding Cephoida

+ remaining Hymenoptera), the anterior furcal arms are either absent, short, or elongate and well separated along their entire length. The anterior arms, or the equivalent region on the lateral arms of the mesofurca, form the posterior attachment sites for the ventral intersegmental muscles (muscle 124, fu_2 - fu_1 , and muscle 127, fu_2 - sps_1). With fusion of the anterior arms, the furca separates the gastric and nervous systems and the ventral nerve cord passes through the foramen bounded by the mesofurcal bridge and the lateral arms of the mesofurca.

In most Neuropterida and Mecopterida, the interfurcal muscles attach directly to the anterior face of the lateral arms of the mesofurca (state 0, no arms) (Snodgrass 1927, Kelsey 1957, Matsuda 1970). In Xyelidae (Fig. 3) and Pamphiliidae (Fig. 6) (and probably Megalodontidae, cf. fig. 187, Rasnitsyn 1969), the interfurcal muscles attach to anterior projections (af, anterior furcal arms) that are long, robust, and separated along their entire length (state 1). Of the outgroup taxa examined, only *Brachynemurus* (Myrmeleontidae) have anterior arms (state 1) similar to Xyelidae, and thus their presence could be plesiomorphic or apomorphic for Hymenoptera. Because anterior arms are present only in a derived member of the outgroup, we consider the presence of long anterior arms in Xyeloidea and Megalodontoida to be apomorphic for Hymenoptera.

In Tenthredinoidea, the anterior arms (af) can be reduced in size (Cimbicidae Fig. 8, Blasticotomidae Fig. 20, and *Nematus* (Tenthredinidae) Fig. 21), modified into supporting cup-like structures (Diprionidae, Fig. 7), or lost entirely so that the interfurcal muscles attach to the anterior face of the lateral furcal arms (Argidae, Pergidae Fig. 5, and most Tenthredinidae). Rasnitsyn (1988) treated "fore arm short" as a character state (his 2-3d) supporting Tenthredinoidea and "fore arm reduced" (his 6-8a) for Argidae + Pergidae. Short arms, as in Blasticotomidae (Fig. 20), are probably plesiomorphic for Tenthredinoidea, and further modifications of the arms or complete loss are derived within Tenthredinidae. It is possible to code for several different character states within Tenthredinoidea (small, absent, cup-shaped, etc.), but this would only introduce unnecessary homoplasy into the analysis (i.e. "absence" derived 2 or more times) or a series of autapomorphic char-

Table 1. Homology and terms for muscles of the mesopostnotum and mesofurca examined in Neuroptera and Hymenoptera. Letter m added to distinguish metathoracic muscles. Muscle fb1 described in text.

Kelsey 1957— <i>Corydalus</i>		Hymenoptera				Notes
No	Name	Matsuda 1970	Daly 1964	Johnson 1988	Present designation	
Mesothoracic dorsal indirect muscles						
112	internal [ventral] longitudinal	t14	1ph-2ph	-	1ph-2ph	longitudinal flight muscle. Kelsey (1957) recognized both ventral (internal, 112) and dorsal (external, 113) muscles. Recognition of the two muscles in Hymenoptera is unnecessary.
112m	metathoracic longitudinal	t14	2ph-3ph	-	2ph-3ph	reduced and attached laterally in most Hymenoptera
114	scutellar-metanotal	t13	t ₂ -t ₃	-	t ₂ -t ₃	in Hymenoptera, paired medial muscles passing from metanotum (t ₁) to scutellum over mesopostnotum (PN ₂), external in some sawflies. From PN ₂ in Neuroptera.
116	second dorsal diagonal	t12	t ₂ -2ph	-	t ₂ -pn ₂	dorsomedial attachment on mesoscutum to anterior face of laterophragma (pn ₂), attachment to dorsal axillar surface where transscutal articulation present.
Mesothoracic ventral muscles						
124	mesothoracic interfurcal	s13	fu ₂ -fu ₁	-	fu ₂ -fu ₁	from lateral face of fu ₁ to anterior face or arms of fu ₂ . Kelsey (1957) treats as three muscles (124-126) and Matsuda (1970) as bundles of the same muscle. Hymenoptera have maximum of two bundles and homology of each is uncertain.
127	mesofurcal-spina	s14	fu ₂ -1sps	-	fu ₂ -sps ₁	spina of profurca to apex of lateral arm of fu ₂ .
181	metathoracic interfurcal	s13	fu ₃ -fu ₂	-	fu ₃ -fu ₂	posterior face of lateral arms of fu ₂ to fu ₃ . Kelsey (1957) treats as three muscles (181-183). Hymenoptera have maximum of two.
180	metafurcal-spina	s14	-	-	fu ₃ -sps ₂	spina of mesofurca to apex of lateral arm of fu ₃ .
Tergopleural muscles						
137	laterophragmal-basalare	t-p8?	-	-	t ₃ -ba ₃	posterior face of laterophragma (=t ₃) to apodeme of basalare (ba ₃). Synonymy with t-p8 is questionable.
Furcal muscles						
150a	posterior furcal-laterophragmal	t-s1	fu ₂ -2ph	-	fu ₂ -pn _{2a}	posterior attachment on lateral arm of fu ₂ to anterior process of laterophragma (ap).
150b	anterior furcal-laterophragmal	t-s1	-	-	fu ₂ -pn _{2p}	attachment anterior to 150a on anterior or lateral arm of fu ₂ to posterior lobe of laterophragma (pn ₂).
151	furcal-pleural arm	p-s1	pl ₂ -fu ₂	-	pl ₂ -fu _{2a}	lateral surface of fu ₂ to pleural ridge.
170	coxal articulation-furcal	s-cx2	-	-	pl ₂ -fu _{2b}	lateral surface of fu ₂ to coxal process on pleuron.
fb1	furcal-basalare	p-s3?	fu ₂ -pl ₃ ?	-	fu ₂ -ba ₃	apex of lateral arm of fu ₂ to basalare (ba ₃); may be homologous with pupal muscle of <i>Apis</i> (Daly 1964); well developed with dorsal cap and apodeme in <i>Diprion</i> (one preparation where ba ₃ dissected with fu ₂ -ba ₃ and pl ₃ -ba ₃ both attached). Possibly homologous with Matsuda's p-s3 from furca to anterior margin of succeeding episternum.
Walking and indirect flight muscles						
169	anterior furcal-coxal	s-cx6	fu ₂ -cx _{2a}	fu-cx _a	fu ₂ -cx _{2a}	anterior base of fu ₂ to median rim of coxa.
173	posterior furcal-coxal	s-cx3	fu ₂ -cx _{2b/c}	fu-cx _p	fu ₂ -cx _{2p}	attachment on fu ₂ posterior to muscle 169 to posteromesal rim of coxa.
174	furcal depressor of trochanter	s-tr1	fu ₂ -tr ₂	-	fu ₂ -tr ₂	anterior base of fu ₂ (or arms) to trochanteral apodeme.

Table 2. Taxa dissected for study of the mesofurcal-mesopostnotal complex.

Section: NEUROPTERIDA		Trigonalynoidea	
Mantispidae	<i>Mantispa</i> sp.	Trigonalynidae	<i>Orthogonalys pulchella</i> (Cresson)
Chrysopidae	<i>Chrysopa</i> sp.		
Corydalidae	<i>Corydalus</i> sp.	Ceraphronoidea	
Myrmeleontidae	<i>Brachynemurus</i> sp.	Megaspilidae	<i>Megaspilus fuscipennis</i> (Ashmead), <i>Trichostereis</i> sp.
Rhaphidiidae	<i>Rhaphidia</i> sp.	Ceraphronidae	<i>Ceraphron</i> sp.
Section: MECOPTERIDA		Evanoidea	
Bittacidae	<i>Bittacus</i> sp.	Aulacidae	<i>Pristaulacus strangaliae</i> (Rohwer)
Meropeidae	<i>Merope tuber</i> Newman	Evaniidae	<i>Hyptia thoracica</i> (Blanchard), <i>Evania</i> sp.
Panorpidae	<i>Panorpa</i> sp.	Gasteruptionidae	<i>Gasteruption</i> sp.
Order: HYMENOPTERA		Ichneumonoidea	
SYMPHYTA		Braconidae	Alysiinae: <i>Coelinius</i> sp.; Hybrizontinae: <i>Hybrizon</i> sp.; Macrocentrinae: <i>Macrocentrus</i> sp.; Miscogasterinae: <i>Apanteles</i> sp.; Rogadinae: genus ?.
Xyeloidea		Ichneumonidae	Ephialtinae: genus ?, <i>Scambus</i> sp., <i>Megarhyssa</i> sp.; Ophioninae: <i>Enicospilus</i> sp.
Xyelidae	Macroxyelinae: <i>Macroxyela ferruginea</i> (Say); Xyelinae: <i>Pleuroneura</i> sp., <i>Xyela</i> <i>minor</i> Norton	Chrysoidea	
Megalodontoidea		Plumariidae	<i>Plumaria</i> sp.
Pamphiliidae	Cephalciinae: <i>Acantholyda</i> sp., Pamphiliinae: <i>Pamphilius</i> sp.	Sclerogibbidae	<i>Probethylus</i> sp.
Tenthredinoidea		Embolemidae	<i>Embolemus nearcticus</i> (Brues)
Blasticotomidae	<i>Blasticotoma</i> sp.	Dryinidae	Anteoninae (female), Gonatopodinae (male)
Tenthredinidae	Heteranthinae: <i>Profenusa canadensis</i> (Marlatt); Nematinae: <i>Nematus</i> sp.; Selandriinae: <i>Aneugmenus flavipes</i> (Norton), <i>Strongylogaster tacita</i> (Norton); Tenthredininae: <i>Filacus</i> sp., <i>Macrophya</i> sp.	Bethylidae	<i>Aniscypris</i> sp., <i>Epyris</i> sp.
Diprionidae	Diprioninae: <i>Diprion similis</i> (Hartig)	Chrysididae	Amiseginae: <i>Adelpho anisomorphae</i> Krombein; Chrysidinae: <i>Chrysis</i> sp., <i>Parnope</i> sp.; Cleptinae: <i>Cleptes</i> sp.
Cimbicidae	Cimbicinae: <i>Cimbex americana</i> Leach; Ambiinae: <i>Zaraea americana</i> Cresson	Vespoidea	
Pergidae	Acordulecerinae: <i>Acordulecera</i> sp., Syzygoninae: <i>Lagideus ?mexicana</i> Smith	Tiphidae	<i>Myzinum</i> sp.
Argidae	Arginae: <i>Arge</i> sp., <i>Durgoa matogrossensis</i> Mal.	Sapygidae	<i>Sapyga</i> sp.
Cephoidea		Mutillidae	Sphaerophthalminae (males, 3 genera)
Cephidae	<i>Cephus cinctus</i> Norton, <i>Hartigia trimaculata</i> (Say)	Sierolomorphidae	<i>Sierolomorpha canadensis</i> Provancher
Siricoidea		Pompilidae	Pepsinae: <i>Calicurgus hyalinatus</i> Fabr.; Pompilinae: <i>Aporinella galapagensis</i> Rohwer, <i>Aporus</i> sp.
Anaxyelidae	<i>Syntexis libocedrii</i> Rohwer	Rhopalosomatidae	<i>Rhopalosoma</i> sp.
Siricidae	Siricinae: <i>Urocerus albicornis</i> (Fabricius); Tremicinae: <i>Tremex columba</i> (Linnaeus)	Bradynobaenidae	<i>Bradynobaenus</i> sp.
Xiphidrioidea		Formicidae	Myrmicinae: <i>Solenopsis invicta</i> Buren (queen & worker); Formicinae: <i>Camponotus planus</i> F. Smith (queen), <i>Paratrechina</i> sp. (queen)
Xiphidriidae	<i>Xiphidria abdominalis</i> Say	Scoliidae	<i>Scolia</i> sp.
Orussoidea		Vespidae	Eumeninae: <i>Odynerus</i> sp., <i>Parancistrocerus</i> sp.; Vespinae: <i>Dolichovespula</i> sp., <i>Vespula</i> sp.
Orussidae	<i>Orussus terminalis</i> Newman	Apoidea	
APOCRITA		Crabronidae	<i>Ectemnius</i> sp., <i>Larra</i> sp.
Stephanoidea		Heterogynaidae	<i>Heterogyna</i> sp.
Stephanidae	<i>Megischus bicolor</i> (Westwood)		

continued on next page

Table 2 continued

Andrenidae	<i>Andrena</i> sp.
Anthophoridae	<i>Nomada</i> sp., <i>Ceratina</i> sp.
Apidae	<i>Apis mellifera</i> L., <i>Bombus</i> sp., <i>Trigona</i> sp.
Halictidae	<i>Agapostemon</i> sp., <i>Lasioglossum</i> sp.
Megachilidae	<i>Megachile</i> sp.
Proctotrupoidea	
Diapriidae	
	Ambositrinae: <i>Dissoxylabis</i> sp.;
	Belytinae: <i>Aclista</i> sp., <i>Acropesta</i> sp.,
	<i>Aneurynchus</i> sp., <i>Oxylabis</i> sp.;
	Diaprinae: <i>Coptera</i> sp., <i>Paramesius</i> sp.,
	<i>Spilomicrus</i> sp., <i>Trichopria</i> sp.
Monomachidae	<i>Monomachus</i> sp.
Vanhorniidae	<i>Vanhornia eucnemidarum</i> Crawford
Heloridae	<i>Helorus</i> sp.
Ropronidae	<i>Roprona</i> sp.
Proctotrupidae	<i>Exallonyx</i> sp., <i>Miota vera</i> (Fouts)
Pelecniidae	<i>Pelecimus polyturator</i> (Drury)
Cynipoidea	
Ibalidae	<i>Ibala</i> sp.
Eucoilidae	genus ?
Alloxystidae	<i>Alloxysta</i> sp.
Platygaстроidea	
Scelionidae	
	Scelioninae: <i>Anteris</i> sp., <i>Calotelea</i> sp.,
	<i>Cremastobaenus</i> sp., <i>Gryon</i> sp. (wingless),
	<i>Macroteleia absona</i> Muesebeck, <i>Sparasion</i>
	sp., Teleasinae: <i>Trimorus</i> sp.
Platygastridae	Inostemmatinae: <i>Isocybus</i> sp., <i>Inostemma</i>
	sp.
Mymarommatoidae	
Mymarommatidae	<i>Palaeomymar</i> sp.
Chalcidoidea (additional dissections for work in progress not listed)	
Mymaridae	<i>Gonatocerus</i> sp.
Pteromalidae	Cleonyminae: <i>Cleonymus</i> sp., <i>Oodera</i> sp.

acter states. Coding of character states must in part reflect the level of analysis. At a different level, for example in an analysis of the relationships of Tenthredinoidea that is associated with a more extensive survey of taxa, it might be appropriate to further partition the various shapes. These modifications are difficult to characterize and here we have combined them into one apomorphic state, the reduction of well-separated anterior arms (state 2).

A clear transformation series leading to the development of the mesofurcal bridge is found within the Symphyta beginning with the Cephidae. In Cephidae (Fig. 9), the anterior arms are narrow and elongate and only the extreme apices of each

arm are joined (state 3). The anterior arms are considered to be homologous with those of Xyeloidea and Megalodontoidea; therefore, state 3 is probably derived from state 1. Rasnitsyn (1988; his character 19b) includes Cephoidae with Siricoidea + Vespina based on having the fore-arms of the mesofurca long and fused for some distance. Although true for Siricoidea + Vespina, the arms are only apically fused in Cephidae.

In Anaxyelidae (Fig. 10) and Siricidae (Fig. 11), the anterior arms are elongate and fused along most of their length (state 4). The anterior arms of Siricidae are laterally flattened (Fig. 11b) and in dorsal view each arm can be distinguished along its entire length (Fig. 11a). Anaxyelidae have a similar structure, including anterior placement of muscle 150b, but fusion of the arms is more complete (Fig. 10a). Posteriorly, the anterior furcal arms of Anaxyelidae are connected by a thin horizontal plate of cuticle.

In Xiphidriidae (Fig. 12), the anterior arms are completely fused and form a transverse mesofurcal bridge (state 5), and the entire dorsal and lateral surfaces form the posterior attachment for muscle 124. Displacement of muscles 150a and 150b to the lateral arms suggests that fusion of the arms in Xiphidriidae may be independent of the fusion in Siricidae and Anaxyelidae.

Orussidae (Fig. 13) exhibit complete fusion of the anterior arms into a smooth and bowed mesofurcal bridge (state 6) with a strong median anterior process that is the attachment site for muscles 150 and 124, as occurs in Anaxyelidae and Siricidae.

The groundplan states for the mesofurca of Apocrita consists of 1) a complete mesofurcal bridge (as in Xiphidriidae and Orussidae), 2) an anterior medial projection supporting muscle 124 (fu_2 - fu_1) (as in Xiphidriidae and Orussidae), and 3) lateral displacement of muscle 150a (fu_2 - pn_{2p}) (as in Xiphidriidae). No Apocrita have muscle 150 originating on the anterior projection of the mesofurca as in Orussidae. Because of the lateral displacement of muscle 150a, which is similar to Xiphidriidae (see character 2), Apocrita with a mesofurcal bridge are coded as character state 4.

The mesofurcal bridge is absent (state 7) in Ceraphronoidea (Fig. 25), Pelecniidae (Fig. 31), some Chalcidoidea (including all Mymaridae), Mymarommatidae, and Platygastridae (Fig. 28). We consider that absence of the bridge is an

apomorphic loss of the type of bridge found in Xiphydriidae (state 5), which is similar to the type found in most Apocrita. Assuming that presence of a bridge is a groundplan state for Apocrita (whether states 4, 5 or 6), losses within each of these taxa are considered irreversible (unlikely that a bridge can be regained) and probably independent. In Ceraphronidae, Pelecinidae, Mymaromatidae, Platygastriidae, and some Mymaridae, the mesofurca is lyre-shaped with the lateral arm terminating in a cup-shaped process that supports muscle 150a. When the furcal bridge is lost in Chalcidoidea (Aphelinidae, Encyrtidae, Rotoitidae, Signiphoridae and Trichogrammatidae), the shape of the mesofurca and attachment of muscle 150a are considerably different.

Synonymy for mesofurcal bridge:

Siricidae & Vespidae: mesofurcal ring (Tenthredinidae, *Vespa*, Weber 1925). Ichneumonoidea: mesofurcal bridge (*Stenobracon*, Alam 1951). Aculeata: mesofurcal bridge (ArF₂) (*Vespula*, Duncan 1939); supraneural bridge (*Apis*, Snodgrass 1942). Chalcidoidea: arch of the furca (*Monodontomerus*, Bucher 1948); tendinous arch of the mesofurca (*Tetramesa*, James 1926).

Character 2. Laterophragma of mesopostnotum (pn₂)

In Neuropterida, Mecopterida, Xyelidae and Pamphiliidae, the laterophragma of the mesopostnotum forms a lobe (pn₂, Figs. 4, 6) (state 0) that extends obliquely into the mesothorax from the lateral corners of the mesopostnotum, medially of the lateral attachment to the upper mesepimeron and lateral to the second phragma. The laterophragma in all of these taxa forms the attachment site for muscle 150 (fu₂-pn₂, see Character 3), muscle 116 (t₂-pn₂, see Character 4) and muscle 137 (pn₂-ba₃). The posterior face of the laterophragma forms the attachment site for muscle 137 (pn₂-ba₃, Fig. 3). Muscle 137 is usually small and difficult to trace, but it is apparently lost in Pergidae and all Apocrita.

In Xyelidae (Figs. 3, 4) and most Symphyta (Figs. 6, 8, 9), an apodeme (ap) is present on the anterolateral margin of the lobe that serves as the attachment site for muscle 150a (fu₂-pn_{2a}). The laterophragma is functionally coupled with

muscles 150 and 116, and the loss of either of these muscles is associated with a corresponding change in structure of the laterophragma. To avoid duplication of character coding, the presence or absence of certain structures of the laterophragma are treated under other characters. For example, the anterior apodeme is lacking in Neuropterida and Mecopterida but this was not coded as a different state for this character because it is reflected in the differentiation of muscle 150a in Hymenoptera, which is dealt with as Character 3. A broad laterophragma with a small anterior apodeme (state 0) occurs in Xyelidae, Pamphiliidae (and probably Megalodontidae), Blasticotomidae, Tenthredinidae, Argidae, Diprionidae, and Cephidae.

The laterophragma of Cimbicidae (Fig. 8) possesses an exaggerated apodeme (ap) and an enlarged posterior lobe (pn₂), which is fused with the second phragma (2ph). The laterophragma is unique in form and apparently autapomorphic.

In Xiphydriidae (Fig. 12), Monomachidae (Fig. 14), Vanhorniidae (Fig. 15), Cynipoidea (Fig. 22), Ceraphronoidea (Fig. 25) and most Diapriidae (Fig. 29), the laterophragma is excised between the elongate apodeme (ap) and the posterior lobe (pn₂) (state 1). In most of these taxa the apodeme of the laterophragma extends medially and horizontally into the thoracic cavity, but in Cynipoidea (cf. Fig. 22), the apodeme is vertical. The posterior lobe is lost in most Apocrita (including some Diapriidae), but this was not coded as an additional state change for this character because it reflects the loss of the muscle 116 (Character 4). The anterior apodeme (=axillary lever) or associated attachment for muscle 150a is present in all Apocrita. Additional character state changes for the laterophragma in Apocrita are based only on changes in the shape of the anterior apodeme.

In Pergidae (Fig. 5) and Orussidae (Fig. 13), the laterophragma is reduced to a narrow triangular process that forms an attachment for the tendon of muscle 150 (state 2). This reduction is also associated with the loss of muscle 116. State 2 could be derived from either state 0 or state 1.

In Apocrita, the axillary lever (ap) occurs in a variety of shapes that probably have different effects on leverage of the laterophragma with respect to the fourth axillary sclerite and the second phragma. In all Apocrita the apex of the axillary lever maintains a connection with muscle 150a

(fu_2-pn_{2a}). The plesiomorphic lever for Apocrita is narrow and inflected medially into the thorax as found in Xiphidriidae (state 1) and occurs either in association with a posterior lobe (most Diapriidae, Monomachidae (Fig. 14), Vanhorniidae (Fig. 15), Ceraphronoidea (Fig. 25) and Cynipoidea (Fig. 22) or without the posterior lobe (Trigonalidae (Fig. 23), Stephanidae (Fig. 24), Diapriidae (Fig. 29), Proctotrupidae (Fig. 32), some Ichneumonidae, Mymaromatidae, and Chrysoidea (Figs. 34-39) (except some Chrysididae). The axillary lever exists in a variety of forms in Apocrita but in shapes that are difficult to separate into discrete states, especially without a more thorough survey of the apocritan taxa. In all cases where the lever was narrow and inflected medially the character was coded as state 1.

In Platygastridae (Fig. 28), some Scelionidae and most Chalcidoidea, the axillary lever is deflected ventrally (state 3). In Mymaromatidae, the lever is robust and inflected medially (state 1). In *Sparasion* (Scelionidae; Fig. 16), the lever is reduced to a small cup-shaped lobe on the laterophragma (autapomorphic and not coded). In other Scelionidae and Mymaridae the lever is short, narrow and medially inflected (state 1).

The axillary lever in Stephanidae (Fig. 24) and most Chrysoidea (Figs. 35-38, also in Fig. 34 but this view is slightly different) is elongate and strongly inflected medially (state 1). This conformation of the lever is likely the precursor to the lever found in Apoidea and Vespoidea, discussed below. However, in Cleptinae and Chrysidinae (Chrysididae) the lever is reduced (state 4) forming a short, broad process attaching to a broad tendon of the shortened muscle 150a (Fig. 40).

In Apoidea (Figs. 45, 46, 54) and Vespoidea (Figs. 41, 42, 44) the axillary lever is robust and strongly appressed to the inner surface of the second phragma (state 5). This type of lever was found in all Apoidea examined and is associated with a robust muscle 150a. Except in Bradynobaenidae and Formicidae, muscle 150a is conical and attached to the lever by a narrow tendon or robust and nearly tubular (Mutillidae and Sapygidae). In Sierolomorphidae, the lever is not closely appressed to the second phragma (inflected medially about 30°), but this was not treated as a different state (intermediate between states 1 and 5). In Bradynobaenidae, the lever is reduced to a rounded knob (attaching to a narrow tendon of

muscle 150a) (state 4?). In Formicidae (Fig. 43), the lever forms a narrow, twisted apodeme (state 1?). Neither Bradynobaenidae and Formicidae were broadly surveyed and other forms may exist.

In Ichneumonidae the axillary lever is either closely appressed to the second phragma and similar to the lever found in Vespoidea and Apoidea (state 5), or rod-like and extending medially into the mesothorax (state 1), or inflected medially and dorsally (Fig. 17a). A robust lever is not found in Braconidae, including Hybrizontinae (Fig. 33), in which it was knob-like or short and slightly deflected ventrally (state 1), similar to Trigonalidae and some Proctotrupeoidea. The lever of Gasteruptiidae (Fig. 26) is similar to some Ichneumonidae but is oriented vertically with respect to the second phragma. In *Oodera* (Pteromalidae), the lever is robust, appressed to the second phragma and horizontal (state 5). This form of the lever appears to be convergent with Ichneumonidae and Aculeata, since in *Oodera* muscle 150a attaches to the entire ventral aspect of the apodeme as in other Chalcidoidea.

All Apiformes have the axillary lever separated (state 6) as an independent sclerite (Snodgrass 1942). This feature was verified in all of the Apiformes examined here. The apical connection of the mesopostnotum is weak and encased by the cup-shaped basal process of the axillary lever (Figs. 45, 54).

Synonymy for laterophragma:

Symphyla: lateral lobe of second phragma (2ph) (Daly 1963). Ichneumonoidea: muscle bearing process of mesopostphragma (*Stenobracon*, Alam 1951); axillary lever (Snodgrass 1942). Cynipoidea: mesopostnotal apodeme (*Ibalia*, Ronquist and Nordlander 1989); 2ph (Daly 1963). Aculeata: axillary lever (*Apis*, Snodgrass 1957; *Bombus*, Pringle, 1957, 1960, 1961); accessory sclerite of the fourth axillary sclerite (*Apis*, Snodgrass 1910); inner process of mesopostphragma (*Vespa*, Weber 1925 [states that lever turns apex of mesophragma and the connected axillary 4]); anterior process of mesopostphragma (MPPh₂) (*Vespa*, Duncan 1939). Hymenoptera: axillary lever (Matsuda 1970).

Character 3. Furcal-laterophragmal muscle

In Neuropterida and Mecopterida, only a

single muscle (150, fu_2-pn_2) acts between the mesofurca and laterophragma of the mesopostnotum (state 0) (Kelsey 1957, Matsuda 1970). In the majority of Symphyta, including Xyelidae and Pamphiliidae, two distinct muscles (150a and 150b) operate antagonistically on the enlarged laterophragma (Figs. 2, 3, 4, 6). The presumed division of muscle 150 into two muscles is considered as an apomorphy for Hymenoptera (state 1). Muscle 150a (fu_2-pn_{2a}) originates on the lateral arms of the mesofurca posterior or lateral to the origin of 150b and inserts onto an anterior apodeme or process of the laterophragmal lobe (Figs. 4, 6, 7, 9). Muscle 150b (fu_2-pn_{2b}) originates anteriorly or medially on the lateral or anterior arms of the mesofurca and broadly attaches to the margin of the laterophragmal lobe (Figs. 4, 6, 7, 9). The fibres of muscle 150b are often arranged so that the anteriormost fibres attach to the posteriormost or innermost margin of the laterophragmal lobe, although this is dependent on the size of the muscle and lobe.

If both muscles are present, muscle 116 (t_2-pn_2) is also present. Loss of muscle 150b (state 2) occurs in Cimbicidae, Monomachidae, Vanhorniidae, Diapriidae, Cynipoidea, and Ceraphronoidea, all of which have retained both the laterophragmal lobe (presumably the former point of insertion of muscle 150b) and muscle 116. All Apocrita have lost muscle 150b. In Anaxyelidae (Fig. 10), muscle 150b is attached to the posterior face of the posterior lobe (versus the margin) and muscle 150a is retained. Because of a similar placement and attachment of muscles in Siricidae (Fig. 11), it can be postulated that muscle 150a is lost and 150b remains (state 3). When both the laterophragmal lobe and muscle 116 are missing, as in Pergidae (Fig. 5) and Orussidae (Fig. 13), it is difficult to assess which muscle, 150a or 150b, has been lost. We could assume that muscle 150b is lost in both families. However, the forward attachment of muscle 150 to the mesofurca in Orussidae suggests that it is homologous with muscle 150b of Anaxyelidae and Siricidae. Therefore, the configuration in Pergidae and Orussidae could also be treated as a parallel loss of muscle 150a. Because of this uncertainty, we code the reduction to a single muscle in Pergidae and Orussidae as of questionable homology (state ?). Based on the presence of muscle 150a in the apocritan families mentioned above, we assume that muscle 150b is

lost in all Apocrita without a posterior laterophragmal lobe. Autapomorphic losses of muscle 150a occurs in workers of *Formica* and *Camponotus* (Märkl 1966, Saini et al. 1982).

Synonymy for muscle 150:

Tenthredinidae: Ilism1 (*Dolerus*, *Schizocerus*, *Tenthredo*, Weber 1927), 25 & 26 (*Euthomostethus*, Maki 1938). Ichneumonidae: 25 (*Psilopsyche*, Maki 1938); 63 (*Stenobracon*, Alam 1951). Aculeata: 25 (*Vespa*, Maki 1938); 78 (*Formica*, Märkl 1966; *Apis*, Snodgrass 1942); Ildv2 (*Vespula*, Duncan 1939); Ilism (*Vespa*, Weber 1925); fu_2-2ph (*Apis*, Daly 1964). Hymenoptera: t-s1 (Matsuda 1970).

Character 4. Second dorsal diagonal (=phragmal flexor) muscle

Muscle 116 (t_2-pn_2) is found attaching between the mesonotum and the anterior face of the laterophragmal lobe in Neuropterida, Mecopterida and most Symphyta (Figs. 2, 3, 12, 14, 15, 20), and is therefore plesiomorphic for Hymenoptera (state 0). Muscle 116, and the associated posterior lobe of the laterophragma, is lost (state 1) in Pergidae, Orussidae and most Apocrita. It seems unlikely that a functional complex composed of both muscle 116 and the corresponding posterior lobe of the laterophragma could be regained, and we consider the apomorphic state (loss of muscle and lobe) to be irreversible. An assumption of irreversibility has obvious consequences for models of character state change which are discussed in the later section on parsimony analyses. Muscle 116 and the corresponding posterior lobe are present in Monomachidae, Vanhorniidae, Cynipoidea, Ceraphronoidea and most Diapriidae, and it is likely that this complex is the groundplan for Apocrita (Daly 1963; Gibson 1985). The loss of this complex in Pergidae and Orussidae is therefore convergent with the loss in most Apocrita.

Synonymy for muscle 116:

Symphyta: 21 (*Euthomostethus*, Maki 1938). Symphyta, Monomachidae, Diapriidae, Vanhorniidae, Ceraphronoidea, Cynipoidea: t_2-2ph (Daly 1963; Gibson 1985). Hymenoptera: t12 (Matsuda 1970).

Character 5. Mesopostnotum and scutellar-metanotal muscle

In Neuropterida and Mecopterida, the mesopostnotum is broadly exposed medially; although in *Corydalus* (Megaloptera) the mesopostnotum is weakly sclerotized medially and appears to be split. The scutellar-postnotal muscle (muscle 114, t_2 - t_3 ; absent in *Bittacus*) passes internally from its origin on the scutellar area of the mesonotum to the anterior medial margin of the mesopostnotum (Kelsey 1957; Matsuda 1970). Within Hymenoptera, changes in the structure of the mesopostnotum and attachment of muscle 114 are correlated; however, the attachment of muscle 114 to the mesopostnotum is unique with respect to the outgroup, and the outgroup is scored as a separate state (state 0).

In Hymenoptera, muscle 114 (t_2 - t_3) arises dorsomedially from a fan-shaped attachment on the mesonotum and passes medially over the mesopostnotum (rarely under), to a narrow medial attachment on the anterior margin of the metanotum. In all Symphyta, our dissections indicate a posterior attachment of muscle 114 to the metanotum. Our observations are supported by illustrations of attachments to the metanotum in Weber (1925) for *Vespa* (his II_{dm_2}) and Märkl (1966) for *Apis* (his 70). In *Eutomostethus* (Tenthredinidae), muscle 114 was described as inserting on the median membrane that divides the mesopostnotum (Maki 1938, his 19 & 20), but in Tenthredinidae muscle 114 passes through the membrane to the metanotum. The attachment of muscle 114 to the metanotum is apomorphic for Hymenoptera.

Determination of the groundplan condition for Hymenoptera is complicated by the presence of different character states in the two extant subfamilies of Xyelidae. In Xyelinae (Xyelidae) (based on *Pleuroneura*, Fig. 47, and *Xyela*), the mesopostnotum (PN_2) is broadly exposed dorsally and the scutellar-metanotal muscle (114, t_2 - t_3) passes under the mesopostnotum through a small emargination of its posterior margin (state 1, broadly exposed and 114 internal). In Macroxyelinae (Xyelidae) (based on *Macroxyela ferrunginea* (Say), *Megaxyela tricolor* Norton, *Megaxyela aviingrata* (Dyar) and *Xyelicia nearctica* Ross), Megalodontoidea (Fig. 48), Tenthredinoidea and Cephioidea (Fig. 49), the mesopostnotum is exposed dorsally (depending on the contortion of

the mesosoma) and muscle 114 passes externally over the mesopostnotum as a tendon enclosed by a sheath of connective tissue (state 2, broadly exposed and 114 external). In groups with an external muscle and an exposed mesopostnotum (state 2), the anterior medial margin may be shallowly or deeply emarginate (appearing split) underneath muscle 114. In some genera of Tenthredinidae and Diprionidae, the mesopostnotum is obscured by posterior development of the scutellum, but otherwise conforms to state 2 (see Character 6).

In Anaxyelidae, the mesopostnotum and muscle 114 are the same as in Xyelinae (Fig. 47). Initially, we coded this as the same character state (state 1). However, this caused problems in developing an additive coding scheme that would force the anaxyelid state to be autapomorphic and not transitional between states 2 and 4. To resolve this problem, Anaxyelidae were assigned a new character state (state 3), which is treated as an autapomorphy. In all of the analyses, coding for Anaxyelidae and Xyelinae as state 1 or state 3 had no effect on tree topology.

In Siricidae, a median vertical process on the anterior margin of the metanotum forms the posterior attachment of muscle 114, which is internal and lacks any connective sheath. Although the process is unique for Hymenoptera, this conformation is considered to be a modification of state 2 even though the mesopostnotum is generally not exposed. The scutellum often extends over the metanotal process and, as in some Tenthredinoidea, the internalization of muscle 114 and mesopostnotum may be secondary. Snodgrass (1910) reported that the mesopostnotum of *Tremex columba* was exposed medially; however, we observed an exposed mesopostnotum only in some specimens of *Urocerus*. Some Cephidae (Fig. 49) also have a similar attachment to a peg-like process (mp) on the metanotum.

In Xiphydriidae (Fig. 50), Orussidae and Apocrita, muscle 114 (t_2 - t_3) and the mesopostnotum (medially) are completely internal and muscle 114 passes medially over the second phragma (state 4). An autapomorphic modification of state 4 is found in Xiphydriidae, in which the cuticle of the second phragma (between the lobes of the pseudophragma) encircles the muscle tendon as it passes through to the metanotum. Further development of the mesopostnotum and its associated

phragma in Apocrita is toward an even greater degree of internalization and a lateral shift of the points of articulation with the scutellum and metanotum (Snodgrass 1910) (see character 10). In Aculeata (Fig. 53), the second phragma is almost entirely disassociated mesally and the notal attachments are reduced to lateral lamellae along the extreme lateral margins (Snodgrass 1942).

Synonymy for muscle 114:

Tenthredinidae: 19 & 20 (*Euthomostethus*, Maki 1938). Ichneumonidae: 20 & 21 (*Psilopsyche*, Maki 1938). Aculeata: IIdlm₂ (*Vespa*, Weber 1925); 23 (*Vespa*, Maki 1938); IIs1 (*Vespula*, Duncan 1939); 70 (*Apis*, Märkl 1966); t₂-t₃ (*Apis*, Daly 1963). Hymenoptera: t13 (Matsuda 1970, Brodskiy 1992).

Character 6. Formation of pseudophragma

The postphragma (2ph) originates at the junction of the mesopostnotum and metanotum and forms the posterior attachment site for the longitudinal flight muscles (112, 1ph-2ph) (Snodgrass 1910). In Mecoptera, Neuroptera, Xyelidae (Fig. 47), Megalodontoidea (Fig. 48) and Tenthredinoidea, the anterior margin of the mesopostnotum is broadly attached to the posterior margin of the mesonotum (scutellum) by a narrow conjunctiva (60, term from Ronquist and Nordlander 1989) (state 0). In Cephidae (Fig. 9b), Anaxyelidae, Siricidae (Fig. 11b), Xiphydriidae and Apocrita, the anterior margin of the mesopostnotum is developed into a broad bilobed internal plate (pseudophragma) that extends anteriorly and dorsally beyond the dorsal attachment of the mesopostnotum to the mesonotum (state 1). The pseudophragma is an extension of the second phragma and both form the posterior attachment for the longitudinal flight muscles (1ph-2ph). A pseudophragma is not apparent in Orussidae (Fig. 13) and some Ichneumonidae and has probably been lost.

Characters 7-8. Furcal-spina muscles

In Xyeloidea (Fig. 3) and Pamphiliidae (Fig. 2, indicated by dashed line), muscles 127 (fu₂-sps₁) and 180 (fu₃-sps₂) connect the spina with the furca of the following segment (state 0). Muscle 127 is present in both Neuroptera and Mecoptera and muscle 180 is found only in Neuroptera (Maki 1938, Kelsey 1957, Matsuda 1970); we veri-

fied their presence only in *Corydalus*. Muscle 127 is lost (state 1, character 7) in all Hymenoptera except the Xyeloidea and Megalodontoidea. Rasnitsyn (1969, fig. 204) illustrates a muscle connection (127?) between sps₁ (his sst) and fu₂ in *Tremex* (Siricidae), but we did not observe this in either *Tremex* or *Urocerus*. The loss of muscle 180 (state 1, character 8) is a synapomorphy of Apocrita.

Synonymy for muscle 127:

Apidae: fu₂-1sps [pupal muscle only] (*Apis*, Daly 1964). Hymenoptera: s12 (Matsuda 1970; not listed by Matsuda for Hymenoptera).

Synonymy for muscle 180:

Symphyta: IIVlm₁ (*Dolerus*, *Schizocerus*, *Tenthredo*, Weber 1927).

Character 9. Furcal-basalare muscle

The furcal-basalare muscle (fb1, fu₂-ba₃) appears to be found only in Hymenoptera (state 1). The muscle is apparently absent in the outgroup (state 0). Muscle fb1 could be homologous with Matsuda's p-s3 which connects the furca to the anterior margin of the succeeding episternum. Muscle p-s3 is found in Neuroptera (IIPm17, Korn 1916 for *Myrmeleon*), but apparently not in other Neuroptera or Mecoptera (Matsuda 1970). In Symphyta (Figs. 2, 3, 5-13) muscle fb1 extends from the extreme lateral apex of the mesofurcal arm to the apodeme of the basalare of the hindwing (ba₃). This muscle was first illustrated, but not discussed, by Rasnitsyn (1969, fig. 204) for *Tremex*. In Diprionidae (Fig. 7), muscle fb1 ends in a sclerotized cap attached to the apodeme of the basalare, along with muscle 137 (t₃-ba₃) which originates from the posterior face of the laterophragma (t₃).

Muscle fb1 is absent (state 0) in most Apocrita. However, what appears to be the same muscle occurs in Mutillidae (Fig. 18), Rhopalosomatidae (Fig. 19) and Bradynobaenidae (state 1). The muscle in these taxa originates laterally on the mesofurcal arms (dorsal to the furcal-trochanteral muscle, muscle 174) and narrows to a fine tendon that enters the pleural area near the base of the hind wing. The dorsal point of insertion was not observed but the muscle enters the pleural area posterior to the subalar muscle of the mesothorax and may insert onto the basalare or axillary sclerites of the hind wing. No such muscle was observed in

other Apocrita. The loss of muscle fb1 in Apocrita could be the result of a shift of the muscle origin from the furca to the pleural wall. Gibson (1986) reported a unique muscle in Eupelmidae and Pteromalidae (pl_2-3ax_3a) that attached between the lower mesepimeron and possibly the metathoracic third axillary sclerite (of uncertain insertion; Gibson pers. comm. 1993). The homology of fb1 with the pleural muscles is beyond the scope of this study.

Character 10. Lateral articulation of mesopostnotum

In Xyeloidea, Megalodontoidea (Fig. 51) and Tenthredinoidea and the outgroup taxa, the mesopostnotum is broadly and evenly joined to the upper mesepimeron (state 0). In Cephidae (Fig. 52), Anaxyelidae and Siricidae, the juncture is invaginated and connected by weak cuticle within the invagination, but maintains a strong cuticular connection at the anteriormost point of attachment (state 1). In Xiphydriidae, Orussidae and Apocrita, the mesopostnotum is completely internal and the lateral connection of the mesopostnotum to the upper mesepimeron is reduced to the anteriormost point of attachment (state 2).

Character 11. Fusion of lateral arms of mesofurca and metafurca

In most Aculeata the lateral arms of the mesofurca and metafurca are closely appressed, but as in most other Hymenoptera and the outgroup taxa, they are broadly separated and joined by the interfurcal muscle 181 (state 0) (Fig. 3). In Apoidea (Figs. 46, 53), the lateral arms of both furcae are fused at the junction with the mesofurcal bridge and the interfurcal muscle is lost (state 1). The lower furcal arms form a four-cornered brace for the furcal complex, and the metafurcal arms are divided lateral to the furcal bridge. A similar fusion of the mesofurca and metafurca occurs in Amiseginae (Chrysididae; Fig. 39) and Gasteruptiidae (Fig. 26), but in both cases muscle 181 is retained and these are considered to be non-homologous and autapomorphic changes. Additional coding as autapomorphic states is unnecessary for this analysis but may be warranted in more extensive studies of related taxa.

Character 12. Furcal process for trochanteral muscle 174

In most Hymenoptera and the outgroup taxa, the furcal depressor of the trochanter (muscle 174, fu_2-tr_2) attaches to the lateral arms of the mesofurca (Fig. 3) (state 0). In Chrysididae (Cleptinae and Chrysidinae), muscle 174 attaches to anterior extensions of the lateral furcal arms (Fig. 40, vp) (state 1). In Pompilidae (Fig. 42), Sapygidae, Scoliidae, Sierolomorphidae and Vespidae (Fig. 41), muscle 174 attaches to similar extensions (vp) that arise instead from the furcal bridge (state 2). In Vespoidea, muscle 174 has two origins - the lateral furcal arms and the ventral process (= scoop shaped processes, schT, Weber 1925; anterior process of mesofurcal bridge, PF_2 , Duncan 1939).

PHYLOGENETIC HYPOTHESIS FOR
HYMENOPTERA

Figs. 55, 56

The higher classification of Hymenoptera has come under increasing scrutiny following reviews published by Königsmann (1977, 1978a) and Rasnitsyn (1969, 1980). Königsmann (1978a) presented evidence that Hymenoptera was comprised of two monophyletic sister taxa, the Symphyta (excluding Cephoidea) and Cephoidea + Apocrita, with most apocritan families presented as a series of unresolved lineages. Although this more traditional concept of the Symphyta is still used (Zessin 1985), it has not been accepted in more recent papers except to present an alternate hypothesis of relationships (Gauld and Bolton 1988). Rasnitsyn (1980) presented evidence that Symphyta is paraphyletic relative to Apocrita with Cephoidea as the sister group of Apocrita. Studies subsequent to Rasnitsyn (1980) (Gibson 1985, 1986; Naumann and Masner 1985; Carpenter 1986) led Rasnitsyn to modify his original hypotheses in a later paper (Rasnitsyn 1988), in which Cephoidea were placed as a more basal lineage of Hymenoptera and Orussidae as the sister group of Apocrita. A far more resolved set of relationships among the parasitic Apocrita (Fig. 56) were presented by Rasnitsyn (1988). Some of Rasnitsyn's hypotheses have been corroborated in recent morphological or phylogenetic treatments (Johnson 1988; Whitfield et al. 1989), although Gibson (1993) presented evidence against the biphyletic origin of Hymenoptera from Xyelidae and Brothers and Carpenter (1993) sup-

ported a different hypothesis for Chrysidioidea and Aculeata. For our data, these modifications affect only the distribution of character 12 in the Aculeata, and have no effect on the parsimony arguments presented in a later section. Cladograms comparing the hypotheses of Rasnitsyn and Königsman are presented in Whitfield (1992).

Rasnitsyn (1980, 1988), Shcherbakov (1980, 1981) and Gibson (1993) have proposed Xyelidae as the most basal extant lineage of Hymenoptera. As well as possessing a branched Rs vein, Xyelidae retain the anepisternum as an integral part of the pleuron and retain the plesiomorphic condition of a relatively equally proportioned meso- and meta-thorax (Gibson 1993). Other than the structure of the antenna, which may be plesiomorphic, there are no features that support the monophyly of the Xyelidae, and Rasnitsyn (1988) proposed that the two subfamilies of Xyelidae belong to two lineages of Hymenoptera (Hymenoptera biphyletic with respect to the two subfamilies). Gibson (1993 and personal communication, 1993) argues that Hymenoptera excluding Xyelidae are monophyletic but that no characters support the monophyly of the Xyelidae. The mesofurcal-mesopostnotal complex of Pamphiliidae and both subfamilies of Xyelidae are basically the same and we consider them to represent the plesiomorphic condition for Hymenoptera.

Rasnitsyn (1988) classified the suborder Siricina into three infraorders that include the following extant families: Xyelomorpha (Xyelidae), Tenthredinomorpha (Argidae, Blasticotomidae, Cimbicidae, Pergidae and Tenthredinidae [including Diprionidae]), and Siricomorpha (including Megalodontoidea [=Pamphilioidea]: Pamphiliidae and Megalodontidae; Cephioidea: Cephidae; Siricoidea: Anaxyelidae, Siricidae and Xiphydriidae). Rasnitsyn (1988) treated Xyelidae as paraphyletic with respect to Tenthredinoidea and remaining Hymenoptera, and the three families of Siricoidea are paraphyletic with respect to the Orussidae + Apocrita (Suborder Vespina). Rasnitsyn (1988) placed Cephioidea as basal to the Siricoidea + Apocrita, rather than sister group to the Apocrita as in his earlier treatments (Rasnitsyn 1969, 1980).

As a framework for evaluating our results, we have compiled the results of Rasnitsyn (1988) and Gibson (1985, 1993) to derive the cladogram presented in Figure 55. Contrary to Rasnitsyn (1988), Hymenoptera excluding Xyeloidea are treated as monophyletic based on the presence of a postspiracular sclerite (=detached anepisternum) (Gibson 1985, 1993) and an apically simple Rs vein that is not bifurcate (Rasnitsyn 1988). Xyelidae are treated as paraphyletic to allow for discussion of Character 5. Tenthredinoidea are monophyletic and placed here as sister group to the remaining Hymenoptera, excluding Xyeloidea and Megalodontoidea, based on a reduction in the number of preapical tibial spurs (from 2-4 spurs on the hind legs in Xyeloidea and Megalodontoidea to less than 1 in Tenthredinoidea, 1-2 in Cephioidea and 0 in remaining Symphyta and Apocrita; H. Goulet and G. Gibson, pers. comm., 1993), and the loss of the ventral mesofurcal-spina muscle, fu_2 - sps_1 , which is present only in Xyeloidea and Megalodontoidea (see Character Analysis).

Remaining infraorders of extant Vespina proposed by Rasnitsyn (1988) include the Orussomorpha, Evaniomorpha (Stephanoidea, Evanioidea), Proctotrupoidea (Proctotrupoidea, Cynipoidea, Chalcidoidea), Ichneumonomorpha (Ichneumonidae), and Vespomorpha (Chrysidioidea, Sphecoidea, Pompiloidea, Scolioidea, Formicoidea and Vespoidea). Recent classifications (Naumann 1992; Huber and Goulet 1993) treat the five families of Rasnitsyn's Stephanoidea as higher taxa (Ceraphronoidea [Ceraphronidae and Megaspilidae], Megalyroidea, Stephanoidea and Trigonalynoidea). Following Brothers (1975) and Huber and Goulet (1993), the Aculeata are referred to only three superfamilies (Chrysidioidea, Apoidea and Vespoidea) and Mymarommatidae are placed as a superfamily.

GROUP ANALYSIS

Character states are referred to in brackets as [character:state]. Relationships are discussed according to the phylogenetic hypotheses illustrated in Figures 55 and 56. The distribution of character states for each taxon are listed in Appendix 2.

Xyeloidea + Megalodontoidea + remaining Hymenoptera

Figs. 1, 2, 3, 4, 6, 47, 48, 51

Four characters of the mesofurcal-mesopostnotal (MF-MPN) complex are not found in the outgroups and therefore support the monophyly of Hymenoptera: long anterior arms of the mesofurca [1:1]; two furcal laterophragmal muscles [3:1]; muscle 114 attaching to the metanotum (part of Character 5, see below); and furcal-basalare muscle (fb1, fu₂-ba₃) present [9:1].

Xyeloidea and Megalodontoidea are plesiomorphic for all characters postulated for Hymenoptera in the mesofurcal-mesopostnotal complex. Megalodontidae were verified for external characters only and the presence of anterior furcal arms [1:1] was based on fig. 189 in Rasnitsyn (1969). Rasnitsyn (1969) also refers to the mesofurco-metapre-episternal muscle as found only in *Xyela*. This muscle was not identified in our dissections, although it may be synonymous with muscle 127 (fu₂-sps₁).

The mesopostnotum is external and broad medially in both Xyeloidea and Megalodontoidea. In extant Xyelinae (Xyelidae), the mesopostnotum is entire medially and muscle 114 is internal [5:1, Fig. 47]. A similar conformation is found in the outgroup, but the attachment of muscle 114 is different [5:0]. In Macroxyelinae (Xyelidae), Megalodontoidea and Tenthredinoidea, the mesopostnotum is almost completely separated medially and muscle 114 passes externally [5:2, Fig. 48]. The deep emargination of the mesopostnotum associated with state 5:2 is visible externally and can be interpreted from fossil Hymenoptera. Based on illustrations in Rasnitsyn (1969), external passage occurs in the fossil xyelids: Archxyelinae: *Asioxyela* (fig. 34), *Leioxyela* (fig. 41), *Triassoxyela* (fig. 32), *Xiphoxyela* (figs. 45, 46); Macroxyelinae: *Agaridyela* Rasn. (fig. 41), *Chaetoxyela* Rasn. (fig. 76), *Ceroxyela* Rasn. (fig. 77); and Xyelinae: *Eoxyela* Rasn. (fig. 59), *Lydoxyela* Rasn. (fig. 68), *Spathoxyela* Rasn. (fig. 42), *Xyelisca* Rasn. (fig. 61), and *Xyela mesozoica* Rasn. (fig. 62). If correctly interpreted in fossil Xyelinae, the internal passage of muscle 114 and an entire mesopostnotum are derived within extant Xyelinae, and the external passage of muscle 114 and an emarginate mesopostnotum are probably apomorphic for Hymenoptera.

Tenthredinoidea + remaining Hymenoptera

Monophyly of Tenthredinoidea and the remaining Hymenoptera is supported by the loss of muscle 127 (fu₂-sps₁) [7:1].

Tenthredinoidea

Figs. 5, 7-8, 20, 21

The anterior mesofurcal arms are reduced or lost in all Tenthredinoidea [1:2].

Blasticotomidae (Fig. 20)

The plesiomorphic combination of muscles is present. Anterior furcal arms are present, but they are short and thin. As discussed earlier (analysis of character 1), because of uncertainties in the homology of reduced arms, we have scored both reduced and absent anterior furcal arms as the same character state (1:2). The anterior apodeme of the laterophragma is absent and both 150a and 150b attach to the apex of the posterior lobe (Fig. 20a). This is considered to be an autapomorphic development, but there is also a general similarity with the laterophragma of *Nematus* (Fig. 19), in which short anterior furcal arms are also present.

Tenthredinidae (Fig. 21)

The plesiomorphic combination of muscles is present in all taxa examined, and the structure of the laterophragma is the same as in Xyelidae and Pamphiliidae. The anterior arms of the mesofurca vary from narrow, elongate apodemes extending from the anterior face of the lateral arms (*Nematus*), to short cup-like structures similar to those found in Diprionidae, to completely absent (most Tenthredinidae). Muscle 180 (fu₃-sps₂) was not found in *Eutomostethus* (Blennocampinae) (Maki 1938).

Diprionidae (Fig. 7)

The plesiomorphic combination of muscles and structures for Tenthredinoidea are present but with the following apomorphic features: anterior arms reduced to cup-like receptacles for muscle 124; anterior process of laterophragma expanded and forming a broad attachment for 150a; and muscle 150b originates medially to 150a on the lateral furcal arms.

Cimbicidae (Fig. 8)

The anterior arms are reduced to small spoon-shaped processes, the posterior lobe of mesopostnotum is fused to second phragma forming attachment for a large muscle 116, and muscle 150b is lost [3:2]. The anterior process of the laterophragma is enlarged and extends ventrally into the cup-shaped lateral arm of the mesofurca (autapomorphy).

Argidae + Pergidae

The lateral arms of mesofurca are tubular and hollow (apomorphic), the anterior arms of the mesofurca are absent, and the attachment site for muscle 124 (fu_2 - fu_1) is to the rounded surface of the lateral arms. Although they would suggest a sister group relationship for these two families, these characters were not surveyed throughout Hymenoptera and were not coded for the parsimony analysis.

Argidae

The laterophragma and its associated muscle attachments are as in Tenthredinidae.

Pergidae (Fig. 5)

This family displays a number of autapomorphies: loss of the tergal depressor muscle (116) [4:1] and the associated posterior lobe of the laterophragma [2:2], and loss of one of the furcal laterophragmal muscles (possibly 150b) [3:2]. The laterophragma is reduced to a small triangular lobe that ends in a narrow attachment to muscle 150. The lateral arms form a cup-shaped attachment for muscles 150 and fb1. A sclerotized apodeme, probably derived from the lateral arm and muscle 151 (pl_2 - fu_{2a}), extends laterally to the pleural ridge. Ventrolateral extensions of the lateral arms are developed as insertions for the enlarged muscle 170 (pl_2 - fu_{2b}).

Cephidae + remaining Hymenoptera

Figs. 9, 49, 52

Monophyly of the Cephidae and the remaining Hymenoptera is supported by a suite of characters: apical connection of the anterior mesofurcal arms [1:3], formation of a pseudophragma [6:1], and invagination of the mesopostnotum laterally [10:1]. The pseudophragma is not present in all Hymenoptera, but its complete absence in the

lower Hymenoptera and presence in Cephidae, Anaxyelidae, Siricidae, Xiphydriidae and most Apocrita suggest that it is a synapomorphy at this level. There are no published accounts which make reference to a pseudophragma occurring elsewhere within Endopterygota.

Cephidae are plesiomorphic for other characters of the mesofurcal-mesopostnotal complex: muscles 116, 150a, 150b, and fb1 are present, and the laterophragma is divided into a large posterior lobe and a small anterior process. The mesopostnotum is usually exposed medially but is sometimes concealed by the scutellum. Muscle 114 passes externally over the mesopostnotum in all genera (plesiomorphic) and may arise dorsomedially from a vertical process on the metatergum (*Calameuta* Konow, *Cephus* Latrielle [mp, Fig. 49], *Monoloplopus* Konow, *Syrista* Konow and *Trachelus* Jurine) as in Siricidae, or from an emargination of the metatergum (*Caenocephalus* Konow and *Janus* Stephens) as in Anaxyelidae.

Anaxyelidae + (Siricidae + (Xiphydriidae + (Orussidae + Apocrita)))

Fig. 10

Monophyly of the Anaxyelidae and remaining Hymenoptera is based on a more complete fusion of the anterior arms of the mesofurca [1:4]. Fusion of the anterior mesofurcal arms in Anaxyelidae (Fig. 10a) appears to be more complete than in Siricidae (Fig. 11a) in which the arms are fused in about the anterior half. The anterior arms of Anaxyelidae (Fig. 10a) are still traceable in dorsal view and they are connected posteriorly by a thin plate of cuticle. The greater degree of fusion of the arms is probably autapomorphic in Anaxyelidae; however, in Anaxyelidae and Siricidae the fusion is intermediate between the apical connection found in Cephidae and the complete fusion including a strong furcal bridge found in Xiphydriidae + Orussidae + Apocrita. In Anaxyelidae, Siricidae and Xiphydriidae, muscle 150b inserts onto the posterior face of the laterophragmal lobe rather than to the ventral margin as in Xyeloidea, Megalodontoidea, Tenthredinoidea and Cephidae. As the muscle is absent in Orussidae and Apocrita, the importance of this unique attachment as a character for supporting monophyly of Siricoidea (including Anaxyelidae and Xiphydriidae) or Siricoidea +

Orussoidea + Apocrita cannot be assessed.

In Anaxyelidae, the presence of both furcal-laterophragmal muscles (150a & 150b) and anterior origin of muscle 150b on the furcal arms is plesiomorphic. The mesopostnotum is broadly exposed medially and muscle 114 (t_2 - t_3) passes under the mesopostnotum medially (autapomorphy; 5:3). The dorsal enclosure of muscle 114 in Anaxyelidae may result from the extension and medial fusion of the anterior margin of the mesopostnotum. Rasnitsyn (1969, fig. 99) illustrates a split mesopostnotum [5:2] for the fossil *Anaxyela gracilis* Martynov. This supports the contention that an internal muscle 114 is derived within Anaxyelidae.

Siricidae + (Xiphydriidae + (Orussidae + Apocrita))

Fig. 11

No characters of the mesofurcal-mesopostnotal complex demonstrate the monophyly of Siricidae and the remaining Hymenoptera. The anterior mesofurcal arms of Siricidae (Fig. 11) are vertically flattened and in dorsal view are distinct along their entire length. The degree of fusion of the anterior arms is intermediate between Cephidae and Xiphydriidae + Orussidae + Apocrita, but, as discussed above, is comparable to that found in Anaxyelidae. Siricidae are autapomorphic for the loss of muscle 150a (along with the anterior process of the laterophragma) [3:3]. The posterior attachment of muscle 114 (t_2 - t_3) to a vertical process of the metanotum is shared with some Cephidae but not with Xiphydriidae, Orussidae or Apocrita, which lack a process. Internal passage of muscle 114 in Siricidae may result from the posterior extension of the scutellum rather than internalization of the mesopostnotum as in Cephidae and Tenthredinoidea.

Rasnitsyn (1988) proposed that Siricidae + remaining Hymenoptera were monophyletic based on four synapomorphies: 1) compound third antennal segment reduced and subequal to the following segments, 2) head capsule with postgenae subcontiguous, divided with narrow hypostomal bridge, 3) transscutal articulation present, and 4) prepectus concealed. In Anaxyelidae, the primitive state of a compound third antennal segment is found only in the fossil anaxyelid genus *Sphenosyntexis* Rasnitsyn; the derived state is found

in the remaining genera of Anaxyelidae including the only extant species, *Syntexis libocedrii* Rohwer. However, the antennal flagellum is apomorphic (reduced and divided) in Xyeloidea, Megalodontoidea, Tenthredinoidea, Cephoidea and within Anaxyelidae, and thus its reduction in Siricidae and remaining Apocrita is not a reliable character. The postgenae meet broadly along the medial line to form a postgenal bridge (=genaponta *sensu* Ross 1937) in Anaxyelidae, Siricidae and Xiphydriidae; we agree with Ross (1937) that the postgenae of Anaxyelidae and Xiphydriidae are similar and thus Anaxyelidae cannot be excluded from Siricoidea based on this character. Gibson (1985) demonstrated that a transscutal articulation is absent in Cephidae, Anaxyelidae and Siricidae. The presence of a concealed prepectus is useful for supporting the monophyly of Siricidae + Xiphydriidae + Orussidae + Apocrita (Rasnitsyn 1988; Gibson 1985).

Xiphydriidae + (Orussidae + Apocrita)

Fig. 12

There is strong support in the MF-MPN complex for the monophyly of Xiphydriidae, Orussidae and Apocrita. The anterior mesofurcal arms are completely fused into an anterior furcal process (fp) and posteriorly strengthened to form a transverse mesofurcal bridge (fb) [1:4], with the exception of some Apocritan taxa in which the mesofurcal bridge is lost. In addition, the mesopostnotum is completely internal medially [5:4] and laterally [10:2], and the laterophragma is strongly incised with the anterior process (ap) developed into a strong apodeme [2:1]. The plesiomorphic combination of muscles in the MF-MPN complex is retained. Among the Cephoidea, Siricoidea and Orussoidea, Xiphydriidae are unique in having muscle 150b attached to the lateral arms of the mesofurca (versus the anterior arms or furcal process). Muscle 124 (fu_2 - fu_1) is broadly attached to the furcal process and bridge. In Xiphydriidae, the tendon of muscle 114 (t_2 - t_3) is enclosed medially, and internally, by the cuticle of the second phragma (autapomorphic).

Orussidae + Apocrita

Fig. 13

No synapomorphies were found in the

mesofurcal-mesopostnotal complex that support the monophyly of Orussidae + Apocrita without Xiphydriidae. It is possible that the loss of muscle 150a supports the monophyly of Orussidae + Apocrita [3:2 = 3:2]. However, the homology of the remaining muscle 150 in Orussidae is uncertain (see discussion of Character 3). Therefore, it is also possible that muscle 150b is lost in Orussidae and 150a is lost in Apocrita.

Orussidae have at least three apomorphic features in the MF-MPN complex, two of which are also found in Pergidae and Cimbicidae. The furcal bridge (fb) is rounded and bowed anteriorly with a distinct median process (fp) [1:6]. The attachment of muscle 150 to the furcal process is found only in Orussidae. In Apocrita, muscle 150a is usually attached to the furcal bridge or lateral arm. Otherwise the furcal bridge and process in Orussidae are similar to Xiphydriidae and other Apocrita. Muscle 116 is lost [4:1] in Orussidae, and there is an associated reduction of the laterophragma to a small triangular lobe that forms the attachment for muscle 150 [2:2]. Additional autapomorphies in Orussidae include loss of the pseudophragma [6:0] and the configuration of muscle 180 (fu_3 - sps_2) which arises from the spina as a single narrow tendon that bifurcates about half-way along its length to the metafurcal arms (the plesiomorphic configuration is completely separated along its entire length).

Apocrita

Figs. 14-19, 22-46, 53, 54

The loss of two muscles in the MF-MPN complex supports the monophyly of the Apocrita: the metafurcal-spina muscle (180, fu_3 - sps_2) [8:1] and the furcal-basalare muscle (fb_1 , fu_2 - ba_3) [9:0]. Muscle 150b (fu_2 - pn_{2a}) [3:2] is lost in all Apocrita including those that retain the posterior lobe of the laterophragma. However, as discussed above, the homology of the remaining muscle 150 in Orussidae is not clear, and therefore loss of 150a is either a synapomorphy of Orussidae + Apocrita or an autapomorphy of Apocrita. Loss of muscle 137 may also support the monophyly of Apocrita (see discussion for Character 2).

Shcherbakov (1981) stated that muscle 170 (pl_2 - fu_{2b} , s - cx_2) is connected to the coxal process of the mesopleuron in all Hymenoptera. Based on our observations, it is well developed in all

Symphyta and attaches laterally to the mesofurcal arms (Figs. 3, 5, 9b, 12b, 13). In Apocrita, the position of muscle 170 shifts from the apex of the furcal arms to the base of the furca and is more nearly horizontal. This is most apparent in Vespoidea (cf. Duncan 1939, muscle $Ilfp_{12}$ (71)).

The laterophragma of Cynipoidea, some Diapriidae, Monomachidae (Fig. 14) and Vanhorniidae (Fig. 15a) are similar in structure with an anterior apodeme (ap) narrowly separated by a deep incision from the posterior lobe (pn_2) [1:5], which supports muscle 116 [4:0]. In Megaspilidae (Fig. 25), the apodeme and lobe may be broadly or narrowly separated. Muscle 116 [4:1] is present only in the families listed above and probably has been lost numerous times within Apocrita (Gibson 1985). It is unlikely that this muscle and associated posterior lobe could be regained once lost. Under the present hypothesis of relationships in Apocrita, muscle 116 and the lobe are lost at least 9 times (10 if also lost in Austroniidae) (Fig. 56). Of these, only in Diapriidae is the muscle lost within an entire family.

Groundplan states for the Apocrita are exemplified by Monomachidae (Fig. 14), Vanhorniidae (Fig. 15), most Diapriidae (Fig. 29) and Cynipoidea (Fig. 22), in which muscle 116 and the posterior lobe of the laterophragma are retained (Daly 1963; Gibson 1985). Plesiomorphic attributes of Apocrita include 1) presence of a median furcal process (fp) forming the attachment for muscle 124, 2) furcal bridge complete (fb) [1:4], 3) muscle 150a originating laterally on the bridge or the lateral arm of the mesofurca, 4) laterophragma divided into an anterior apodeme and posterior lobe [2:1], 5) presence of the tergal depressor muscle (116) [4:0], 6) mesopostnotum internal [10:2] and 7) prephragma present [6:1]. Ceraphronoidea (Fig. 25) have lost the mesofurcal bridge [1:7] but retain a divided laterophragma, and in some Diapriidae (Fig. 22) the posterior lobe of the laterophragma is lost [4:1].

Apart from changes in the laterophragma, apomorphic changes of the MF-MPN complex in Apocrita include loss of the mesofurcal bridge [1:7] and changes in the structure of the anterior apodeme (=axillary lever) of the laterophragma [2:3-6]. Changes in the shape of muscle 150a, lateral arms, furcal bridge and second phragma are homoplastic and probably related to changes in thoracic shape. Notable exceptions in Aculeata include development of an axillary lever [2:5] that

is separated in Apiformes [2:6], fusion of the lateral arms of the mesofurca and metafurca [11:1], development of processes on the mesofurca for the furcal-trochanteral muscle [12:1,2], and a medial reduction of the attachment points (60 & 61) between the second phragma and terga.

The cladogram presented in Figure 56 is consistent with the relationships proposed by Rasnitsyn (1988) and Brothers and Carpenter (1993) for extant Apocrita, and is used as the model for examination of character state change within Apocrita. Apart from the modifications in Aculeata, the MF-MPN complex offers little support for phylogenetic relationships proposed for Apocrita. Within Apocrita a total of 22 steps are required to explain the distribution of character states as modelled on Figure 56 (excluding changes in the Chalcidoidea + Platygastroidea + Mymarommatoida trichotomy, Austroniidae and Peradeniidae). Given that the tergal depressor muscle and posterior lobe of the laterophragma are present [4:0] in what are assumed to be relatively derived groups (e.g., Cynipoidea, Diapriidae and Monomachidae), this complex must be lost a minimum of 9 times (or 10 times if it is absent in Austroniidae). Only 8 losses are required if Pelecinidae and Vanhorniidae are monophyletic (Fig. 56). An additional 3 losses of muscle 116 [4:1] are required using Königsman's (1978a) hypothesis for Apocrita. Obviously, loss of this muscle does not offer strong evidence for the monophyly of Megalyroidea, Stephanoidea and Trigonoidea (Fig. 56).

Among the parasitic families of Apocrita, the mesofurcal complex of Gasteruptiidae (Fig. 26) and Evaniidae (Fig. 27) were very different from each other. However, the mesofurcal bridge of Aulacidae and Evaniidae are similar in shape (broad and flattened with muscle 124 attaching under the anterior margin of the bridge). In all three families the axillary lever is strongly inflected and perpendicular to the lateral wall of the mesosoma (Figs. 26, 27), and the lever is connected by a long thin tendon to muscle 150a. Scelionidae and Chalcidoidea both have a similar mesofurcal bridge (bowed with the median process virtually absent) which may indicate a sister-group relationship between Chalcidoidea and Platygastroidea. However, given that the bridge is lost in Platygastriidae, Mymarommatidae, Mymaridae and some Chalcidoidea [1:7], it is not clear what

the groundplan state of this character is in either superfamily. Also, the axillary lever is deflected [2:3] in Platygastriidae, some Scelionidae and most Chalcidoidea. Almost all Chalcidoidea including Mymaridae are unique in that muscle 150a attaches to the entire length of the deflected axillary lever (versus only apical attachment). Mymarommatidae have a medially inflected lever [2:1] and muscle 150a is conical and attaches only to the apex of the lever (plesiomorphic). Proctotrupidae (Fig. 32) have a similar axillary lever to that of Platygastriidae (Fig. 28), although it is shorter and not as strongly deflected (Figs. 29-32). In Heloridae (Fig. 30) and Pelecinidae (Fig. 31), the lever is followed by a short spine (pn₂?) that has no muscle connection and may be the remnant of the posterior lobe of the laterophragma. Some Proctotrupidae have a blunt triangular lobe in a homologous position. Heloridae, Pelecinidae and Proctotrupidae are the only Hymenoptera with a vestigial posterior lobe of the mesopostnotum. Roproniidae were identical to Heloridae internally except for the lack of a vestigial posterior lobe.

Most Ichneumonoidea (Fig. 17) have a mesofurca consisting of a broad mesofurcal bridge and a strong medial projection. The furcal bridge of Hybrizontinae (Braconidae) (Fig. 33) lacks a median process but this could be autapomorphic. The axillary lever in Ichneumonidae is similar to Vespoidea and Apoidea [2:5]. This may be evidence for the close relationships to Aculeata that have been proposed (Rasnitsyn 1988, Sharkey and Wahl 1992), but a similar lever has not been found in Braconidae or Chrysididae.

Chrysididae do not have any defining apomorphies of the mesofurca or axillary lever. The arched bridge of Plumariidae (Fig. 34), Sclerogibbidae (Fig. 35) and Embolemidae (Fig. 36) are similar but this feature may be plesiomorphic, as this shape is similar to Stephanidae. The furcal bridge of the single female dryinid examined (Anteoninae) was similar to Bethyidae (Fig. 38) (relatively straight with a strong apical projection), and the bridge of the male dryinid (Fig. 35) was reduced to a straight bar. Obviously more taxa need to be surveyed to understand the importance of furcal shape in Chrysididae. Chrysididae have apomorphies that distinguish taxa at the subfamily level: the fusion of the lateral arms of the mesofurca and metafurca

in Amiseginae (Fig. 39), and extensions of the furca that support the furcal depressor of the trochanter [12:1] in Chrysidinae (Fig. 40) and Cleptinae. These latter two subfamilies also share a reduction of the axillary lever [2:4]. Reduction of the axillary lever and presence of ventral processes in Cleptinae and Chrysidinae do not support the hypothesis of relationships among Chrysididae proposed by Kimsey and Bohart (1990) of Cleptinae + (Amiseginae + Chrysidinae). Based on relationships for Chrysididae proposed by Brothers and Carpenter (1993), Carpenter (1986) and Rasnitsyn (1988), the plumariid type of bridge is plesiomorphic, Dryinidae have an independently derived bridge, and Chrysididae + Bethylinidae have a relatively broad, straight furcal bridge with a strong medial projection.

Monophyly of the Vespoidea and Apoidea is supported by the development of an axillary lever [2:6], which is subsequently reduced in Bradynobaenidae [2:4] and modified in Formicidae [2:1]. Most Aculeata also have a broad, flattened furcal bridge with muscle 124 attaching to the dorsal and lateral surfaces (Fig. 18), although the bridge is not as well developed in Rhopalosomatidae (Fig. 19), Sierolomorphidae and some Sphecidae (Fig. 46). In Tiphidae (Fig. 44), the furca is convoluted and broadly excavated dorsally. The furcal bridge has several shapes in Vespoidea but their importance for assessing relationships will require a much broader survey of taxa. A strong ventral process (vp) for the furcal depressor of the trochanter ($174, fu_2-tr_2$) confluent with the furcal bridge [12:2] is present in Sapygidae, Sierolomorphidae, Pompilidae (Fig. 42), Scoliidae and Vespidae (Fig. 41). Under the most recent hypothesis of relationships for Vespoidea (Brothers and Carpenter 1993), the ventral process is derived independently in Sapygidae, Pompilidae and Scoliidae + Vespidae, although several models of state change are possible. Mutillidae (Fig. 18), Rhopalosomatidae (Fig. 19) and Bradynobaenidae have apparently retained muscle fb1 (fu_2-ba_3) [9:1] and have a characteristically shaped mesofurca, however these families are not regarded as sister taxa (Brothers 1975, Carpenter and Brothers 1993).

Apoidea have been separated into two groups, the Apiformes and the Spheciformes (Goulet and Huber 1993). Heterogynaidae have been included either within the Spheciformes (see Goulet and

Huber 1993) or as the sister group of Spheciformes + Apiformes (Carpenter and Brothers 1993). Apoidea (Figs. 45, 53), including Heterogynaidae, have the arms of the mesofurca and metafurca fused at the junction with the mesofurcal bridge and muscle 181 (fu_3-fu_2) is lost [11:1]. This feature is unique in Hymenoptera. In Vespoidea (Figs. 41, 42, 44), Spheciformes (Fig. 46) and Heterogynaidae, the base of the axillary lever is broadly fused to the lateral arm of the mesopostnotum. All Apiformes have the axillary lever separated from the mesopostnotum as an independent sclerite [2:6] (Fig. 45) (Snodgrass 1942).

PARSIMONY ANALYSIS

The mesofurcal-mesopostnotal complex represents a single system of inter-related characters, and it should not be used alone to form new hypotheses of relationships. However, it is of interest to determine if our interpretations of character state evolution are in fact the most parsimonious for these data. We tried two approaches to explore this question. First, we superimposed the data in Appendix 2 on existing hypotheses of relationships. PAUP Version 3.0s (Swofford 1985) was used to optimize the character state data in Appendix 2 on Figure 55 for Symphyta and Figures 55 and 56 for the entire Hymenoptera (using one fully resolved tree for Apocrita based on Rasnitsyn (1988) and Brothers and Carpenter (1993)). Iballidae was used to represent the groundplan of Apocrita in the former case, and each matrix included the outgroup (Appendix 2). All most parsimonious models of character state evolution were examined on these tree topologies.

Characters 1 and 4 are sensitive to assumptions about transformation series. As discussed above (Character Analysis), it seems most reasonable to assume that character 1 can evolve from state 0 to state 1 (unique for Hymenoptera), from state 1 to state 2 or state 3, from state 3 to state 4 and from state 4 to state 5; states 6 and 7 are independent derivations from state 5. Character 1 was ordered using a character state tree (or "stepmatrix" in PAUP) that specified the above transformation series. As discussed earlier, character 4 is treated as irreversible. The assumptions of additive coding for characters 1 and 4 are referred to as the Ordered Characters. Other characters were always treated as nonadditive (unordered).

For Symphyta, the models of character state change shown in Figure 55 are in fact the most parsimonious for that tree topology. 27 steps are required to explain the data (indices of homoplasy are not possible for characters ordered using step matrices). Different models of state change are possible for character 3 (because it is scored as missing in Pergidae and Orussidae) and character 5 (unknown polarity for ingroup). For character 5, the presence of state 2 in fossil Xyelinae argues that this condition is groundplan for Hymenoptera, but it is equally parsimonious (at least for extant taxa) to assume that state 1 is groundplan and state 2 arises in the interval below Macroxyelinae and remaining Hymenoptera (dashed line, Fig. 55). The latter solution would make Xyelidae paraphyletic. Treating all characters as nonadditive (unordered) does not change the tree length (27 steps, consistency index 0.81, retention index 0.77). In fact, the only effect is to allow for a number of alternate models of state change for character 1. In this case, it is equally parsimonious to assume any of states 0, 1, 2 or 3 in the nodes below Tenthredinoidea + remaining Hymenoptera and Cephidae + remaining Hymenoptera, a result that essentially discards the information in the transformation series. Optimizing the ordered data onto alternate hypotheses of Symphyta resulted in longer trees. Rasnitsyn's (1988) tree, with Macroxyelinae as sister group to Tenthredinoidea, is one step longer, because of the parallel loss of muscle 127 [7:1]. Königsmann's (1977) tree, with Symphyta monophyletic and Cephidae as sister group to Apocrita, requires 37 steps (character 3 optimized).

For Hymenoptera, similar results were obtained for optimizing the Ordered Character data onto one tree, which is summarized for Apocrita in Figure 56. 58 steps were required to explain the data. Different optimizations were possible for Character 1 for Chalcidoidea + Mymarommatoidea + Platygastroidea (if parallel loss of mesofurcal bridge [1:7] is preferred), and Character 9 in Vespoidea. In the former case, although it is equally parsimonious to assume loss of the mesofurcal bridge (1:7) followed by a gain [1:6], parallel loss of the bridge seems more likely. Likewise, it seems more likely to postulate a parallel loss of the furcal-basalare muscle [9:0] in Vespoidea. Treating all characters as nonadditive decreases the length of the hymenopteran tree by 5 steps because of a

different optimization for Character 4 (treated as irreversible in the ordered analysis) and reversals (4:1 to 4:0) are favoured. For this result, the loss of the posterior lobe of the laterophragma and associated muscle 116 (4:1) would be a synapomorphy of Orussidae and Apocrita and then the presence of both structures (4:0) would have to be regained at least 4 times within Apocrita. Although this may be a more parsimonious solution in terms of the number of steps, we feel it is an unacceptable model of character evolution and the assumption of irreversibility should be invoked.

Parsimony analysis using the branch and bound algorithm (Symphyta) or branch-swapping (Hymenoptera) was then performed on these data to determine if another tree topology would result in a more parsimonious solution. When characters are ordered as above, for Symphyta, 24 trees of 27 steps result (after derooting, condensing and rerooting the resulting trees in PAUP, which is necessary when using directed characters). Coding Anaxyelidae as state 1 (homoplastic) or state 3 (autapomorphic) had no effect on the number of steps or resulting trees. As should be apparent from Figure 55, the basal taxa (Xyelinae, Macroxyelinae and Pamphiliidae) are unresolved in each of the 24 trees. Tenthredinoidea is always resolved as monophyletic but with little or no further resolution and Cephidae is consistently placed as sister group to remaining Hymenoptera, as in Figure 55. Anaxyelidae and Siricidae form a trifurcation with Xiphydriidae + Orussidae + Apocrita while the latter three taxa are essentially unresolved. In other words, there is no more parsimonious interpretation of these data and the most parsimonious solutions are congruent with the data shown on Figure 55. When characters are unordered for Symphyta, 138 trees of 26 steps result. The strict consensus solution for these trees is almost completely unresolved. For Hymenoptera, the lack of character support in Apocrita resulted in a considerably shorter tree (40 steps for the Ordered Characters) but also provided no resolution of Apocritan relationships; the structure of the Symphyta portion remained unchanged.

CONCLUSIONS

The mesofurcal-mesopostnotal complex is a conservative character system that generally ex-

hibits few changes within families of Hymenoptera but undergoes considerable change at higher taxonomic levels. The most significant changes occur in the Symphyta, but additional characteristics of the mesofurcal-mesopostnotal complex provide characters that are useful in inferring relationships within Apocrita.

Of the competing hypotheses for relationships of Symphyta, those in Figure 55 are the most parsimonious using the hypotheses of character state transformation discussed in this paper. Exact search methods using additive (ordered) characters reproduce these relationships with the same number of steps and identical indices of character homoplasy and fit. Siricoidea are recognized as a paraphyletic group with respect to Apocrita. If Xyelidae are paraphyletic with the rest of Hymenoptera (Rasnitsyn 1980, 1988) and Macroxyelinae + Tenthredinoidea are monophyletic, then a minimum of one extra step is required for character 7 (loss of $fu_2\text{-sps}_1$). In sharp contrast, a monophyletic grouping for Symphyta with Cephidae as sister group to the Apocrita (Königsmann 1977) requires 11 additional steps for the same data. The phylogenetic hypothesis for Apocrita proposed by Rasnitsyn (1988; Fig. 56) was shorter than Königsmann's by only three steps (for character 4). Hypotheses based on parsimony are much shorter for Apocrita, even when characters are ordered, but these hypotheses should not be accepted until they can be included in a larger data set with other character systems.

Monophyly of Orussidae + Apocrita (*Vespina sensu* Rasnitsyn) is supported by 10 external characters of adults (Rasnitsyn 1988) and a shift of the furcal-coxal muscles from a posterior to an anterior attachment on the discriminial lamella of the mesosoma (Johnson 1988). No features of the mesofurcal-mesopostnotal complex discussed here provide support for the monophyly of Orussidae + Apocrita, without Xiphydriidae. The mesofurca and laterophragma of Orussidae is highly derived and the only potential synapomorphy for *Vespina* (Character 3: loss of muscle 150b, $fu_2\text{-pn}_{2p}$) is probably not homologous. The lack of 2ph-3ph in Siricidae and Xiphydriidae has been proposed as a potential synapomorphy for Xiphydriidae + Siricidae (Whitfield et al. 1992), but this muscle has also been lost independently in *Goniozus* (Bethyridae), *Cleptes* (Chrysididae), Formicidae and *Ampulex* (Sphecidae) (Daly 1963). Monophyly of

Xiphydriidae, Orussidae and Apocrita is supported by four synapomorphies. No evidence in the mesofurcal-mesopostnotal complex supports the inclusion of Xiphydriidae or Orussidae within Siricoidea or the monophyly of Anaxyelidae + Siricidae.

The monophyly of Apocrita is supported based on losses of the muscles $fu_2\text{-pn}_{2p}$, $fu_3\text{-sps}_2$, $fu_2\text{-ba}_3$, $pl_2\text{-fu}_{2b}$, and probably $t_3\text{-ba}_3$. Using the evolutionary scheme proposed by Rasnitsyn (1988), characters of the mesofurca and mesopostnotum were less useful for demonstrating relationships within Apocrita. Taxa which have retained the posterior lobe of the laterophragma and the associated muscle 116 are treated by Rasnitsyn (1988) as relatively derived taxa (especially Diapriidae and Cynipoidea). Rasnitsyn's hypothesis requires at least nine independent losses of character 4, if loss of both lobe and muscle is irreversible. This appears to be a poor character for postulating relationships. Loss of the mesofurcal bridge [1:7] could indicate support for the monophyly of Ceraphronoidea, but it is homoplastic within both Chalcidoidea and Platygastroidea. Some changes in shape of the axillary lever or mesofurcal bridge within Apocrita are difficult to categorize or to place into distinct transition series. Distinctive features such as the vestigial posterior laterophragmal lobe of Pelecinidae, Heloridae and Proctotrupidae are reductions and possibly convergent. The development and separation of the axillary lever, fusion of the mesofurca and metafurca, and the retention (or redevelopment) of muscle fb1 provide strong support for relationships within the Aculeata.

Changes in the mesofurcal-mesopostnotal complex probably result from an increased emphasis on the fore wings for flight, reduction of the metathorax and fusion of the first abdominal segment. Although the indirect flight muscles are the main wing depressors, the direct muscles of the mesothorax control flight through modifications of the pronation and rotation of the wings during the downstroke and by controlling the tension of the longitudinal flight muscles, thereby affecting the amplitude of the wing beat (Pringle 1957, 1960, 1961). In Apocrita, the axillary lever acts to turn the apex of the mesophragma and the associated fourth axillary sclerite (Weber 1925). This is a shift in function from the lower Hymenoptera where muscles 150a and 150b twist the posterior lobe of

the laterophragma, initiating a greater force upon the indirect phragmal flexor (muscle 116, t_2 - pn_2). The excision of the laterophragma in Xiphydriidae would reduce the effect of the anterior apodeme (= axillary lever) on the posterior lobe. Pringle (1960, 1961) proposed that the pleurosternal and axillary lever muscles control the power generated by the indirect flight muscles and thus the amplitude of the wing beat. The flexibility of the axillary lever reaches a maximum in the Apiformes in which complete separation from the laterophragma results in more powerful leverage upon the associated axillary sclerites of the forewing (Snodgrass 1942).

Homologies may not be clear in taxa from opposite ends of a phylogenetic tree. For example, Weber (1925) discusses the mesofurcal ring (=mesofurcal bridge) of Siricidae and Vespidae as non-homologous. Superficially they do look different, but by examining the intermediate stages the homologies can be verified. Changes in the mesofurca and mesopostnotum provide a number of characters that show informative transitions from the plesiomorphic states in Xyelidae, but only by comparing a large number of taxa do these transformation series become apparent. Nonadditive multistate characters are not as useful in building a classification because unlinked character states support only their inclusive members. However, *a priori* ordering of transformation series are dependent on previous classifications or on the presumed homology of sometimes very divergent character states. For example, placement of Cephidae as sister group to the Apocrita led to a misinterpretation of the hypostomal bridge by Ross (1937) and the mesofurcal bridge was not discussed as an important character by Rasnitsyn (1969, 1980, 1988). Present interpretations of changes in the mesofurca and mesopostnotum would have made little sense without the direction provided from new classifications for Symphyta proposed by Gibson (1985) and Rasnitsyn (1988). The current distribution of character states of the mesofurca and mesopostnotum within Apocrita seems incongruent with other character information. Perhaps as more characters are used to construct improved classifications of Apocrita, this will also change.

ACKNOWLEDGEMENTS

Gary Gibson and two anonymous reviewers provided valuable comments and criticisms. We thank Henri Goulet, John Huber, Lubomir Masner and especially Gary Gibson (all CNC) for providing specimens and guidance. Jeff Cumming (CNC) and Dave Smith (USNM) provided specimens of miscellaneous families that were important additions to the material examined. This study was supported by Hatch Project TEXO-6705 of J.B.W. for initial work carried out at Texas A&M University and an NSERC grant to D.C.D. for subsequent work done in Ottawa

LITERATURE CITED

- Alam, S.M. 1951. The skeleto-muscular mechanism of *Stenobracon deesae* Cameron (Braconidae, Hymenoptera) - An ectoparasite of sugarcane and juar borers of India. Part I Head and thorax. *Aligarh Muslim University Publications (Zoological Series)* 3: 76 pp. + 9 pls.
- Brodskiy, A.K. 1992. Structure, function, and evolution of the terga of wing-bearing segments of insects. II. Organizational features of the terga in different orders of insects. *Entomological Review* 71: 8-28.
- Brothers, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *Kansas University Science Bulletin* 50: 483-648.
- Brothers, D. J. and J. M. Carpenter. 1993. Phylogeny of Aculeata: Chrysoidea and Vespoidea. *Journal of Hymenoptera Research* 2: 227-304.
- Bucher, G. E. 1948. The anatomy of *Monodontomerus dentipes* Boh., an entomophagous chalcid. *Canadian Journal of Research (D)* 26: 230-281.
- Carpenter, J. M. 1986. Cladistics of the Chrysoidea (Hymenoptera). *Journal of the New York Entomological Society* 94: 303-330.
- Chapman, R. F. 1992. General anatomy and function. pp. 33-67. In *The Insects of Australia*, 2nd edition. Volume I. Melbourne University Press, Carlton. 1137 pp.
- Daly, H. V. 1963. Close-packed and fibrillar muscles of the Hymenoptera. *Annals of the Entomological Society of America* 56: 295-306.
- Daly, H. V. 1964. Skeleto-muscular morphogenesis of the thorax and wings of the honey bee *Apis mellifera* (Hymenoptera: Apidae). *University of California Publications in Entomology* 39: 77 pp.
- Duncan, C. D. 1939. A contribution to the biology of North American vespine wasps. *Stanford University Publications (Biological Sciences)* 8 (1): 272 pp.
- Gauld, I. and B. Bolton. 1988. *The Hymenoptera*. Oxford University Press, New York. 332 pp.
- Gibson, G. A. P. 1985. Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. *Canadian Entomologist* 117: 1395-1443.
- Gibson, G. A. P. 1986. Mesothoracic skeleto-musculature and mechanics of flight and jumping in Eupelminae (Hymenoptera, Chalcidoidea: Eupelminidae). *Canadian Entomologist* 118: 691-728.

- Gibson, G. A. P. 1993. Groundplan structure and homology of the pleuron in Hymenoptera based on a comparison of the skeletomusculature of Xyelidae (Hymenoptera) and Rhaphidiidae (Neuroptera). *Canadian Entomologist* 165: 165-187.
- Huber, J. T. and H. Goulet. 1993. *Families of Hymenoptera of the World Research Branch, Agriculture Canada. Publication 1894/E.* 668 pp.
- James, H. C. 1926. The anatomy of a British phytophagous chalcidoid of the genus *Harmolita* (*Isosoma*). *Proceedings of the Zoological Society of London* [1926] 75-182.
- Johnson, N.F. 1988. Midcoxal articulations and the phylogeny of the order Hymenoptera. *Annals of the Entomological Society of America* 81: 870-881.
- Kelsey, L.P. 1957. The skeleto-motor mechanism of the Dobson Fly, *Corydalus cornutus*. Part II. Pterothorax. *Memoirs of the Cornell University Agricultural Experimental Station* 346: 31 pp. + 55 figs.
- Kimsey, L. and R.M. Bohart 1990. *The Chrysidid Wasps of the World*. Oxford University Press: Oxford. 652 pp.
- Korn, W. 1916. Die muskulatur des Kopfes und des thorax von *Myrmelion europaeus* und ihr metamorphose. *Zoologische Jahrbucher* 68: 273-330.
- Königsmann, E. 1977. Das phylogenetische System der Hymenoptera. Teil 2: "Symphyta." *Deutsche Entomologische Zeitschrift (N.S.)* 24: 1-40.
- Königsmann, E. 1978a. Das phylogenetische System der Hymenoptera. Teil 3 "Terebrantes" (Unterordnung Apocrita). *Deutsche Entomologische Zeitschrift (N.S.)* 25: 1-55.
- Königsmann, E. 1978b. Das phylogenetische System der Hymenoptera. Teil 4 Aculeata (Unterordnung Apocrita). *Deutsche Entomologische Zeitschrift (N.S.)* 25: 365-435.
- Kristensen, N.P. 1992. Phylogeny of extant Hexapods. pp. 125-140. In *The Insects of Australia*, 2nd edition. Volume 1. Melbourne University Press, Carlton. 1137 pp.
- Lawrence, J.F., E.S. Nielson and I.M. Mackerras. 1992. Skeletal anatomy and key to orders. pp. 3-32. In *The Insects of Australia*, 2nd edition. Volume 1. Melbourne University Press, Carlton. 1137 pp.
- Maki, T. 1938. Studies on the thoracic musculature of insects. *Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University* 24: 343 pp. + 17 pls.
- Markl, H. 1966. Peripheres Nervensystem und Muskulatur im Thorax der Arbeiterin von *Apis mellifera* L., *Formica polyctena* Foerster und *Vespa vulgaris* L., und der Grundplan der Innervierung des Insektenthorax. *Zoologische Jahrbücher* 83: 107-184.
- Matsuda, R. 1970. Morphology and evolution of the insect thorax. *Memoirs of the Entomological Society of Canada* 76: 431 pp.
- Michener, C.D., 1944 Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History* 82: 157-326.
- Naumann, I.D. 1992. Hymenoptera. pp. 916-1000. In *The Insects of Australia*, 2nd edition. Volume 1. Melbourne University Press, Carlton. 1137 pp.
- Naumann, I.D. and L. Masner. 1985. Parasitic wasps of the proctotrupoid complex: a new family from Australia and a key to world families (Hymenoptera: Proctotrupeoidea *sensu lato*). *Australian Journal of Zoology* 33: 761-783.
- Pringle, J. W. S. 1957. *Insect Flight*. University Press, Cambridge. 132 pp.
- Pringle, J. W. S. 1960. The function of the direct flight muscles in the bee. *Proceedings of the 12th International Congress of Entomology* p. 660.
- Pringle, J. W. S. 1961. The flight of the Bumblebee. *Natural History* 70 (7): 20-29.
- Rasnitsyn, A. P. 1969. [Origin and evolution of the lower Hymenoptera.] *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 123: 196 pp.
- Rasnitsyn, A. P. 1980. [Origin and evolution of Hymenoptera.] *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 174: 190 pp.
- Rasnitsyn, A. P. 1988. An outline of evolution of the hymenopterous insects (Order Vespida). *Oriental Insects* 22: 115-145.
- Ronquist, F. and G. Nordlander. 1989. Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibalidae). *Entomologica Scandinavica, Supplement* 33: 60 pp.
- Ross, H. H. 1937. A generic classification of the Nearctic sawflies (Hymenoptera, Symphyta). *Illinois Biological Monographs* 34: 173 pp.
- Saini, M.S., S.S. Dhillon, and R. Agarwal. 1982. Skeletomuscular differences in the thorax of winged and non-winged forms of *Camponotus camelinus* (Smith) (Hym., Formicidae). *Deutsche Entomologische Zeitschrift (N.S.)* 29: 447-458.
- Sharkey, M. J. and D. B. Wahl. 1992. Cladistics of the Ichneumonoidea (Hymenoptera). *Journal of Hymenoptera Research* 1: 15-24.
- Shcherbakov, D. E. 1980. [Morphology of the pterothoracic pleura in Hymenoptera. 1. Groundplan]. *Zoologicheskii Zhurnal* 59: 1644-1653.
- Shcherbakov, D. E. 1981. [Modifications of the pterothoracic pleura in Hymenoptera. 2. Modifications of the groundplan]. *Zoologicheskii Zhurnal* 60: 205-213.
- Snodgrass, R. E. 1910. The thorax of Hymenoptera. *Proceedings of the United States National Museum* 39: 37-91 + 16 pls.
- Snodgrass, R. E. 1927. Morphology and mechanism of the insect thorax. *Smithsonian Miscellaneous Collections* 80 (1): 108 pp.
- Snodgrass, R. E. 1942. The skeleto-muscular mechanisms of the honey bee. *Smithsonian Miscellaneous Collections* 103 (2) 120 pp.
- Tulloch, G. S. 1935. Morphological studies of the thorax of the ant. *Entomologica Americana* 15: 93-130.
- Weber, H. 1925. Der thorax der Hornisse. *Zoologische Jahrbücher* 67: 1-100 + 4 pls.
- Weber, H. 1927. Die Gliederung der Sternalregion des Tenthredinidenthorax. Ein Beitrag zur vergleichenden Morphologie des Insektenthorax. *Zeitschrift für wissenschaftliche Insektenbiologie* 22: 161-198 + 6 pls.
- Whitfield, J. B. 1992. Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera *Journal of Hymenoptera Research* 1: 3-14.
- Whitfield, J. B., N. F. Johnson and M. R. Hamerski. 1989. Identity and phylogenetic significance of the

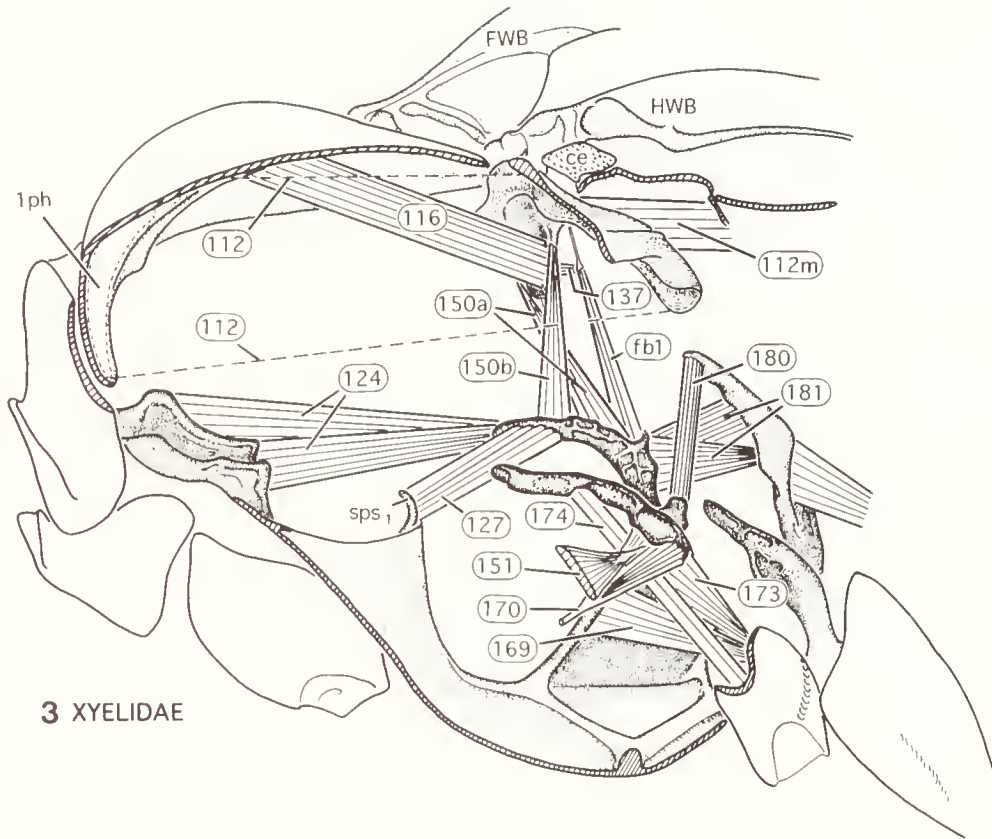


1 PAMPHILIIDAE

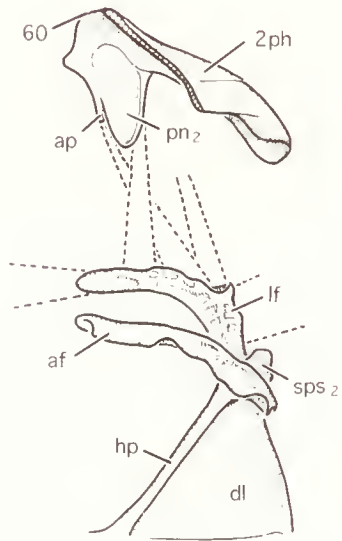


2

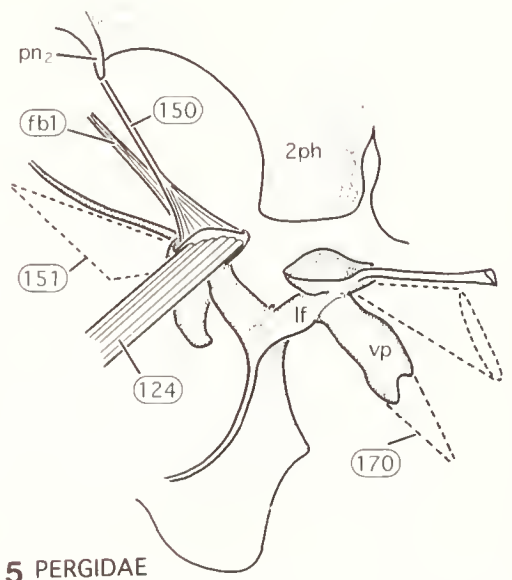
Figs. 1-2. Pamphiliidae. 1, *Pamphilius* sp., lateral habitus of mesosoma; 2, *Acantholyda* sp., sagittal section of mesosoma. Muscle 127 removed and location indicated by dashed line. Abbreviations as listed in Table 1 and Appendix 1.



3 XYELIDAE

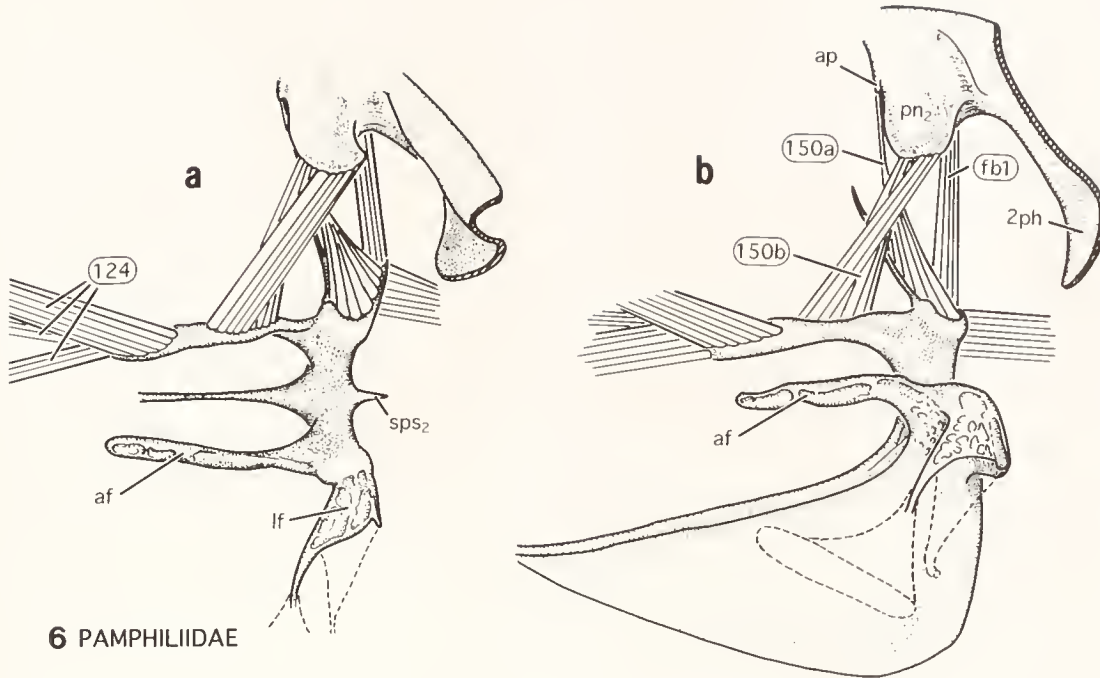


4 XYELIDAE

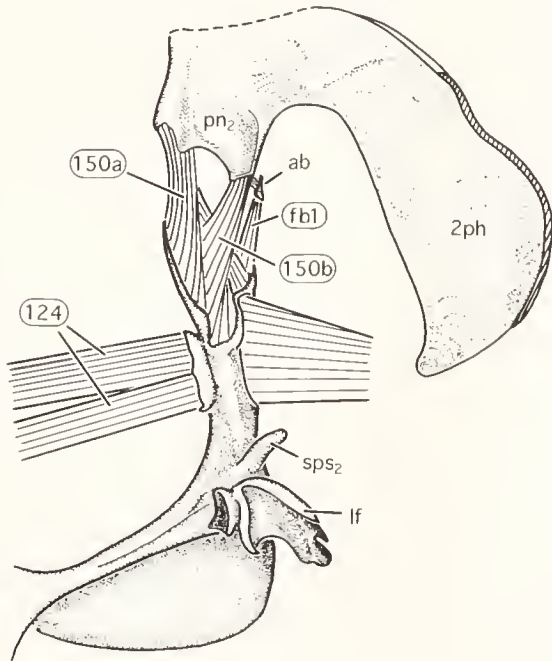


5 PERGIDAE

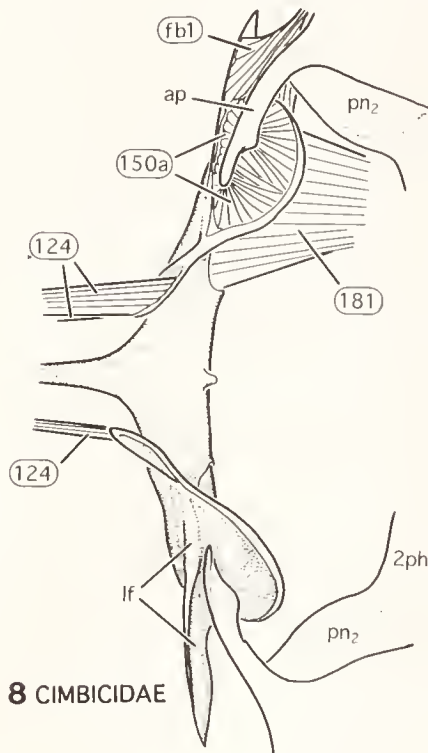
Figs. 3-5. 3, *Xyela minor*, oblique subsagittal section of mesothorax. 4, *Xyela minor*, skeletal components of Fig. 3, musculature removed. 5, *Acordulecera* sp., frontolateral view of MF-MPN complex. Abbreviations as listed in Table 1 and Appendix 1.



6 PAMPILIIDAE

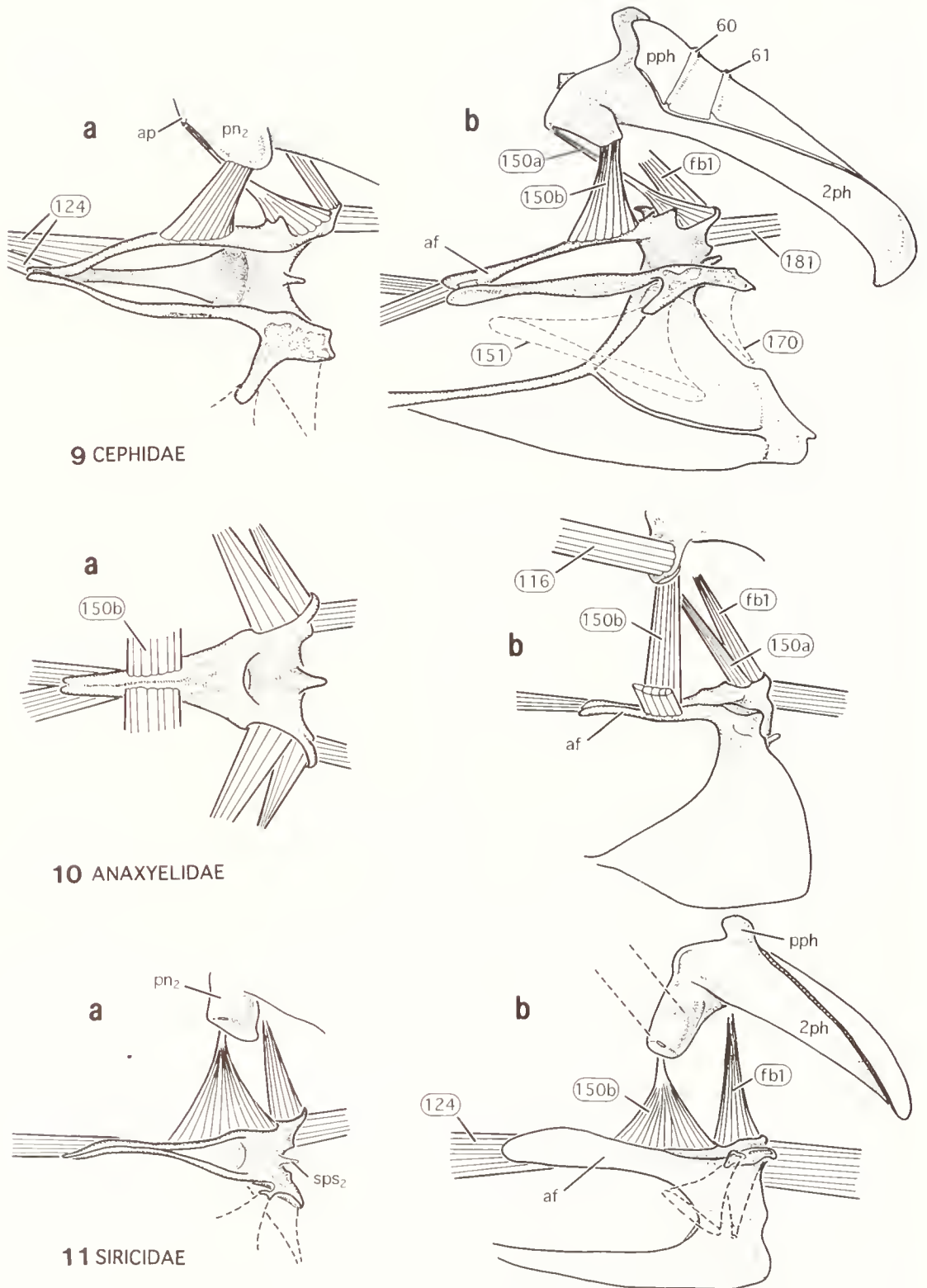


7 DIPRIONIDAE

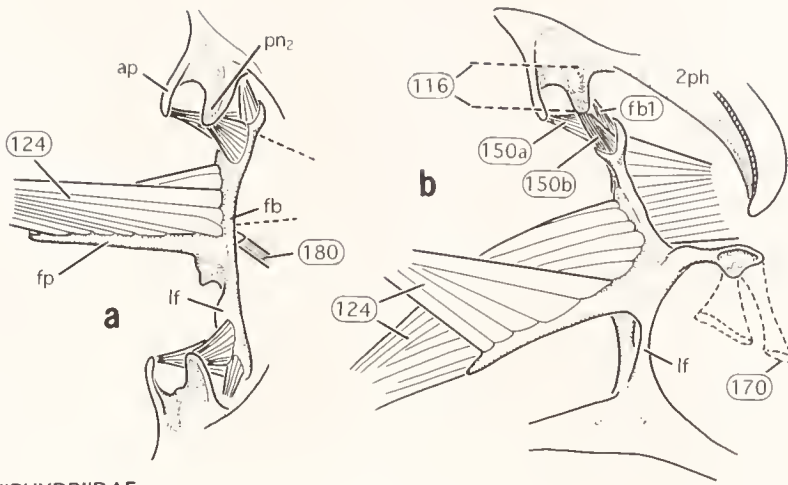


8 CIMBICIDAE

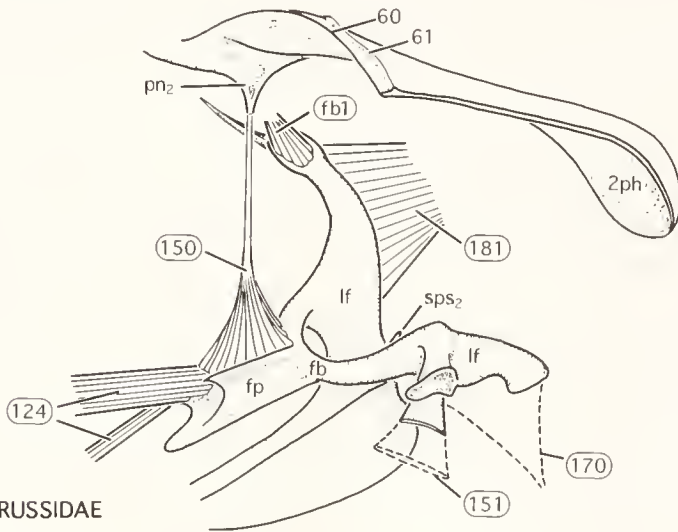
Figs. 6-8. 6, *Pamphilius* sp.: a, dorsal view of MF-MPN complex; b, lateral view of MF-MPN complex. 7, *Diprion* sp., supralateral view of MF-MPN complex. 8, *Zareaa* sp., dorsal view of MF-MPN complex. Abbreviations as listed in Table 1 and Appendix 1.



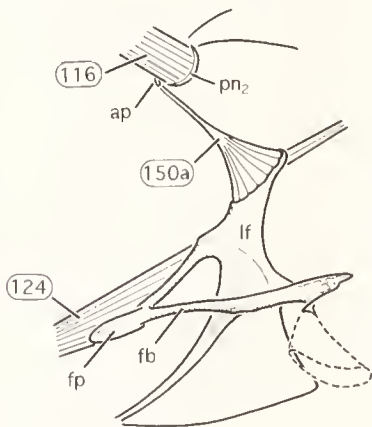
Figs. 9-11 MF-MPN complex. 9, *Cephus cinctus*: a, dorsal view; b, supralateral view. 10, *Syntexis libocedrii*: a, dorsal view; b, supralateral view. 11, *Tremex* sp.: a, dorsal view; b, lateral view. Abbreviations as listed in Table 1 and Appendix 1.



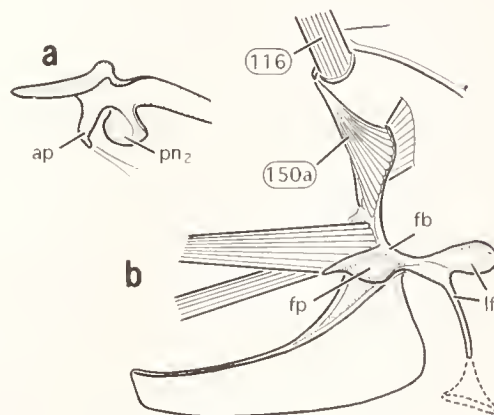
12 XIPHYTRIIDAE



13 ORUSSIDAE

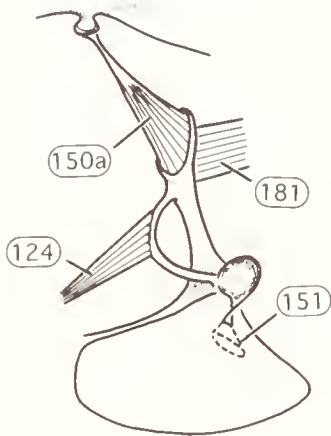


14 MONOMACHIDAE

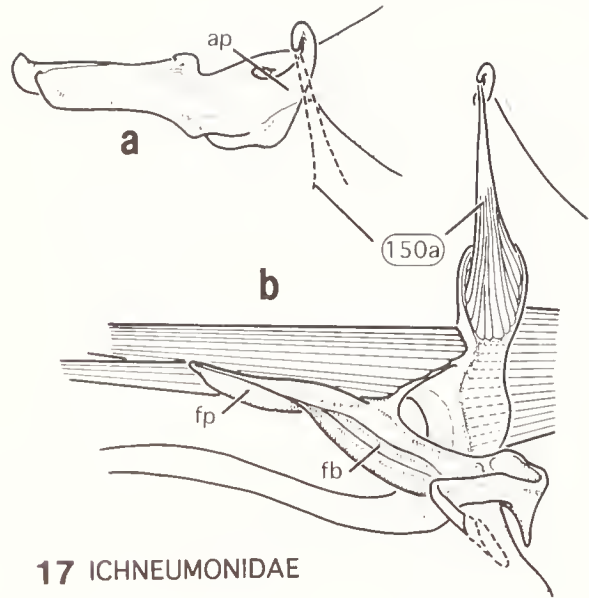


15 VANHORNIIDAE

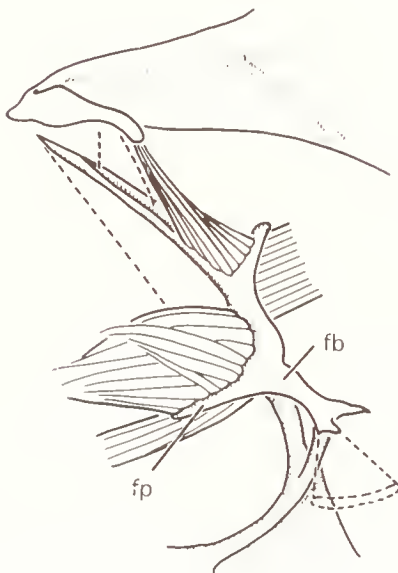
Figs. 12-15. MF-MPN complex. 12, *Xiphytria abdominalis*: a, dorsal view; b, supralateral view. 13, *Orussus sayii*, supralateral view. 14, *Monomachus* sp., supralateral view. 15, *Vanhornia cucnemidarum*: a, laterophragma; b, supralateral view. Abbreviations as listed in Table 1 and Appendix 1.



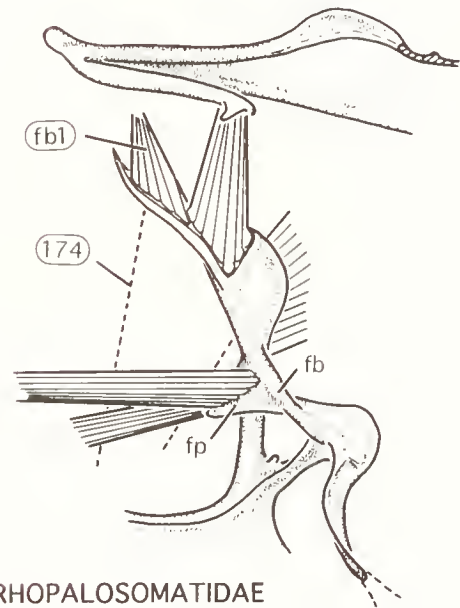
16 SCELIONIDAE



17 ICHNEUMONIDAE

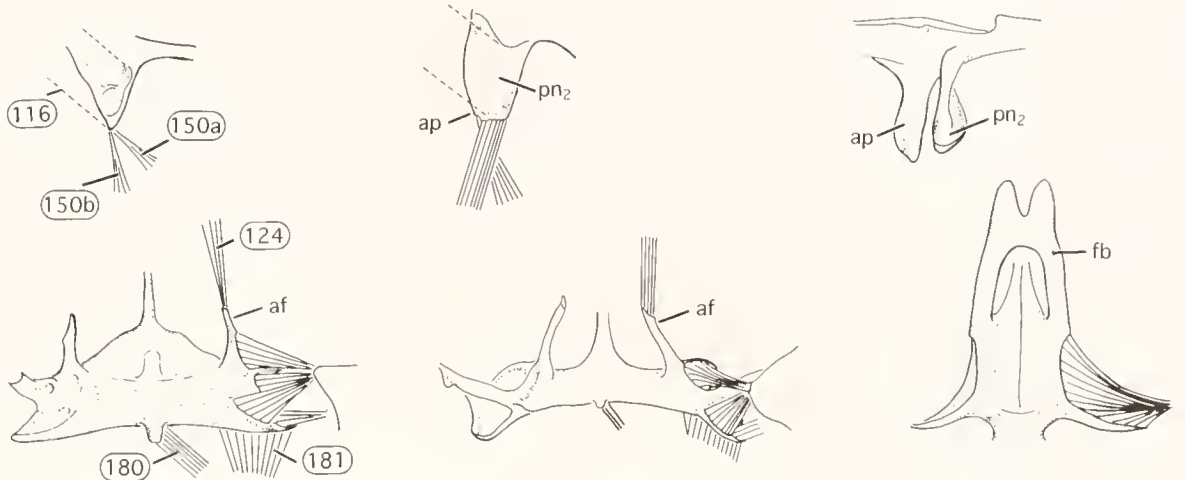


18 MUTILLIDAE



19 RHOPALOSOMATIDAE

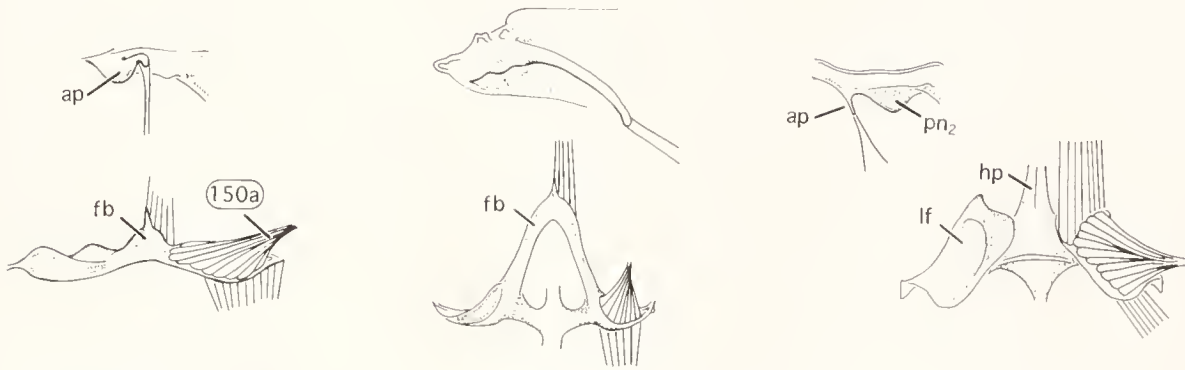
Figs. 16-19. MF-MPN complex. 16, *Sparasion* sp., supralateral view. 17, *Megarhyssa* sp. (Ichneumonidae): a, laterophragma (inner view); b, supralateral view. 18, Mutillidae (male), supralateral view. 19, *Rhopalosoma* sp., supralateral view. Abbreviations as listed in Table 1 and Appendix 1.



20 BLASTICOTOMIDAE

21 TENTHREDINIDAE

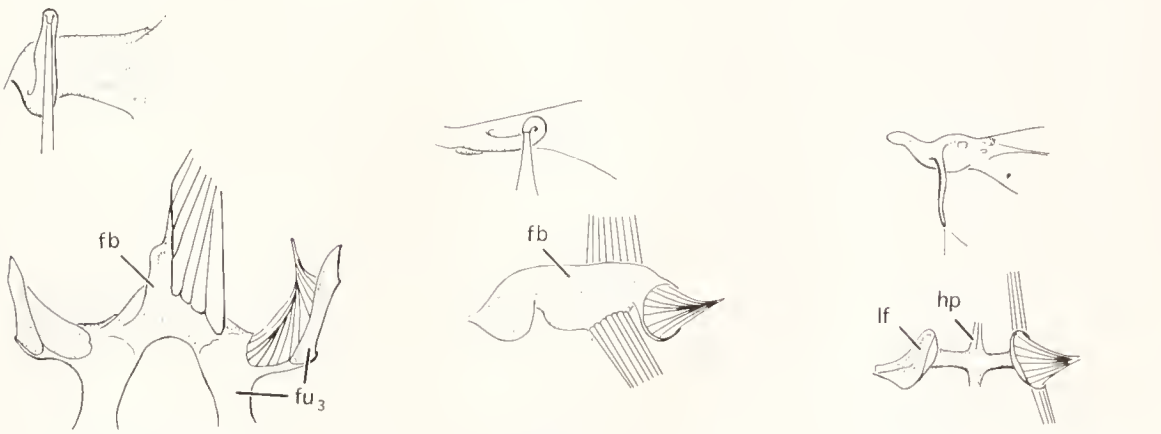
22 IBALIIDAE



23 TRIGONALYIDAE

24 STEPHANIDAE

25 MEGASPILIDAE

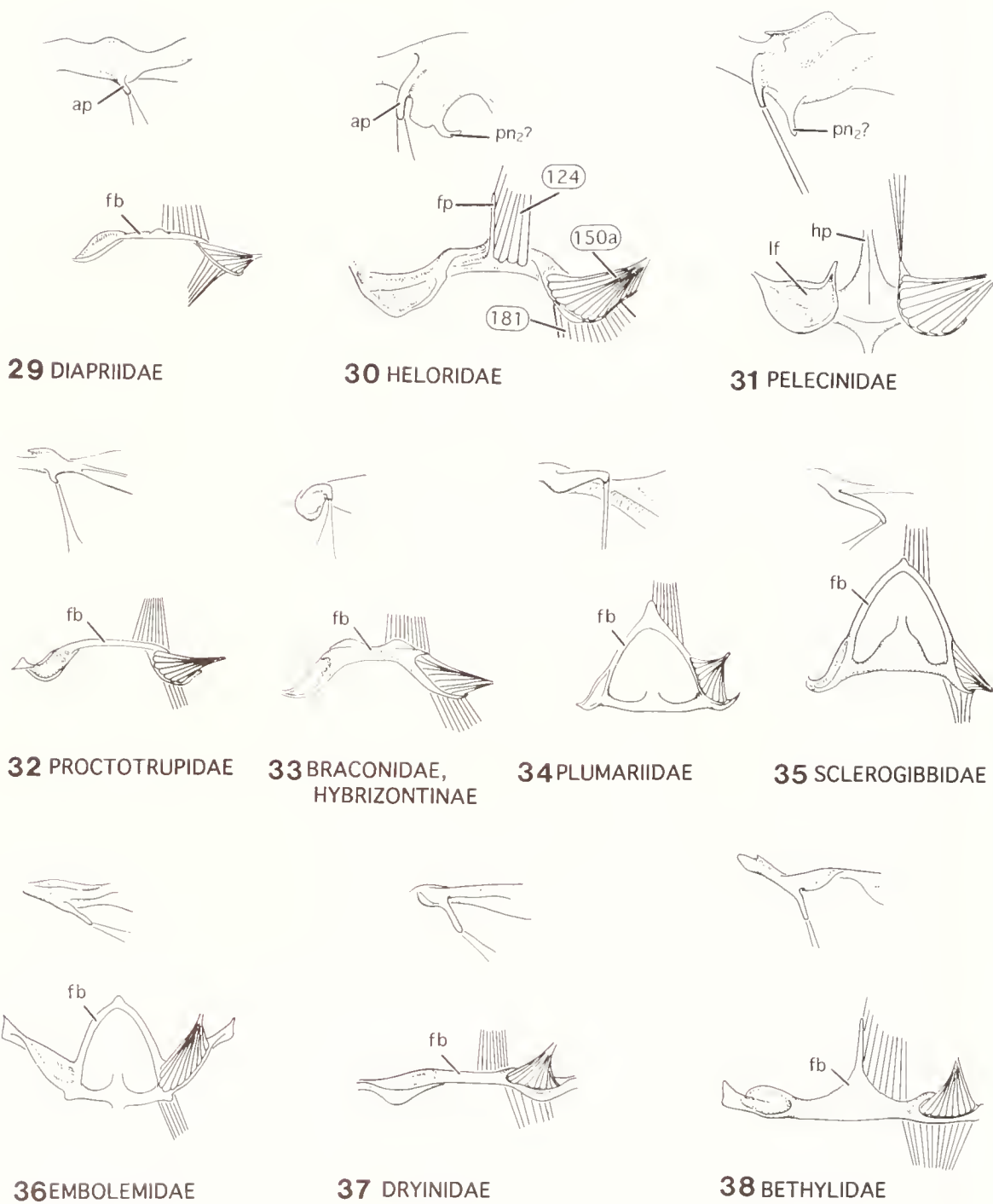


26 GASTERUPTIIDAE

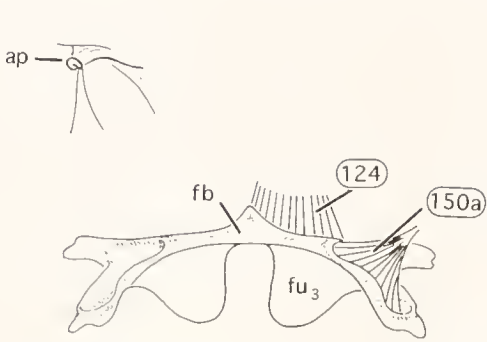
27 EVANIIDAE

28 PLATYGASTRIDAE

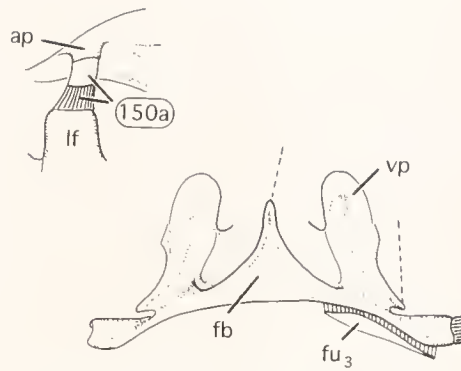
Figs. 20-28. MF-MPN complex of Apocrita: right laterophragma (upper figure); mesofurca in dorsal view (lower figure). 20, *Blasticotoma* sp.; 21, *Nematus* sp.; 22, *Ibalia* sp.; 23, *Orthogonalys pulchella*; 24, *Megischus* sp.; 25, *Megaspilus* sp.; 26, *Gasteruption* sp.; 27, *Hyptia* sp.; 28, *Isocybus* sp.



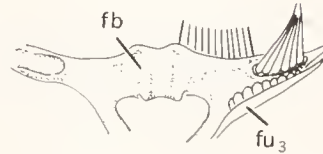
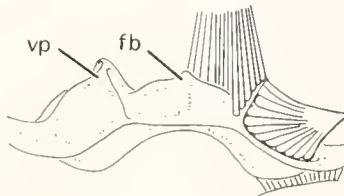
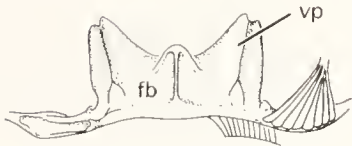
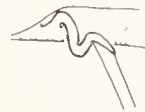
Figs. 29-38. MF-MPN complex of Apocnita. right laterophragma (upper figure); mesofurca in dorsal view (lower figure). 29, *Oxylabis* sp.; 30, *Helorus* sp.; 31, *Pelecimus polyturator*; 32, Proctotrupidae; 33, *Hybrizon* sp.; 34, *Plumaria* sp.; 35, Sclerogibbidae; 36, *Embolemus* sp.; 37, Gonatopodinae (male); 38, *Gontozus* sp



39 CHRYSIDIDAE, AMISEGINAE



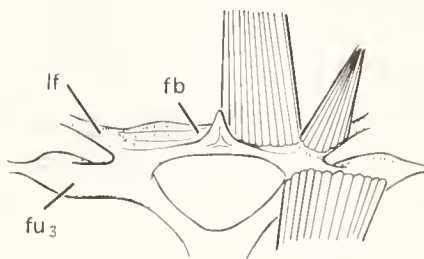
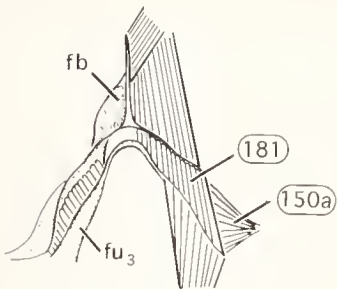
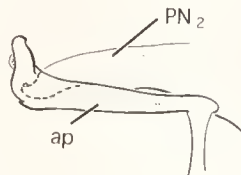
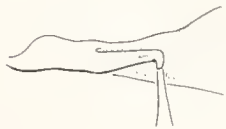
40 CHRYSIDIDAE, CHRYSIDINAE



41 VESPIDAE

42 POMPILIDAE

43 FORMICIDAE

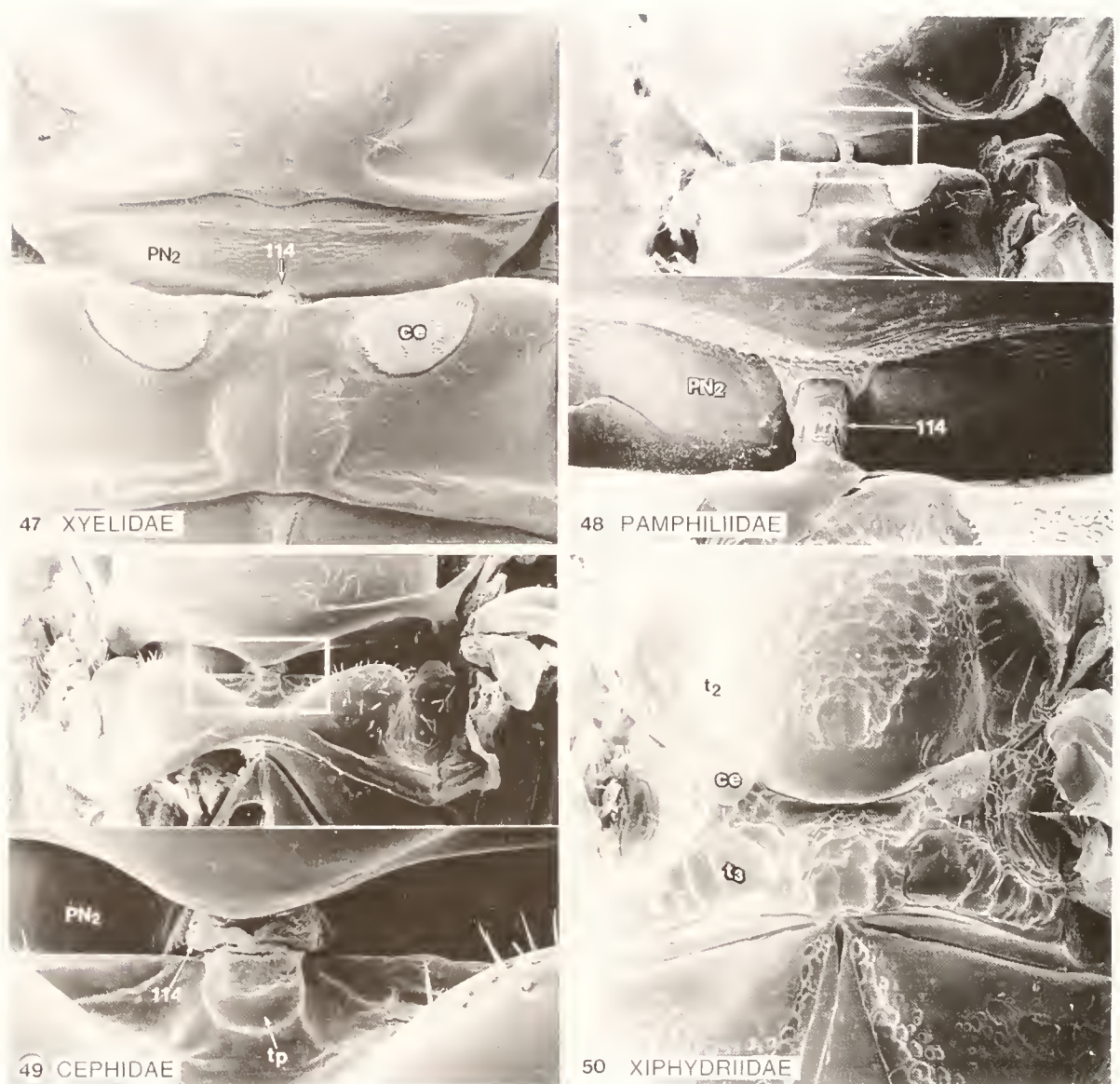


44 TIPHIIDAE

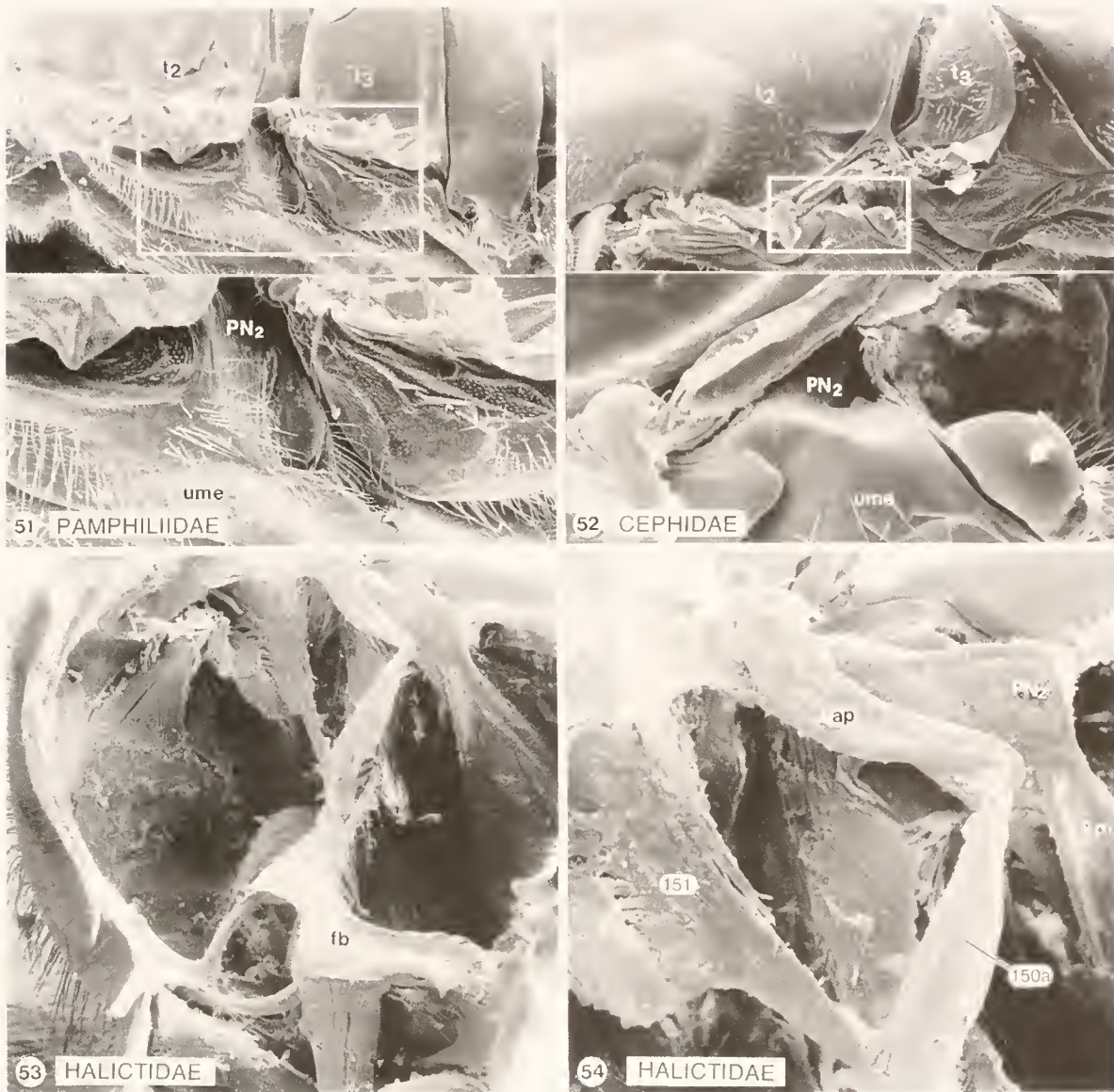
45 APIDAE

46 LARRIDAE

Figs. 39-46. MF-MPN complex of Apocrita: right laterophragma (upper figure); mesofurca in dorsal view (lower figure). 39, Amiseginae; 40, *Chrysis* sp.; 41, *Vesputa* sp.; 42, *Aporinella galapagoensis*; 43, *Camponotus planus*; 44, *Myzinum* sp.; 45, *Trigona* sp.; 46, *Larra* sp.



Figs. 47-50. Mesopostnotum, dorsal view. 47, *Pleuroneura* sp.; 48, *Pamphulus* sp.; 49, *Cephus cinctus*; 50, *Xiphydria abdominalis*. Abbreviations as listed in Appendix 1. Split figures are magnifications of highlighted area in upper figure.



Figs. 51-54. 51-52, Mesopostnotum in lateral view with magnification of connection to upper mesepimeron. 51, *Pamphilus* sp.; 52, *Cephus cinctus*. Arrow indicates articulation of laterophragma with upper mesepimeron. 53-54, MF-MPN complex of *Lasioglossum*, dorsolateral view. 53, fused meso- and metafurca; 54, magnification of axillary lever (ap). Other abbreviations as listed in Table 1 and Appendix 1. Split figures are magnifications of highlighted area in upper figure.

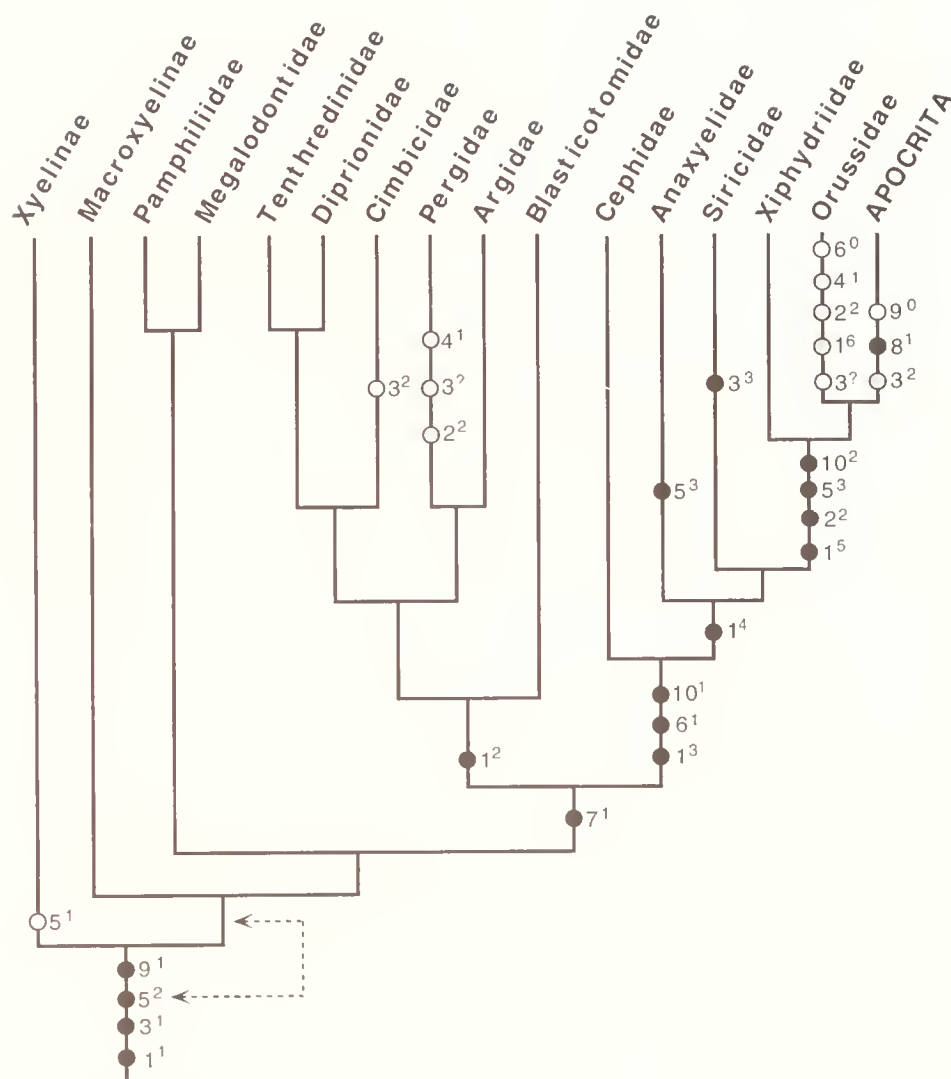


Fig. 55. Phylogenetic hypothesis for extant Hymenoptera based on Rasnitsyn (1988) and Gibson (1985, 1993), with characters of the MF-MPN complex superimposed. Characters and states discussed in text. Solid circles are unique apomorphies; shaded circles indicate convergence; open circle indicates reversal. Xyelidae are not demonstrably paraphyletic, but under some optimizations character 5:2 is treated as a synapomorphy of Macroxyelinae and the remaining Hymenoptera (dotted line to alternate placement, see text for discussion). Character 3:2 was not optimized, and this tree is two steps longer than found in the parsimony analyses (see text).

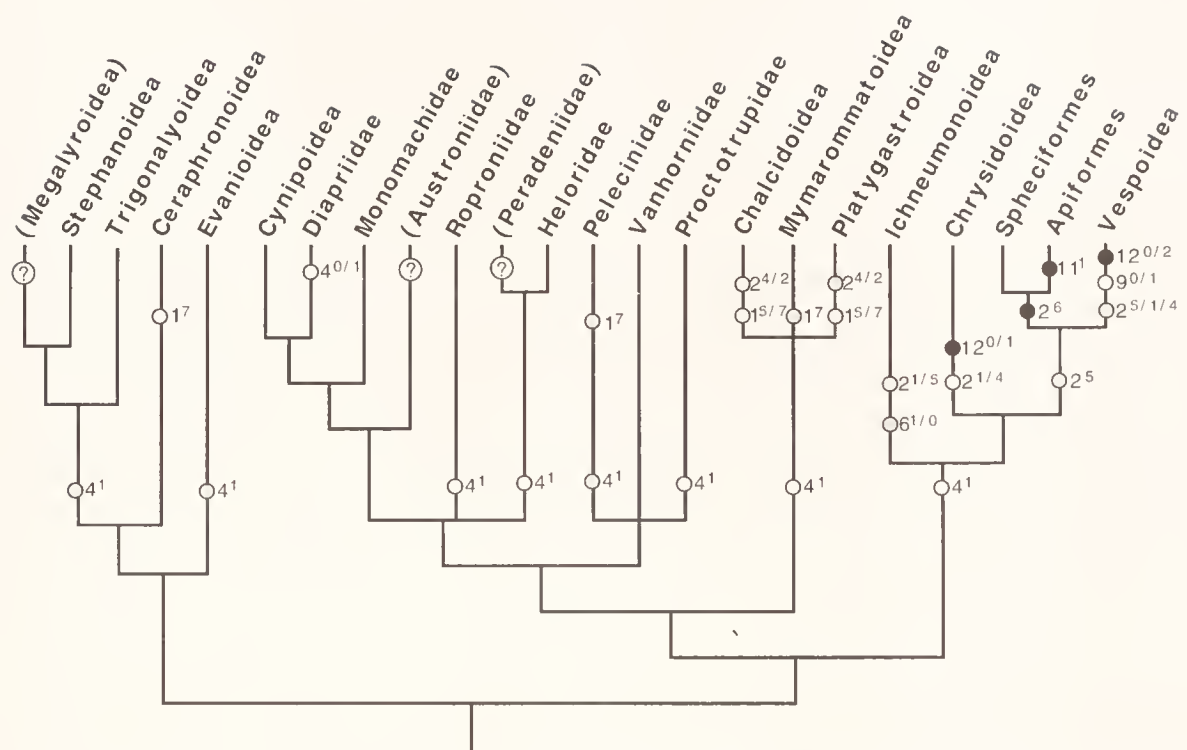


Fig. 56. Phylogenetic hypothesis for Apocrita based on Rasnitsyn (1988), with characters of the MF-MPN complex superimposed. Characters and states discussed in text. Placement of Peradeniidae and Vanhorniidae by Masner (pers. comm., 1993). Superfamily names follow Huber and Goulet (1993), those names in parentheses were not examined for internal characters and question marks indicate unknown character states. Solid circles are unique apomorphies; shaded circles indicate convergence; open circle indicates reversal. Multiple states indicate groundplan first followed by proposed derived state changes; changes listed in Appendix 2.

A Taxonomic Study of the genus *Ascogaster* in China* (Hymenoptera: Braconidae: Cheloninae)

YUQUING TANG AND PAUL M. MARSH

(YT) Biological Control Research Institute, Fujian Agricultural College, Fuzhou, Fujian, People's Republic of China; (PMM) Cooperating Scientist, Systematic Entomology Laboratory, U. S. Department of Agriculture (present address: P. O. Box 384, North Newton, Kansas 67117)

Abstract.—The chelonine genus *Ascogaster* is studied for the first time from the largely unknown area of mainland China and Taiwan. Twenty-three species are described and keyed, of which 13 are new to science and six are recorded for the first time from this area.

INTRODUCTION

Ascogaster Wesmael is a cosmopolitan braconid genus whose species are parasitic upon microlepidoptera, predominantly Tortricidae. Some species have been recorded frequently as parasitoids of several economically important insect pests and have been considered for use in biological control programs. About 110 species of *Ascogaster* have been recorded in the world. Huddleston (1984) revised the 30 Palaearctic species; Tobias (1986a, 1986b, 1988) and Papp (1989) added 12 species to this region. Shaw (1983) reviewed 11 species for the Nearctic Region and described a related new genus, *Leptodrepana* (4 species). Walker and Huddleston (1987) recorded 12 species of *Ascogaster* in New Zealand. The fauna of the Indo-Australian Region is largely unknown, although Baker (1926) and Szépligeti (1905, 1908) described a few species. The *Ascogaster* fauna of China is especially poorly studied with only five species recorded, three from mainland China (Fahringer 1934; He, *et al* 1989) and two from Taiwan (Sonan 1932). In this work 23 species of *Ascogaster* in China are treated, of which 13 species are new to science and six are recorded for the first time from China.

MATERIALS AND METHODS

Approximately 1,200 specimens of Chinese *Ascogaster* were examined in this study, mostly from the collections of the Fujian Agricultural College, the Zhejiang Agricultural University, the Zoology Research Institute of Academia Sinica, the Taiwan Agricultural Research Institute and the American Entomological Institute. The following acronyms are used to identify collections that provided specimens for this study and several as the depositories for type material:

- AEIG American Entomological Institute, Gainesville, Florida, USA
- BM Bishop Museum, Honolulu, Hawaii, USA
- CNC Canadian National Collection, Agriculture Canada, Ottawa, Canada
- ELKU Entomological Laboratory, Kyushu University, Fukuoka, Japan
- FAC Biological Control Research Institute, Fujian Agricultural College, Fuzhou, China
- HNHM Hungarian Natural History Museum, Budapest, Hungary
- IRSNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
- TARI Taiwan Agricultural Research Institute, Wufeng, Taiwan
- UEI Entomological Institute, Hokkaido University, Sapporo, Japan
- USNM National Museum of Natural History, Washington, D. C., USA
- ZAU Department of Plant Protection, Zhejiang Agricultural University, Hangzhou, China

*Throughout this paper, China includes mainland China and Taiwan.

ZRI Zoology Research Institute, Academia Sinica, Beijing, China

We also examined available Palaearctic and Indo-Australian material in the U. S. National Museum of Natural History and some type material from other institutions as follows: USNM - *abdominator* Dahlbom, *albitarsus* Reinhard, *annularis* Nees von Esenbeck, *atamiensis* Ashmead (holotype, synonymized with *bidentula* Wesmael by Huddleston 1984), *bicarinata* Herrich-Shaffer, *bidentula* Wesmael, *brevicornis* Wesmael, *canifrons* Wesmael, *cinctus* Baker (holotype), *coelioxoides* (Baker) (holotype), *consobrina* Curtis, *detectus* Baker (holotype), *distinctus* Baker (holotype), *fullawayi* (Baker) (type series), *inconspicuus* Baker (holotype), *intensus* Baker (holotype), *laeviventris* Baker (holotype), *longulus* Baker (holotype), *luzonensis* Baker (holotype), *maculaticeps* Baker (holotype), *malayanus* (Baker) (holotype), *modestus* Baker (holotype), *philippinensis* Baker (type series), *quadridentata* Wesmael, *reticulata* Watanabe (type series), *rufidens* Wesmael, *rufipes* (Latreille), *vividus* Baker (holotype); BM - *argentea* Fullaway (syntypes); *rugosa* Fullaway (holotype); IRSNB - *armata* Wesmael (lectotype), *bidentula* Wesmael (lectotype), *brevicornis* Wesmael (lectotype), *canifrons* Wesmael (lectotype); *limitatus* Wesmael (syntypes, synonymized with *scabricula* (Dahlbom) by Huddleston 1984), *quadridentata* Wesmael (type-series), *rufidens* Wesmael (type-series), *varipes* Wesmael (type series); UEI - *epinotiae* Watanabe (type series, synonymized with *quadridentata* Wesmael by Huddleston 1984); *reticulata* Watanabe (type series); ELKU - *longicornis* Huddleston (holotype, synonymized with *formosensis* Sonan, new synonymy); HNHM - *nilena* Papp (holotype).

The general braconid morphological terminology and measurements used in this study are mostly after van Achterberg (1988). The terminology used for wing veins is illustrated and explained in Sharkey (1988). Microsculpture terms are based on Harris (1979). Two character states of the ocellar triangle are defined after Huddleston (1984) as follows: where a straight line drawn between the anterior borders of posterior ocelli also touches the anterior ocellus, the ocelli are referred to as being 'on line'; where a line between the posterior ocelli passes behind the anterior ocellus without touching it, the ocelli are referred to as being 'not on line'. The measurements OO and OD refer,

respectively, to the ocellar-ocular distance and the diameter of the posterior ocellus. The ratio CL/CW is carapace length (CL) to carapace width (CW). Shaw (1983) and Huddleston (1984) discussed the important taxonomic characters of *Ascogaster* in detail and we have used most of the specific characters used by Huddleston (1984) for the description of new species in this study (see discussion under generic diagnosis). All dates from labels on specimens examined have been standardized thus, I-1-93, to avoid confusion.

BIOLOGY

Members of *Ascogaster*, like all the chelonines, are internal egg-larval parasitoids of microlepidoptera, principally Tortricidae. They lay their eggs into the host egg, but their larval development is delayed at the first instar until the host larva is mature. Little detailed work has been done on the biology of *Ascogaster*. Huddleston (1984) and Shaw (1983) reviewed the hosts of *Ascogaster* for the Palaearctic and Nearctic Regions respectively. Cox (1932), Rosenberg (1934) and Boyce (1936) gave fairly detailed accounts of the biology of *A. quadridentata* Wesmael. A research group in Japan has recently studied in some detail host-searching, host-preference, mating and oviposition behavior of *A. reticulata* Watanabe, an important parasitoid of the smaller tea tortrix, *Adoxophyes* sp., in Japan (Kainoh 1986, 1988; Kainoh, *et al.* 1982; Kainoh, *et al.* 1991; Kainoh and Tamaki 1982, 1988; Kainoh, *et al.* 1990; Kainoh, *et al.* 1989; Kamano, *et al.* 1989; Kawakami 1985; Kawakami and Kainoh 1985, 1986). Little is known at present about the biology of the Chinese *Ascogaster* species, however He *et al.* (1987) gave a full host list of *A. reticulata* in mainland China.

SYSTEMATICS

The Cheloninae are distinguished from all other subfamilies of Braconidae by the combination of having the first three metasomal terga fused to form a carapace (Figs. 21-26), having a complete postpectal carina and three submarginal cells in the forewing (Fig. 1). Two tribes of the Cheloninae, Chelonini and Phanerotomini, are represented in the Palaearctic and Indo-Australian regions. In the Phanerotomini the carapace is divided into three tergites by two transverse su-

tures; in the Chelonini the carapace has no trace of sutures. The Chelonini are represented in the Palaearctic and Indo-Australian regions by three genera, *Ascogaster* Wesmael, *Megascogaster* Baker and *Chelonus* Panzer. The former two genera can be separated from *Chelonus* by having the first submarginal cell always separated from the discal cell by vein 1-Rs+M (Rs+M of some authors) (Fig. 1). Many authors (e.g. Baker 1926; Shaw 1983; Huddleston 1984; Walker and Huddleston 1987; van Achterberg 1990b; Zettel 1990) state that *Ascogaster* is also characterized by having hairless eyes. However, we have described one new species, *A. setula* from Taiwan, with eyes densely and distinctly setose (Fig. 8), but with most of the other characters of typical *Ascogaster*. We include it within *Ascogaster* until more species with this unusual character have been found. *Megascogaster* Baker is distinguished from *Ascogaster* only by having a very elongate carapace (distinctly longer than head and thorax) and a slender stigma in the forewing. The taxonomic position of *Megascogaster* Baker must wait until more material from the Indo-Australian region has been studied. Shaw (1983) cited thirteen characters for distinguishing *Ascogaster* and *Leptodrepana*, however intermediate forms of most characters occur in many undescribed Indo-Australian *Ascogaster* which we have

examined and we have chosen to follow van Achterberg's synonymy. This concept makes *Ascogaster* an apparent polyphyletic group and we feel that a thorough phylogenetic study of the entire genus is needed before the correct position of *Leptodrepana* and the many other unusual forms from the Indo-Australian Region can be settled. That is beyond the scope of this limited study which aims only to identify species from the previously unknown area of China.

Ascogaster Wesmael

Ascogaster Wesmael 1835:226. Type-species: *Ascogaster instabilis* Wesmael [= *abdominator* (Dahlbom)], subsequently designated by Foerster (1862).

Cascogaster Baker 1926:482. Type-species: *Cascogaster fullawayi* Baker, original designation; syn. by Watanabe (1937).

Leptodrepana Shaw 1983:37. Type-species: *Leptodrepana opuntiae* Shaw, original designation; syn. by van Achterberg (1990b).

Diagnosis.—Distinguished from all other braconid genera by having: (a) the first three metasomal terga fused into a rigid carapace without transverse sutures; and (b) the forewing with three submarginal cells and vein 1-Rs+M present, separating the first submarginal and discal cells.

KEY TO THE ASCOGASTER SPECIES OF CHINA

- 1 Face punctate or rugose-punctate, occasionally nearly smooth; mesonotum usually predominantly punctate, notauli usually distinct 2
- Face strongly areolate or areolate-rugose, at least finely areolate-rugose; mesonotum usually coarsely areolate-rugose so that notauli often are indistinct 13
- 2(1) Setae on upper part of face pointing upwards; ocellar triangle acute, ocelli usually not on line or almost on line; propodeum without mediodorsal and apicolateral tubercles 3
- Setae on upper part of face pointing downwards; ocellar triangle always obtuse, ocelli usually on line; propodeum with distinct mediodorsal and apicolateral tubercles 6
- 3(2) Clypeus with conspicuous dentate flanges laterally; legs completely black or sometimes fore tibia reddish-brown; ovipositor sheaths broad, knife-like *semenovi* Telenga
- Clypeus without dentate flanges laterally; legs mostly yellow or yellow-brown; ovipositor sheaths not conspicuously broad and knife-like 4
- 4(3) Clypeus with a large median incision apically; female carapace with a conspicuous dorsal prominence at base *dimorpha* Tang and Marsh, new species
- Clypeus without any medial apical tubercle or incision; carapace without a dorsal prominence at base 5
- 5(4) Vein r of forewing about 1.0-1.2 times as long as 3-RS; hind coxa of male completely yellow *townesi* Tang and Marsh, new species
- Vein r of forewing about twice as long as 3-RS; hind coxa of male mostly black *yunnanica* Tang and Marsh, new species

- 6(2) Eyes distinctly setose; antennae short, with 26-29 flagellomeres; body 2.9-3.1 mm
 *setula* Tang and Marsh, new species
- Eyes without setae or at most with only a few minute setae; antennae longer, generally with more than
 30 flagellomeres; body generally more than 3.2 mm 7
- 7(6) Mesopleuron completely coarsely areolate-rugose so that precoxal suture not distinct; antennae very
 long, 45-49 flagellomeres; apical border of clypeus weakly marginate medially ..*formosensis* Sonan
- Mesopleuron at least in part smooth or punctate, precoxal suture usually distinct (except *varipes*);
 antennae shorter, at most with 40 flagellomeres; apical border of clypeus either produced or with one
 or two small tubercles 8
- 8(7) Apical border of clypeus transversely impressed and produced medially but without medial excision or
 tubercles 9
- Apical border of clypeus with one or two distinct teeth medially 11
- 9(8) Hind coxa strongly strigate; carapace short, oval in dorsal view; mandible at base with a deep,
 semicircular depression *varipes* Wesmael
- Hind coxa largely smooth or finely punctate; carapace elongate, clavate in dorsal view; mandible at base
 with vertical, parallel-sided depression 10
- 10(9) Legs yellow except hind coxa at base black, apex of hind femur and tarsi infusate *consobrina* Curtis
- Legs black except tibiae at base and basal tarsus of hind leg ivory or pale yellow *albitarsus* Reinhard
- 11(8) Apical border of clypeus with two medial tubercles, generally with a small excision between them; if
 excision absent, then medial clypeal border with a narrow, spatulate projection, but never a medial
 tooth *arisanica* Sonan
- Apical border of clypeus with a single medial pointed tooth 12
- 12(11) Carapace short, oval, broadest at about middle point in dorsal view; ventral opening of carapace shorter
 in front of apex; hind coxa completely yellow *perkinsi* Huddleston
- Carapace longer, clavate, broadest in posterior third in dorsal view; ventral opening of carapace long at
 apex of carapace; hind coxa predominantly black *lini* Tang and Marsh, new species
- 13(1) Carapace elongate, CL/CW more than 2.0 14
- Carapace shorter, usually oval, CL/CW generally 1.7 or less, never more than 2.0 15
- 14(13) Hind coxa strigate and black; ventral opening of carapace short, reaching only slightly beyond middle
 of carapace *grandis* Tang and Marsh, new species
- Hind coxa smooth or finely punctate, yellow; ventral opening of carapace longer, reaching apical 1/4 of
 carapace *macrogaster* Tang and Marsh, new species
- 15(13) Gena long and straight in face view; hind coxa strigate and yellow *chaoi* Tang and Marsh, new species
- Gena more or less rounded in face view; hind coxa often punctate or if strigate, then always mostly black
 16
- 16(15) Interantennal carina strongly raised into an erect triangular flange between scapes 17
- Interantennal carina present but never strongly raised into a triangular flange between scapes 19
- 17(16) Carapace rounded, without a tubercle apically; clypeus matte, rugose-punctate, its apical border straight
 with no medial tooth *armatoides* Tang and Marsh, new species
- Carapace apically pointed, with a tubercle at apex; clypeus smooth, sparsely punctate, its apical border
 pointed with a medial tooth 18
- 18(17) Carapace oval; face and temple areolate-rugose *acutus* Tang and Marsh new species
- Carapace acutely pointed; face and temple strongly and coarsely rugose *fullawayi* (Baker)
- 19(16) Hind coxa smooth, or finely punctate, yellow or infusate at base; hind tibia with a medial pale colored
 band; clypeus transversely impressed apically, without a medial tooth or if with a medial tooth, then
 lower part of face smoother than upper part 20
- Hind coxa strigate, at least at part, always black; hind tibia generally completely black or pale at base,
 but never with a medial pale-colored band medially; clypeus always with a distinct medial tooth; face
 evenly areolate or strongly areolate-rugose 21
- 20(19) Clypeus matte, rugose-punctate, straight apically, with no medial tooth; face strongly areolate
 *reticulata* Watanabe
- Clypeus smooth, finely and sparsely punctate, with a distinct medial apical tooth; face finely areolate-
 rugose *rugulosa* Tang and Marsh, new species
- 21(19) Anterior corners of middle mesonotal lobe swollen, notauli distinct; palpi black
 *gibbosa* Tang and Marsh, new species

- Anterior corners of middle mesonotal lobe not swollen, notauli indistinct; palpi yellow or reddish-brown 22
- 22(21). Temple short, about equal in width to eye in dorsal view; carapace short, oval in dorsal view, deep in lateral view *quadridentata* Wesmæl
- Temple rounded, distinctly longer than eye in dorsal view; carapace longer, clavate in dorsal view, not so deep in lateral view *hei* Tang and Marsh, new species

***Ascogaster acutus* Tang and Marsh,**
new species
Fig. 23

Female.—Length of forewing 2.5-2.7 mm, of body 3.0-3.2 mm.

Head.—Antenna with 28-32 flagellomeres, slightly dilated medially, medial flagellomeres slightly broader than long, apical ones longer than broad. Temple slightly contracted behind eyes, distinctly longer than length of eye in dorsal view. Occiput strongly concave. Ocelli small, on line, OO= 4.0 OD. Frons strongly depressed, finely rugose or smooth, medial carina distinct, extending from upper part of face between antennae to anterior ocellus and strongly expanded between antennae into an erect triangular lamella. Eyes protuberant, glabrous. Face slightly protuberant, about twice as broad as high, strongly areolate-rugose. Clypeus punctate, strongly divided from face, apical border produced medially into a small pointed tooth.

Mesosoma.—Pronotum slightly projecting in front of mesonotum, dorsolaterally rugose-punctate. Notauli not distinct; mesonotum completely coarsely rugose. Precoxal suture indistinguishable; mesopleuron strongly rugose. Propodeum coarsely areolate-rugose, divided by a transverse carina which is raised into a medial pair and a lateral pair of dentate flanges. Hind coxa strigate. Vein r of forewing about 1.0-1.5 times as long as 3-RS.

Metasoma.—Carapace (Fig. 23) short, with pointed tubercle at apex, areolate-rugose. Ventral opening of carapace longer, not distinctly in front of apex. Ovipositor concealed.

Color.—Black; carapace yellow at base; all legs yellow except hind coxa at base, tibia at apex and tarsi black.

Male.—Same as females except antenna not dilated medially, smaller yellow spot at basal carapace.

Holotype Female.—BEIJING CITY: Mentougou, VIII-25-81, M. S. Shi. Deposited in ZAU.

Paratypes.—BEIJING CITY: 1 female, Lugouqiao, IX-57, T. L. Chen; 1 male, IX-78, J. H. He. GUIZHOU PROVINCE: 1 female, Guiyang, V-13-85, Q. H. Luo. FUJIAN PROVINCE: 1 female, Shaowu, VII-20-45, H. F. Chao; 1 female, Shanhan, VII-19-21-88, Y. Ma. TAIWAN: 1 female Dutuanpi, VIII-5-82, K. C. Chou and C. N. Lin; 1 female, Wushe, IV-13-83, H. Townes; 1 female, Wushe, IV-19-83, H. Townes; 1 female, Wushe, V-3-83, H. Townes; 2 females, Wushe, V-10-83, H. Townes; 1 male, Wushe, V-15-83, H. Townes. Deposited in AEIG, FAC, TARI, ZAU and ZRI.

Host.—Unknown.

Distribution.—China (Beijing City, Guizhou Province, Fujian Province), Taiwan.

Remarks.—This species is very close to *fullawayi* (Baker) from which it can be distinguished by the characters mentioned in the key.

Etymology.—The specific name is from the Latin *acutus* meaning pointed in reference to the pointed tubercle at the apex of the carapace.

***Ascogaster albitarsus* Reinhard**

Ascogaster albitarsus Reinhard 1867: 364. Lectotype male, POLAND: Gdansk (designated by Huddleston 1984). Shenefelt 1973: 815; Huddleston 1984: 364; Papp 1989: 297.

Ascogaster leptopus Thomson 1874: 584. Lectotype female, SWEDEN (designated by Huddleston 1984 and syn. by Hellen 1953)

Diagnosis.—Length of forewing 3.3-3.5 mm, of body 3.9-4.0 mm. Antenna with 36-38 flagellomeres, slightly dilated medially (female); ocelli almost on line; face about 1.5 times as broad as high, rugose-punctate; clypeus with its apical border produced medially and slightly reflexed forwards; notauli distinct, foveolate, coalescing posteriorly in a large areolate-rugose area, rest of mesonotum densely areolate-punctate; precoxal suture strongly areolate-rugose anteriorly, rather weak posteriorly, mesopleuron anterodorsally strongly rugose, rest of mesopleuron finely punctate; hind leg predominately dark with base of

tibia and tarsus pale-yellow; hind coxa finely punctate; carapace long, clavate and widest in posterior third.

Specimens Examined.—HEBEI PROVINCE: 2 females. SICHUAN PROVINCE: 2 females.

Additional Specimens Examined.—WESTERN EUROPE: 1 male, det. by Huddleston, 1983.

Host.—A tortricid moth on pine tree.

Distribution.—China (Hebei Province, Sichuan Province), Korea and some European countries.

Remarks.—Our specimens from China have the mesopleuron with a polished impunctate area posteroventrally, but otherwise agreeing with the redescription of Huddleston (1984)

Ascogaster arisanica Sonan

Fig. 3

Ascogaster arisanicus Sonan 1932: 79. Holotype male, TAIWAN: Alishan (=Arisan). Watanabe 1937: 77 (as syn of *rufipes* (Latreille)); Chou 1981: 72 (notes on the locality of types).

Ascogaster arisanica Sonan: emended by Huddleston 1984: 365.

Diagnosis.—Length of forewing 2.9-3.2 mm, of body 3.3-3.7 mm. Antenna with 34-38 flagellomeres, moderately dilated medially (female); ocellar triangle obtuse, ocelli almost on line; face (Fig. 3) about 1.5 times as broad as high, densely punctate or rugose-punctate; apical border of clypeus produced, with a distinct medial excision flanked by two small tubercles; notauli shallow, coarsely rugose, coalescing posteriorly in an areolate-rugose area, rest of mesonotum punctate or rugose-punctate; precoxal suture broad, shallow, foveolate; rest of mesopleuron sparsely punctate except dorsally rugose; hind coxa finely punctate; carapace elongate, broadest in distal half; ventral opening of carapace conspicuously in front of apex.

Specimens Examined.—ZHEJIANG PROVINCE: 16 females, 9 males. SICHUAN PROVINCE: 2 females. YUNNAN PROVINCE: 1 male. GUANGXI PROVINCE: 1 female. HAINAN PROVINCE: 1 female. TAIWAN: 115 females, 35 males.

Host.—Unknown.

Distribution.—China (Zhejiang Province, Sichuan Province, Yunnan Province, Guangxi Province, Hainan Province), Taiwan, Japan.

Remarks.—Huddleston (1984) stated that "This

species is structurally very close to *bidentula*, but it can be distinguished by the more massive head and the more elongate carapace." However, our specimens generally have the heads not so massive as described by Huddleston. In Chinese specimens examined here, the temple is only 1.0-1.3 times as long as eye in dorsal view. Sonan (1932) named this species as *arisanicus*, however, the holotype is labelled '*Ascogaster arisensis* Sonan'.

Ascogaster armatoides Tang and Marsh, new species

Fig. 19

Female.—Length of forewing 3.5-3.6 mm, of body 4.2-4.4 mm.

Head.—Antenna with 42 flagellomeres, moderately dilated medially, medial segments about as broad as long. Temple constricted behind eyes, slightly shorter than length of eye in dorsal view. Occiput strongly concave. Ocelli very small, on line, OO = 4.0 OD. Frons strongly excavate behind antennae, smooth, with a distinct medial carina which is expanded between antennae into an erect triangular flange (Fig. 19). Eyes glabrous, strongly protuberant. Face slightly protuberant, about 1.5 times as broad as high, strongly areolate-rugose. Clypeus dull, rugose-punctate, not very distinctly divided from face; apical border convex, not produced medially and without distinct tooth or tubercle.

Mesosoma.—Pronotum slightly projecting in front of mesonotum, areolate-rugose laterally. Notauli indistinct; mesonotum strongly rugose. Precoxal suture indistinct; mesopleuron completely areolate-rugose. Propodeum strongly areolate-rugose, divided into dorsal and posterior surfaces by a transverse carina which is raised into a pair of medial blunt teeth and laterally a pair of less stout teeth. Hind coxa strongly strigate. Vein r of forewing about as long as 3-RS.

Metasoma.—Carapace short, CL/CW = 1.6, oval in dorsal view, somewhat pointed in lateral view, areolate-rugose. Ventral opening of carapace short, in front of apex. Ovipositor concealed.

Male.—Unknown.

Holotype Female.—GUANGXI PROVINCE: Longzhou, V-18-82, J. H. He. Deposited in ZAU.

Paratypes.—INDIA: 4 females, Anumatti, S. Coorg, II-52, P. S. Nathan. Deposited in CAN, USNM.

Host.—Unknown.

Distribution.—China (Guangxi Province), India.

Remarks.—This species is very close to *armata* Wesmael from which it can be distinguished by its longer antenna and less massive head.

Etymology.—The specific name is in reference to the similarity of this species to *armata*.

***Ascogaster chaoi* Tang and Marsh, new species**

Female.—Length of forewing 3.0-3.4 mm, of body 3.5-4.0 mm.

Head.—Antenna with 40-42 flagellomeres, strongly dilated medially, tapered at apex, medial segments slightly broader than long, apical segments about as long as broad. Temple constricted behind eyes, slightly longer than length of eyes in dorsal view. Occiput deeply concave. Ocelli small, $OO=3.5OD$, on line. Frons moderately depressed, finely punctate, with distinct medial carina. Eyes slightly protuberant, glabrous without distinct setae. Gena long and straight in face view. Face slightly protuberant, about 1.5 times as broad as high, areolate-rugose. Clypeus protuberant, punctate, distinctly divided from face; apical border slightly impressed laterally, produced medially into stout dentate flange.

Mesosoma.—Pronotum projecting in front of mesonotum, dorsolaterally areolate-rugose. Notauli indistinguishable; mesonotum strongly areolate-rugose. Mesopleuron completely rugose so that precoxal suture not distinct. Propodeum strongly areolate-rugose, with a medial transverse carina raised into a pair of medial stout dentate and a pair of lateral less stout dentate. Hind coxa strigate. Vein r of forewing 1.0-1.5 times as long as 3-RS.

Metasoma.—Carapace shorter, $CL/CW = 1.5-1.7$, somewhat pointed in dorsal view, rounded and deep in lateral view, areolate-rugose. Ventral opening of carapace short, distinct in front of apex. Hypopygium short. Ovipositor sheath clavate.

Color.—Black; carapace yellow at base; all legs yellow except hind femur and tibia black at apex.

Male.—Unknown.

Holotype Female.—FUJIAN PROVINCE: Huanggangshan, VII-14-85, Y. Q. Tang. Deposited in FAC.

Paratypes.—FUJIAN PROVINCE: 1 female, same as holotype; 6 females, Tongmuguan

(Wuyishan), VII-11-82, J. C. Huang; 1 female, Wuyishan, VI-80, H. F. Chao; 2 females, Shanguan (Wuyishan), VII-5-85, D. H. Huang and G. Zheng; 1 female, Wuyishan, VII-15-86, J. S. Wang. GUANGXI PROVINCE: 1 female, Tainlin, V-30-82, J. H. He; 1 female, Longsheng, VI-24-84, J. H. He. ZHEJIANG PROVINCE: 5 females, Songyang, VII-15-89, J. H. He and H. L. Chen; 1 female, Tianmushan, VI-17-83, Y. Ma. ANHUI PROVINCE: 1 female, Huangshan, VII-30-86, S. C. Zhang. JILING PROVINCE: 1 female, Dongliao, VII-20-31-88, X. M. Luo. Deposited in FAC, USNM, ZAU.

Host.—Unknown.

Distribution.—China (Jiling Province, Anhui Province, Zhejiang Province, Guangxi Province, Fujian Province).

Remarks.—This species is close to *quadridentata* from which it can be easily distinguished by its longer antenna, straight and long gena, and yellow hind coxa.

Etymology.—This species is named for Prof. H. F. Chao, Fujian Agricultural College, in appreciation for his outstanding contribution to the taxonomy of parasitic Hymenoptera in China.

***Ascogaster consobrina* Curtis**

Figs. 20, 27

Ascogaster consobrinus Curtis 1837: 672. Holotype male, GREAT BRITAIN: England. Shenefelt 1973: 819; Huddleston 1984: 367; Papp 1989: 297.

Diagnosis.—Antenna with 32-34 flagellomeres, slightly dilated medially (female); ocellar triangle obtuse, ocelli almost on line; face (Fig. 20) about 1.5 times as broad as high, areolate-punctate, hairs downwards; apical border of clypeus not retracted, medially produced into a broad, blunt point, without impression or tubercle; notauli distinct, foveolate, rest of mesonotum punctate except with a broad areolate-rugose area posteromedially; precoxal suture distinct foveolate, mesopleuron (Fig. 27) dorsally finely rugose-punctate except for a polished and impunctate area just dorsal precoxal suture, ventrally always sparsely punctate, shining; carapace rather long, clavate, widest in posterior third, with a downwardly directed anterior flange; hind coxa punctate, sometimes weakly rugose dorsally; hind leg yellow except coxa at base black, apex of femur and sometimes of tarsus infusate. Length of forewing 3.3-3.6 mm, of body 3.8-4.3 mm.

Specimens Examined.—ZHEJIANG PROVINCE: 1 female. TAIWAN: 89 females, 12 males.

Additional Specimens Examined.—Western European countries, 6 females, 10 males, det. by Huddleston, 1983.

Hosts.—No reared material was examined. Shenefelt (1973) recorded *Chelonia caja* and *Gelechia vulgella* as its hosts, but these records need to be confirmed.

Distribution.—China (Zhejiang Province), Taiwan., Japan, Korea, and several European countries (see Huddleston 1984: 367)

Remarks.—All specimens examined agree well with the redescription given by Huddleston (1984) except for the slightly shorter medial flagellar segments of the female, which are generally about as long as broad.

***Ascogaster dimorpha* Tang and Marsh,
new species**

Fig. 4

Female. Length of forewing 3.8 mm, of body 4.4 mm.

Head. Antenna, with 26 flagellomeres, flagellum slightly dilated medially, all segments longer than broad. Temple more or less rounded behind eyes, slightly longer than eye in dorsal view. Occiput strongly concave. Ocelli large, OO = 4.5 OD; ocellar triangle acute, ocelli not on line. Frons behind antenna moderately excavated, smooth anteriorly, rugose-punctate posteriorly. Eyes moderately protuberant, nearly glabrous with only few scattered minute setae. Gena contracted below in face view. Face (Fig. 4) slightly protuberant, about twice as broad as high, densely and regularly rugose-punctate, moderately hairy, the hairs on the upper part of the face pointing upwards. Clypeus moderately protuberant, rugose-punctate, but less densely than that of face, its apical border strongly incised medially.

Mesosoma.—Pronotum projecting in front of mesonotum, rugose-foveolate dorsolaterally. Notauli not very distinct, mesonotum finely punctate except with an areolate-rugose area posteromedially. Precoxal suture shallow foveolate, rest of mesopleuron punctate. Propodeum slightly impressed and punctate medially, strongly areolate-rugose laterally, but without distinct tubercles. Hind coxa smooth and shining. Vein r of forewing about 2.5 times as long

as 3-RS.

Metasoma.—Carapace long, CL/CW = 2.2, areolate-rugose, but finely and sparsely punctate apically, with a distinct dorsal prominence at base. Hypopygium large and broad. Ovipositor long slender, upcurved.

Color.—Black; legs yellow-brown except hind coxa at base and tarsis black, and hind tibia infusate with a pale-yellow band medially; carapace with yellow-pale spots at anterolateral sides; papli yellow-pale,

Males.—Same as female except antenna longer, not dilated medially, with 30-31 flagellomeres and carapace more slender, CL/CW = 2.3-2.5, more rounded and deeper apically, without a dorsal prominence at base. Length of forewing 3.6-3.9 mm, of body 4.3-4.5 mm.

Holotype Female.—ZHEJIANG PROVINCE: Songyang, VII-18-31-89, J. H. He. Deposited in ZAU..

Paratypes.—ZHEJIANG PROVINCE: 3 males, Songyang, VII-15-17-89, J. H. He. TAIWAN: 5 males, Meifeng 2150 m, -24-26-81, K. S. Lin and W. S. Tang (TARI); 1 male, Meifeng, VI-22-26-83, K. S. Lin and S. C. Lin. Deposited in TARI, ZAU.

Hosts.—Unknown.

Distribution.—China (Zhejiang Province), Taiwan.

Remarks.—This species belongs to the *caucasica*-group (*sensu* Huddleston 1984) by virtue of its punctate face, hair on the upper part of the face pointing upwards and the bidentate clypeus. It appears to be related to *caucasica* Kokujev and *bicarinata* Herrich-Schaffer, but is easily distinguished from the later two species by the characteristics of the carapace.

Etymology.—The specific name refers to the sexual dimorphism of the metasomal carapace.

***Ascogaster formosensis* Sonan**

Fig. 5

Ascogaster formosensis Sonan 1932:78. Holotype female, TAIWAN: Arisan, Kunkiko. Watanabe 1937:76; Shenefelt 1973: 822; Chou 1981: 72 (notes on the locality of types); Papp 1989: 297.

Ascogaster formosanus (!): Watanabe 1934: 198.

Ascogaster longicornis Huddleston 1984: 368. Holotype female, JAPAN: Mt. Tachibana (ELKU). New synonymy.

Diagnosis.—Antenna with 45-49 flagellomeres, medial segment weakly dilated; ocelli on line or

almost on line; face (Fig. 5) rugose-punctate, 1.2-1.5 times as broad as high; clypeus with its apical border rounded except its medial 1/4 weakly emarginate; notauli foveolate, rest of mesonotum densely punctate except posteromedially areolate-rugose; mesopleuron coarsely rugose so that precoxal suture not distinct; propodeum areolate-rugose with 4 prominent tubercles; hind coxa finely punctate; carapace always yellow at base, oval in dorsal view, clavate in lateral view, ventral opening of carapace distinctly in front of apex. Larger species, length of forewing 5.0-5.4 mm, of body 5.8-6.4 mm.

Specimens Examined.—YUNNAN PROVINCE: 1 female. TAIWAN: 15 females, 7 males.

Additional Specimens Examined.—NEPAL: 1 female, 1 male. INDIA: 6 females, 6 males. JAPAN: Holotype of *longicorinis* Huddleston.

Hosts.—Unknown.

Distribution.—China (Yunnan Province), Taiwan, India, Japan, Nepal.

Remarks.—This species is easily distinguished from other species of Chinese *Ascogaster* by its conspicuously long antennae and by the characteristics of its face and clypeus. It is very similar to *philippinensis* Baker from which it differs only in the sculpture of the mesonotum. We treat it here as a valid species given no intermediate forms are known.

Ascogaster fullawayi (Baker)

Figs. 7, 24

Cascogaster fullawayi Baker 1926: 483. Holotype female (cited as male), PHILIPPINES: Baguio, Benguet.

Ascogaster fullawayi: Shenefelt 1973: 822.

Diagnosis.—Antenna with 34-35 flagellomeres, slightly dilated medially; scrobes outwardly margined by high, thin and complete carina middle of which is raised into sharply angulate teeth; ocelli almost on line; face (Fig. 7) narrow, less 1.5 times as broad as long, strongly and coarsely rugose; clypeus smooth and shining, sparsely punctate, apical border acute; mesonotum between notauli swollen, strongly areolate-rugose; mesopleuron coarsely areolate-rugose, precoxal suture indistinguishable; hind coxa rugose-punctate; carapace (Fig. 24) acute with a tubercle at apex; ventral opening of carapace short, distinctly in front of apex.

Specimens Examined.—TAIWAN: 2 females.

Additional Specimens Examined.—Holotype of *fullawayi* (Baker), female, PHILIPPINES: Baguio, Benguet (USNM). Holotype of *fullawayi* var. *maquilingensis* (Baker), female, PHILIPPINES: Mt. Makiling, Luzon (USNM). Paratype of *fullawayi* (Baker), 1 female, PHILIPPINES: Imugin, N, Viscaya (USNM).

Hosts.—Unknown.

Distribution.—Taiwan, Philippines.

Remarks.—Two Taiwanese specimens examined agree well with the type of *fullawayi* (Baker) except that the antennae are shorter. This species is the only Philippine *Ascogaster* described by Baker (1926) found in China. It is distinguished from the other Chinese *Ascogaster* by the characteristics of the carapace and sculpture of the head.

Ascogaster gibbosa Tang and Marsh, new species

Fig. 28

Females.—Length of forewing 3.0-3.2 mm, of body 3.5-3.8 mm.

Head.—Antenna with 37-40 flagellomeres, slightly dilated medially, medial segments about as long as broad. Temple rounded behind eye, slightly shorter than eye in dorsal view. Occiput concave. Ocelli small, OO = 3.5-4.0 OD, on line. Frons moderately depressed, smooth, with a weak medial carina. Eyes protuberant, without distinct setae. Gena in face view contracted. Face about 1.5 times as broad as high, coarsely areolate-rugose. Clypeus distinctly divided from face, punctate, apical border produced medially into a strongly pointed large tooth.

Mesosoma.—Pronotum slightly projecting in front of mesonotum, dorsolaterally areolate-rugose. Notauli present, areolate-rugose; mesonotum (Fig. 28) between notauli strongly protuberant, rugose-punctate, rest of mesonotum areolate-rugose. Precoxal suture indistinguishable; mesopleuron completely areolate-rugose. Propodeum strongly areolate-rugose, divided by transverse carina which is raised medially and laterally into prominent dentate flanges. Hind coxa dorsally strigate. Vein r of forewing about as long as 3-RS.

Metasoma.—Carapace moderately long, CL/CW = 1.6-1.7, oval in dorsal view, somewhat pointed in lateral view. Hypopygium short.

Ovipositor short, straight.

Color.—Almost completely black except extreme apex of hind coxa and of femur yellow.

Male.—Unknown.

Holotype Female.—TAIWAN: Tsuifeng, VI-3-80, L. Y. Chou and C. C. Chen. Deposited in TARI.

Paratypes.—TAIWAN: 2 females, same as holotype; 2 females, Tsuifeng, VII-16-82, S. C. Lin and C. N. Lin; 1 female, Tsuifeng, VI-21-79, K. S. Lin and B. H. Chen; 1 female, Meifeng, VII-31-IX-2-82, L. Y. Chou and K. C. Chou; 1 female, Tayuling, IX-12-15-80, K. S. Lin and C. H. Wang. Deposited in TARI, USNM.

Host.—Unknown.

Distribution.—Taiwan.

Remarks.—This species can be easily distinguished from other species of the *quadridentata*-group (see Huddleston 1984:371) by the characteristics of the mesonotum and by the strongly pointed clypeus tooth and completely black body.

Etymology.—The specific name is from the Latin *gibbosus* meaning hunched or humped in reference to the strongly humped mesonotum.

***Ascogaster grandis* Tang and Marsh,
new species
Fig. 6, 21**

Females.—Length of forewing 4.0-4.1 mm, of body 4.8-5.0 mm.

Head.—Antenna with 37 flagellomeres; flagellum dilated medially, strongly tapered at apex, medial segments about as long as broad. Temple slightly constricted behind eyes, at least 1.5 times as long as eye in dorsal view. Occiput deep, concave. Ocelli very small, on line, $OO = 4.0 OD$. Frons strongly depressed, rugose-punctate. Eyes protuberant, glabrous, without distinct setae. Gena swollen in lateral view. Face (Fig. 6) slightly protuberant, about 1.5 times as broad as high, areolate-rugose, with medial carina dorsally. Clypeus slightly protuberant, punctate, distinctly divided from face, apical border impressed laterally, produced medially into a very small pointed tooth.

Mesosoma.—Pronotum strongly projecting in front of mesonotum, dorsolaterally rugose-punctate, smooth ventrally. Notauli not distinct, mesonotum strongly areolate-rugose. Precoxal suture indistinguishable, mesopleuron strongly areolate-rugose. Propodeum completely coarsely areolate-rugose, divided by a transverse carina

produced into medial and postero-lateral pairs of stout teeth. Hind coxa strongly strigate or areolate-rugose. Vein *r* of forewing about as long as 3-RS.

Metasoma.—Carapace (Fig. 21) very long, $CL/CW = 2.3-2.5$, areolate-rugose. Ventral opening of carapace very short, ending almost in middle of carapace. Ovipositor concealed.

Color.—Black; fore and middle legs yellow except coxae and femora black basally, hind leg black except trochanters reddish-brown; papli pale yellow.

Male.—Same as female except antenna not dilated medially.

Holotype Female.—ZHEJIANG PROVINCE: Xitianmushan, VII-29-84, X. J. Wu. Deposited in ZAU.

Paratypes.—ZHEJIANG PROVINCE: 1 male, same as holotype; 1 female, Xitianmushan, VII-27-84, X. J. Wu; 1 female, Xitianmushan, VII-22-87, X. M. Lou. Deposited in USNM, ZAU.

Host.—Unknown.

Distribution.—China (Zhejiang Province).

Remarks.—Both this species and *macrogaster*, new species, run into the *quadridentata*-group in the key of Huddleston (1984), but both of them are distinguished from species of this group by the characteristics of head shape and their elongate carapaces.

Etymology.—The specific name is from the Latin *grandis* meaning large in reference to the large expanded temple.

***Ascogaster hei* Tang and Marsh, new species
Figs. 15, 16**

Females.—Length of forewing 4.0-4.2 mm, of body 4.6-5.0 mm.

Head.—Antenna with 33-37 flagellomeres, moderately dilated medially, medial flagellomeres slightly broader than long. Temple rounded behind eyes, distinctly longer than length of eye in dorsal view. Occiput deeply concave. Ocelli small, $OO = 3.5-4.0 OD$, almost on line. Frons (Fig. 15) moderately depressed behind antennae, rugose-punctate, with a weak medial carina. Eyes protuberant, nearly glabrous but with a few scattered setae. Gena in face view contracted. Face (Fig. 16) about twice as broad as high, strongly areolate-rugose. Clypeus distinctly divided from face, punctate; apical border produced medially into a small

pointed tooth.

Mesosoma.—Pronotum projecting in front of mesonotum, dorsolaterally areolate-rugose. Notauli not distinct; mesonotum strongly areolate-rugose; precoxal suture indistinguishable; mesopleuron coarsely areolate-rugose. Propodeum strongly areolate-rugose, divided by a transverse carina which is raised medially and laterally into stout dentate flanges. Hind coxa strongly strigate. Vein r of forewing about as long as 3-RS.

Metasoma.—Carapace longer, CL/CW = 1.6-1.7, clavate in dorsal view. Ventral opening of carapace longer, not very distinctly in front of apex. Hypopygium short. Ovipositor sheaths clavate.

Color.—Almost completely black except fore tibia, and sometimes middle and hind coxae testaceous apically.

Male.—Same as females except antennae not dilated medially, with 34-35 flagellomeres.

Holotype Female.—ZHEJIANG PROVINCE: Fengyangshan, VIII-12-84, L. R. Sheng. Deposited in ZAU.

Paratypes.—JILING PROVINCE: 2 females, 3 males, Dongjiang, VII-20-31-88, X. M. Luo. HEILONHJANG PROVINCE: 1 female, Qingdinzhi, V-77, Y. Y. Hun. ZHEJIANG PROVINCE: 1 male, same as holotype; 1 female, Xitainmushan, VIII-3-84, L. K. Sheng; 1 female, Songyang, VII-15-17-89, J. H. He; 1 male, Zhuji, VI-10-85, X. X. Chen. FUJAIN PROVINCE: 1 female, 1 male, Guadun (Wuyishan), VI-11-82, J. H. Xiu; 1 female, Wuyishan, VI-20-80, N. Q. Lin; 1 female, Wuyishan, VI-30-80, J. H. Xiu; 1 female, Wuyishan, VIII-3-83, Y. Ma; 1 male, Wuyishan, VII-30-81, J. S. Weng. Deposited in FAC, USNM, ZAU.

Host.—Unknown.

Distribution.—China (Heilongjiang Province, Jiling Province, Zhejiang Province, Fujian Province).

Remarks.—This species can be distinguished from other species of the *quadridentata*-group by the more massive head, strongly strigate-rugose hind coxa, and larger and stout body.

Etymology.—This species is named for Prof. J. H. He, Zhejiang Agricultural University, in appreciation for his helpfulness in this work.

Ascogaster lini Tang and Marsh, new species Fig. 9

Females.—Length of forewing 3.9-4.3 mm, of body 4.4-4.8 mm.

Head.—Antenna with 33-36 flagellomeres, weakly dilated medially, slightly tapered at apex, medial segments about as broad as long, basal segments distinctly longer than broad, apical segments slightly longer than broad. Temple strongly constricted behind eyes, slightly shorter than eye in dorsal view. Occiput deeply concave. Ocelli small, on line, OO = 4.0 OD. Frons with two depressed, polished impunctate areas behind antenna, median carina distinct. Eyes moderately protuberant, glabrous. Face (Fig. 9) slightly protuberant, about 1.5 times as broad as high, finely punctate, with a median carina in upper part; Clypeus weakly divided from face, protuberant, sparsely punctate, smoother than face; apical border of clypeus strongly impressed laterally, medial area raised and produced forwards into a distinct pointed tooth.

Mesosoma.—Pronotum projecting in front of mesonotum, laterally shining and smooth, dorsally rugose-foveolate. Notauli strong, foveolate, coalescing posteriorly in an areolate-rugose area; rest of mesonotum rugose-punctate. Precoxal suture shallow, foveolate; mesopleuron above precoxal suture rugose-foveolate anteriorly, smooth and punctate posteriorly, rest of mesopleuron ventrally densely punctate. Propodeum completely areolate-rugose divided medially by a transverse carina with medial and lateral tubercles, the medial pair broad and stout, lateral tubercles more prominent. Hind coxa finely punctate. Vein r of forewing about 1.5-2.0 times as long as 3-RS.

Metasoma.—Carapace long, CL/CW = 1.8-2.0, clavate in dorsal view, finely areolate-rugose, with two weak medial carinae at base. Ventral opening of carapace longer, almost at apex of carapace. Hypopygium short. Ovipositor sheaths clavate, short.

Color.—Black except carapace yellow at base; antenna infusate except scape yellow; legs yellow except hind coxa at base, mid and hind femur at apex, and all tarsi infusate.

Males.—Same as females except medial flagellomeres not dilated, carapace completely black and scape infusate as in flagellum.

Holotype Female.—TAIWAN: Tsuifeng 2300m, malaise trap, VI-84, K. S. Lin and K. C. Chou. Deposited in TARI.

Paratypes. TAIWAN: 1 female, 3 males, Tsuifeng, VI-21-79, K. S. Lin and B. H. Chen; 3 males, Tsuifeng, VI-3-80, L. Y. Chou and C. C. Chen; 1 male, Tsuifeng, V-8-81, K. S. Lin and S. C. Lin; 1 female, Tsuifeng, VII-1-3-81, T. Lin and W. S. Tang; 12 females, 4 males, VI-25-27-81, K. S. Lin and W. S. Tang; 2 females, 1 male, Tsuifeng, V-23-82, L. Y. Chou; 9 females, 1 male, VII-16-82, S. C. Lin and C. N. Lin; 4 females, 5 males, Tsuifeng, VI-23-25-83, K. S. Lin and S. C. Lin; 13 females, 14 male, same as holotype; 20 females, 8 males, Tsuifeng, VII-XI-84, Malaise trap, K. S. Lin and K. C. Chou; 1 male, Tsuifeng, IX-85, Malaise trap, K. S. Lin; 1 female, 1 male, Meifeng, V-10-79, K. C. Chou; 2 females, Meifeng, VI-20-22-79, K. S. Lin and B. H. Chen; 2 females, 1 male, Meifeng, VI-2-4-80, L. Y. Chou and C. C. Chen; 1 female, Meifeng, VI-5-8-80, C. C. Chen; 1 female, Meifeng, VI-8-80, K. S. Lin and B. H. Chen; 1 female, Meifeng, X-5-9-80, C. C. Chen and C. C. Chien; 1 female, 10 males, Meifeng, V-7-9-81, K. S. Lin and S. C. Lin; 2 females, Meifeng, VI-24-26-81, K. S. Lin and W. S. Tang; 2 males, Meifeng, V-22-82, L. Y. Chou; 1 male, Meifeng, V-3-83, H. Townes; 5 males, Meifeng, V-10-83, H. Townes; 2 males, Meifeng, V-15-83, H. Townes; 1 female, 4 males, V-22-83, H. Townes; 4 females, Meifeng, VI-22-26-83, K. S. Lin and S. C. Lin; 1 male, Meifeng, V-8-11-84, K. C. Chou and C. C. Pan; 1 female, 3 males, Meifeng, VI-84, Malaise trap, K. S. Lin and K. C. Chou; 1 female, Meifeng, VIII-84, Malaise trap, K. S. Lin and K. C. Chou; 1 female, Meifeng, X-84, Malaise trap, K. S. Lin and K. C. Chou; 1 female, Meifeng, X-85, Malaise trap, K. S. Lin; 1 female, Sungkang 2100 m, X-84, Malaise trap, K. S. Lin and K. C. Chou; 1 female, 2 males, Sungkang, X-XI-85, Malaise trap, K. S. Lin; 8 females, 3 males, Tayuling 2560 m, VI-9-16-80, Malaise trap, K. S. Lin and B. H. Chen; 1 female, 2 males, Alishan 2400 m, VI-12-16-65, T. Maa and K. S. Lin; 4 females, Anmashan 2275m, VII-6-9-79, L. Y. Chou. Deposited in AEIG, FAC, TARI, USNM.

Host.—Unknown.

Distribution.—Taiwan.

Remarks.—This species is very similar to *perkinsi* in the characteristics of the face and clypeus, but it is rather different in the shape of the carapace and color patterns of both legs and antennae.

Etymology.—It is a pleasure to name this species in honor of its collector, Mr. K. S. Lin, who also collected a large amount of Braconidae in Taiwan.

***Ascogaster macrogaster* Tang and Marsh,
new species**

Females.—Length of forewing 3.5-4.2 mm, of body 4.3-4.9 mm.

Head.—Antenna with 33 flagellomeres, slightly dilated medially, medial segments about as long as broad. Temple slightly contracted behind eyes, slightly longer than eyes in dorsal view. Occiput concave. Ocelli larger, $OO = 3.0OD$, on line. Frons slightly excavated, rugose-punctate; medial carina distinct. Eyes not protuberant, glabrous without distinct setae. Gena expanded in lateral view. Face slightly protuberant, about 1.5 times as broad as high, areolate-rugose. Clypeus punctate; apical border impressed laterally, produced medially into a small pointed tooth.

Mesosoma.—Pronotum strongly projecting in front of mesonotum, dorsolaterally areolate-rugose. Notauli not distinct; mesonotum rugose-punctate anteriorly, rest of mesonotum foveate. Mesopleuron deep punctate, but precoxal suture not distinguishable. Propodeum strongly areolate-rugose, not distinctly divided into dorsal and posterolateral surfaces. Hind coxa smooth, shining. Vein r of forewing about 1.5 times as long as 3-RS.

Metasoma.—Carapace very long, $CL/CW = 2.5$, areolate-rugose, rounded apically in lateral view. Ventral opening of carapace at $1/4$ apex of carapace. Hypopygium broad. Ovipositor short, pointed apically; ovipositor sheath clavate.

Color.—Black; carapace sometimes yellow at base; all legs yellow except hind femur and tibia brownish apically; palpi pale yellow.

Male.—Same as female except antenna not dilated medially, all flagellomeres longer than broad, and smaller yellow spot at basal carapace.

Holotype Female.—FUJIAN PROVINCE: Tongmugun (Wuyishan), VI-23-82, J. C. Huang. Deposited in FAC.

Paratypes.—FUJIAN PROVINCE: 1 female, same as holotype; 1 female, Wuyishan, VI-80, H. F. Chao; 1 female, Wuyishan, VI-80, J. C. Huang; 1 male, Huanxi, V-30-86, N. Q. Lin. Deposited in FAC.

Host.—Unknown.

Distribution.—China (Fujian Province).

Remarks.—This species is very close to *grandis* from which it can be distinguished not only by the characters mentioned in the key but also by the lack of distinct tubercles on the propeodum.

Etymology.—The specific name is from the Greek makros meaning long and gaster meaning stomach in reference to the long metasomal carapace.

Ascogaster perkinsi Huddleston

Figs. 10, 22

Ascogaster perkinsi Huddleston 1984: 368. Holotype female, JAPAN: Mt. Tachibana, Fukuoka.

Diagnosis.—Length of forewing 2.6–2.9 mm, of body 3.0–3.5 mm. Antenna with 34–36 flagellomeres, slightly dilated medially (female); ocellar triangle obtuse, ocelli almost on line; face (Fig. 10) about 1.5 times as broad as high, rugose-punctate; apical border of clypeus strongly impressed laterally, medial area projecting and produced forwards into a distinct pointed tooth; notauli weak, foveolate, rest mesonotum rugose-punctate; precoxal suture foveolate, mesopleuron above precoxal suture areolate-foveolate anteriorly, sparsely punctate posteriorly, rest of mesopleuron densely punctate; carapace short, oval in dorsal view, clavate in lateral view, generally yellow at base; ventral opening of carapace (Fig. 22) short, distinctly in front of apex; hind coxa finely punctate; all legs yellow except middle tibia dark at base, hind femur and tibia dark at base, mid and hind tarsi infuscate.

Specimens Examined.—ZHEJIANG PROVINCE: 41 females, 24 males. HUNAN PROVINCE: 1 male. FUJIAN PROVINCE: 4 females, 3 males. TAIWAN: 11 females, 6 males.

Host.—Unknown.

Distribution.—China (Zhejiang Province, Hunan Province, Fujian Province), Taiwan, Japan.

Remarks.—All specimens examined agree well with the description of Huddleston (1984). This is a new species record for the fauna of China.

Ascogaster quadridentata Wesmael

Figs. 17, 18

Ascogaster quadridentatus Wesmael 1835: 237. Lectotype female, BELGIUM: Brussels (designated by Shaw 1983).

Chelonus impressus Herrich-Schaffer 1838: 153. Syntypes, GERMANY (syn. by Reinhard 1867)

Ascogaster nigricornis Thomson 1892: 1719. Lectotype female, SWEDEN (designated and syn. by Huddleston 1984). Shenefelt 1973: 826.

Ascogaster cynipum Thomson 1892: 1720. Holotype male, SWEDEN (syn. by Huddleston 1984). Shenefelt, 1973: 820.

Ascogaster egregius Kokujev 1895: 83. Holotype male, USSR (syn. by Huddleston 1984). Fahringer 1934: 525; Shenefelt 1973: 821.

Chelonus nigrator Szépligeti 1896: 303. Holotype female, YUGOSLAVIA: Buccari (syn. by Huddleston 1984). Shenefelt 1973: 859.

Chelonus carpocapsae Viereck 1909: 43. Holotype female, USA: Michigan (syn. by Rosenberg 1934).

Ascogaster epinotiae Watanabe, 1937: 76. Holotype female, JAPAN: Hokkaido, Sapporo (syn. by Huddleston 1984). Shenefelt 1973: 821.

Ascogaster quadridentata; Shenefelt 1973: 828; Shaw 1983: 32; Huddleston 1984: 376 Walker and Huddleston 1987: 343; Papp 1989: 258.

Diagnosis.—Antenna with 27–32 flagellomeres, slightly dilated medially; ocelli on line or almost on line (Fig. 17); face (Fig. 18) about twice as broad as high, generally finely rugose; clypeus finely punctate, apical border produced medially into a pointed tooth; notauli and precoxal suture indistinguishable, mesonotum and mesopleuron completely areolate-rugose; hind coxa always mostly black and strongly strigate-rugose; carapace oval, short, generally deep in lateral view, sometimes yellow at base; ventral opening of carapace short, usually distinctly in front of apex.

Specimens Examined.—BEIJING CITY: 1, female, 1 male. JILING PROVINCE: 1 male. HUNAN PROVINCE: 2 females. JIANGXI PROVINCE: 1 male. GUANGXI PROVINCE: 1 female, 1 male. YUNNAN PROVINCE: 2 females, 2 males. GUIZHOU PROVINCE: 3 females, 2 males. ZHEJIANG PROVINCE: 29 females, 30 males. FUJIAN PROVINCE: 18 females, 11, males. TAIWAN: 26 females, 7 males.

Additional Specimens Examined.—Lectotype of *quadridentatus* Wesmael, female, BELGIUM: Brussels (IRSNB). Lectoparatypes of *quadridentatus* Wesmael, 1 female, 5 males, same as lectotype (IRSNB). USA: 1 female, 1 male, WA, Pullman, August 30, 1989, ex. *Cydia pomonella*, det. by Shaw, 1990 (FAC).

Hosts.—Huddleston (1984) and Shaw (1983) recorded the following hosts in the Palearctic and Nearctic Regions: *Cydia fumebrana* (Treitsche), *Cydia nigricana* Steph., *Cydia pallifrontana* (Lienig & Zeller), *Cydia pomonella* (L.), *Epiblema uddmanniana*

(L.), *Grapholitha molesta* (Busck), *Grapholitha prunivora* (Walsh), *Spilonota ocellana* (Denis & Schiffermuller) (Lepidoptera: Tortricidae); *Endopiza viteana* (Clem.); *Yponomeuta padella* (L.) (Lepidoptera: Yponomeutidae).

Distribution.—China (Beijing City, Jiling Province, Jiangsu Province, Zhejiang Province, Yunnan Province, Guizhou Province, Guangxi Province, Fujian Province), Taiwan, Japan, Korea, New Zealand, West Palaearctic Region, Nearctic Region.

Remarks.—This species has been studied widely as a parasitoid of several economically important insect pests in Europe and North America. Its hosts and biology were reviewed by Huddleston (1984) and Shaw (1983). There is very little published work on this species in China. Fahringer (1934) recorded it in Jiangsu Province (=Kiangfu). This species is characterized by its coarse sculpture, short oval and deep carapace, short temple and antenna, highly strigate and black hind coxa, and the single tooth on its clypeus.

Ascogaster reticulata Watanabe

Ascogaster reticulatus Watanabe 1967: 41. Holotype male (cited as female), JAPAN: Hokkaido, Ashigawa. He, Chen and Ma 1989: 438.

Ascogaster reticulata: Huddleston 1984: 377; Papp 1989: 298.

Diagnosis.—Length of forewing 2.8-3.2 mm, of body 3.4-3.8 mm. Antenna with 34-36 flagellomeres, weakly dilated medially; ocelli large, on line; face about 1.5 times as broad as high, coarsely irregularly rugose; clypeus strongly punctate, matt and its apical border almost flat without any trace of tooth or tubercle; mesonotum areolate-rugose, notauli indistinct; precoxal suture indistinguishable, mesopleuron strongly areolate-rugose; carapace short, deep, sometimes yellow at base; ventral opening of carapace short, distinctly in front of apex; hind coxa yellow, smooth or sometimes finely punctate; hind tibia black with a pale yellow medial band.

Specimens Examined.—BEIJING CITY: 2 females. HENAN PROVINCE: 13 females. SHANDONG PROVINCE: 8 females, 5 males. SHANXI PROVINCE: 8 females. SHAANXI PROVINCE: 3 females, 1 male. ANHUI PROVINCE: 1 male. JIANGSHU PROVINCE: 9 females, 2 males. JIANGXI PROVINCE: 2 females. ZHEJIANG PROVINCE: 7 females, 4 males.

YUNNAN PROVINCE: 3 females. GUANHXI PROVINCE: 1 female. FUJIAN PROVINCE: 1 female, 1 male. TAIWAN: 31 females, 36 males.

Additional Specimens Examined.—Holotype of *reticulatus* Watanabe, male, JAPAN: Hokkaido, Asahigawa, June 15, 1966 (UEI). Paratypes of *reticulatus* Watanabe: 3 females, JAPAN, May 16-July 20, 1966 (UEI); 1 female, 1 male, JAPAN, July 20-23, 1966 (USNM).

Hosts.—*Acleris fimbriana* (Thunberg), *Adoxophyes orana* (Fischer von Roslerstamm), *Archips issikii* Kodama, *Archips oporana* (L.), *Archips pulchra* (Butler), *Carposiana nipponensis* Walsingham (Lepidoptera: Tortricidae).

Distribution.—China (Beijing City, Henan Province, Shandong Province, Shanxi Province, Shannxi Province, Anhui Province, Jiangsu Province, Jiangxi Province, Zhejiang Province, Yunnan Province, Guangxi Province, Fujian Province), Taiwan, Japan, Korea, Czechoslovakia.

Remarks.—This species is easily distinguished from other species of the *quadridentata*-group by the matt and no tooth clypeus and by the yellow and smooth hind coxa and the hind tibia with a yellow-pale band medially.

Ascogaster rugulosa Tang and Marsh, new species Fig. 13

Females.—Length of forewing 3.0-3.2 mm, of body 3.4-3.7 mm.

Head.—Antenna with 31-35 flagellomeres, slightly dilated medially, flagellomeres 1-11 longer than broad, rest of flagellum about as broad as long. Temple rounded behind eyes, about equal to length of eye in dorsal view. Occiput concave. Ocelli small, OO=3.5-4.0 OD, on line. Eyes protuberant, glabrous. Frons moderately concave, smooth, with a weak medial carina. Face (Fig. 13) about 1.5 times as broad as high, finely areolate-rugose, generally more finely sculptured ventrally than dorsally. Clypeus punctate, apical border produced medially into a pointed tooth.

Mesosoma.—Pronotum little projecting in front of mesonotum, rugose-punctate dorsolaterally. Notauli present but not very distinct; mesonotum rugose-punctate except an areolate-rugose area posteromedially. Precoxal suture very weak, shallow foveolate; rest of mesopleuron sparsely but coarsely punctate. Propodeum coarsely areolate-

rugose, divided by a tranverse carina which is raised into a pair of medial dentate flanges and a pair of lateral dentate flanges. Hind coxa finely punctate. Vein r of forewing about as long as or slightly longer than 3-RS.

Metasoma.—Carapace short, oval in dorsal view, clavate in lateral view, areolate-rugose. Ventral opening of carapace less distinctly in front of apex. Ovipositor short, tapered apically.

Color.—Black; fore and middle legs yellow except middle tibia at apex and all tarsi infuscate, hind leg black except apex of coxa and base of femur yellow and with a pale yellow medial band on tibia; carapace always yellow laterally at base, but black medially.

Males.—Same as females except antenna not dilated medially.

Holotype Female.—TAIWAN: Meifeng, V-7-9-81, K. S. Lin and S. C. Lin. Deposited in TARI.

Paratypes.—ZHEJIANG PROVINCE: 1 male, Xitainmushan, VI-2-4-90, L. G. Weng. HAINAN PROVINCE: 1 male, Shuiman, V-26-60, X. F. Li. TAIWAN: 7 females, 1 male, same as holotype; 1 female, Meifeng, VII-26-78, K. C. Chou; 1 female, Meifeng, IV-8-9-78, K. S. Lin; 1 male, Meifeng, VII-18-79, K. C. Chou; 1 female, Meifeng, V-15-22-79; 1 female, Meifeng, VI-20-21-79, K. S. Lin and B. H. Chen; 1 female, Meifeng, X-5-9-80, C. C. Chen and C. C. Chien; 1 male, Meifeng, VI-24-26-81, K. S. Lin and W. S. Tang; 3 males, Meifeng, VIII-28-29-81, L. Y. Chou and S. C. Lin; 1 female, 1 male, VII-31-IX-2-82, L. Y. Chou and S. C. Lin; 2 females, 2 males, Meifeng, V-8-11-82, K. C. Chou and C. C. Pan; 1 male, Meifeng, VII-30-83, L. Y. Chou; 1 female, Meifeng, VI-22-26-83, K. S. Lin and S. C. Lin; 1 female, Meifeng, X-4-7-82, K. C. Chou; 1 male, V-8-11-84, K. C. Chou and C. C. Pan; 1 female, Meifeng, VII-84, Malaise trap, K. S. Lin and K. C. Chou; 1 female, Tungpu, X-18-21-82, K. C. Chou and S. C. Lin; 1 female, Tungpu, VI-20-24-83, K. C. Chou and C. Y. Wong; 1 female, Tungpu, VII-85, Malaise trap, K. S. Lin; 1 female, Tsuifeng, VI-21-79, K. S. Lin and B. H. Chen; 1 female, Tsuifeng, VI-3-80, L. Y. Chou and C. C. Chen; 1 female, Tsuifeng, V-8-81, K. S. Lin and S. C. Lin; 4 females, 1 male, Tsuifeng, VI-25-27-81, K. S. Lin and W. S. Tang; 1 male, Tsuifeng, VIII-27-81, L. Y. Chou and S. C. Lin; 1 male, Tsuifeng, IX-1-3-82, L. Y. Chou and K. C. Chou; 3 females, Tsuifeng, VI-23-25-83, K. S. Lin and S. C. Lin; 2 females, Tsuifeng, VI-VII-84, Malaise trap, K. S. Lin and K. C. Chou; 3 males,

Tsuifeng, IX-85, Malaise trap, K. S. Lin; 4 males, Tsuifeng, IX-12-14-84, K. S. Lin and S. C. Lin; 3 males, Wushe, IV-26-83, H. Townes; 1 male, Wusha, VII-25-78, K. C. Chou; 1 female, Sungkang, VIII-6-84, K. S. Lin; 1 female, 1 male, Sungkang, X-84, Malaise trap, K. S. Lin and K. C. Chou; 2 males, Sungkang, Malaise trap, IX-X-85, K. S. Lin; 1 female, 2 males, Shengkuang, IX-20-68, K. S. Lin; 1 female, Wuling, VI-27-29-79, K. S. Lin and L. Y. Chou; 1 female, Tayuling, VI-9-16-80, K. S. Lin and B. H. Chen; 1 male, Lishan, IX-12-68, K. C. Chou. Deposited in AEIG, FAC, TARI, USNM, ZAU, ZRI.

Host.—Unknown.

Distribution.—China (Zhejiang Province, Hainan Province), Taiwan.

Remarks.—This species is close to *reticulata* from which it can be distinguished not only by its characters mentioned in the key but also by its smooth mesopleuron, less deep carapace and mostly black hind coxa.

Etymology.—The specific name is in reference to the rugulose sculpturing on the clypeus.

Ascogaster semenovi Telenga

Figs. 11, 25

Ascogaster semenovi Telenga 1941: 310, 453. Holotype female, MONGOLIA: Alashan, Dyn-juan-in. Shenefelt 1973: 825, Huddleston 1984: 352.

Ascogaster kyushuensis Yoneda 1978: 291. Holotype female, JAPAN: Kyushu, Fukuoka Pref., Fukuoka City, Hakozaki (syn. by Huddleston 1984).

Diagnosis.—Length of forewing 4.3-4.7 mm, of body 5.2-5.6 mm. Antenna of female with 20 flagellomeres and medial segments dilated, generally broader than long, male with 25-26 flagellomeres, medially not dilated, all segments longer than broad; ocellar triangle acute, ocelli not on line; face (Fig. 11) about twice as broad as high, rugose-punctate, the hairs on the upper part of face pointing upwards; clypeus with its apical border rounded medially, produced laterally into broad dentate flanges, without tooth or incision; notauli distinct, foveolate, rest of mesonotum punctate with an areolate-rugose area posteromedially; precoxal suture deep foveolate, rest of mesopleuron punctate with a deep foveolate groove anterodorsally; hind coxa finely and sparsely punctate; carapace (Fig. 25) long, CL/CW = 2.2-2.4, pointed in dorsal and lateral views; ovipositor

sheaths broad, knife-like. Almost completely black except sometimes fore tibia reddish-brown.

Specimens Examined.—JIANGSU PROVINCE: 2 females, 6 males. SHANGHAI CITY: 8 females, 3 males. ZHEJIANG PROVINCE: 2 females, 8 males.

Hosts.—Unknown.

Distribution.—China (Jiangsu Province, Shanghai City, Zhejiang Province), Mongolia, Japan.

Remarks. This remarkable species is easily distinguished from other species of *Ascogaster* by the lateral dentate flanges on its clypeus and by the broad and knife-like ovipositor sheaths. It is new to the fauna of China.

Ascogaster setula Tang and Marsh, new species
Fig. 8

Females.—Length of forewing 2.4-2.7 mm, of body 2.9-3.1 mm.

Head.—Antenna with 26-29 flagellomeres; flagellum moderately dilated medially, medial segments slightly broader than long, apical segments about as broad as long. Temple rounded behind eyes, about equal to or slightly shorter than eye in dorsal view. Occiput concave. Ocelli small, OO = 4.0 OD, almost on line. Frons moderately depressed behind antenna. Eyes slight protuberant, with dense and distinct hairs. Malar space shorter, about 0.5 time as eye high. Gena strongly constricted in face view. Face (Fig. 8) protuberant, coarsely rugose-punctate, about 1.5 times as broad as high. Clypeus not distinctly divided from face, slightly convex, its apical border more or less straight, with a very small tooth medially.

Mesosoma.—Pronotum protecting in front of mesonotum, dorsolaterally foveate. Notauli shallow foveolate, rest of mesonotum punctate except an areolate-rugose area posteromedially. Precoxal suture not very distinct, mesopleuron generally coarsely rugose-punctate, sometimes areolate-rugose. Propodeum coarsely areolate-rugose, divided by a transverse carina which is raised into a medial pair and a lateral pair of stout dentate flanges. Hind coxa smooth. Vein r of forewing 1.0-1.3 times as long as 3-RS.

Metasoma.—Carapace shorter, CL/CW = 1.5-1.8, areolate-rugose, oval, deeper in lateral view. Ventral opening of carapace distinctly in front of apex. Hypopygium short. Ovipositor short, its sheath clavate.

Color.—Black; carapace always yellow at base; all legs yellow except hind femur and tibia apically infusate.

Males.—Same as female except antennae not dilated medially and carapace black at base.

Holotype Female.—TAIWAN: Tungpu, XI-18-21-82, K. C. Chou and S. C. Lin. Deposited in TARI.

Paratypes.—TAIWAN: 4 females, 1 male, same as holotype; 3 females, 2 males, Tungpu, IX-25-29-80, L. Y. Chou and T. Lin; 1 female, Tungpu, IV-28-V-2-81, T. Lin and C. J. Lee; 2 females, 1 male, Tungpu, X-5-8-81, T. Lin and W. S. Tang; 1 female, Tungpu, XI-18-23-81, T. Lin and W. S. Tang; 6 females, Tungpu, X-XI-85, Malaise trap, K. S. Lin; 4 males, Tungpu, IV-16-VII-27-84, K. C. Chou and C. H. Yung; 2 females, 2 males, Lienhuachi, III-VII-84, Malaise trap, K. S. Lin and K. C. Chou. Deposited in FAC, TARI, USNM.

Hosts.—Unknown.

Distribution.—Taiwan.

Remarks.—Previous authors (Baker 1926, Shaw 1983, Zettel 1990) treated glabrous eyes as a character to distinguish *Ascogaster*. Strikingly this species has distinct and dense setae on its eyes, but except for this character it agrees well with typical *Ascogaster*. Its very small body and the characteristics of the clypeus are also useful to distinguish this species from other Chinese *Ascogaster*.

Etymology.—The specific name is the diminutive form of the Latin seta meaning bristle in reference to the unusually hairy eyes.

Ascogaster townesi Tang and Marsh,
new species
Figs. 12, 26

Females.—Length of forewing 4.3-4.5 mm, of body 4.6-4.9 mm.

Head.—Antenna with 23 flagellomeres, medial segments not dilated, all segments longer than broad. Temple rounded behind eyes, slightly longer than eye in dorsal view. Occiput deeply concave. Ocelli small, OO = 4.0-4.5 OD, ocellar triangle acute, ocelli not on line. Frons behind antenna slightly depressed, sparsely punctate. Eyes moderately protuberant, glabrous with few scattered minute setae. Malar space short. Gena in face view strongly constricted. Face (Fig. 12) slightly convex, about twice as broad as high, less hairy, the hairs on the upper part of face pointing upwards, finely punctate, with a medial carina on the

upper part. Clypeus slightly protuberant, more scatteredly punctate than face; apical border straight, without medial teeth or flanges.

Mesosoma.—Pronotum projecting little in front of mesonotum, dorsolaterally smooth, shallow foveate. Notauli deep, foveolate, rest of mesonotum punctate except with a depressed and areolate-rugose area posteromedially. Precoxal suture shallow foveate; rest of mesopleuron sparsely punctate, smooth except anterodorsally foveolate. Propodeum not distinctly divided into dorsal and posterolateral surfaces; strongly rugose with no tubercles. Hind coxa smooth. Vein r of forewing 1.0-1.2 times as long as 3-RS.

Metasoma.—Carapace (Fig. 26) very long, CL/CW = 2.3-2.5, clavate in dorsal view, flat in lateral view, areolate-rugose, apically polished. Ventral opening of carapace at apex of carapace. Hypopygium large and broad. Ovipositor long, slender and upcurved.

Color.—Black; legs yellow-brown except hind coxa basally, hind and middle femora and tibia apically and tarsi brownish; antenna infusate except scape reddish brown; palpi yellowish brown.

Males.—Same as females except antennae longer with 32 flagellomeres, flatter carapace and yellow hind coxa.

Holotype Female.—TAIWAN: Meifeng 2150 m, V-10-83, H. Townes. Deposited in AEIG.

Paratypes.—TAIWAN: 1 male, Meifeng 2150 m, IV-19-21-83, K. C. Chou and P. Huang; 4 males, Meifeng 2150 m, IV-26-83, H. Townes; 1 female, 30 males, Meifeng 2150 m, V-3-83, H. Townes; 2 females, 17 males, same as holotype. Deposited in AEIG, FAC, TARI, USNM.

Host.—Unknown.

Distribution.—Taiwan.

Remarks.—This species is easily distinguished from other species of *Ascogaster* by the hairs on the upper part of the face, very flat carapace, no tubercle on its clypeus, and long, upcurved ovipositor.

Etymology.—It is a pleasure to name this species in honor the late Henry Townes who collected many of the type series and who contributed greatly to our knowledge of the World Ichneumonoidea during his lifetime.

Ascogaster varipes Wesmael

Fig. 14

Ascogaster varipes Wesmael 1835: 234. Lectotype female, BELGIUM: Brussels (designated by Huddleston 1984). Shenefelt 1973: 837; Huddleston 1984: 370; Tobias 1986: 305; Papp 1989: 298.

Ascogaster cavifrons Thomson 1874: 585. Lectotype female, SWEDEN: Skane, Torekov (designated and syn. by Huddleston 1984). Shenefelt 1973: 818.

Ascogaster sternalis Thomson 1874: 587. Lectotype female, SWEDEN: Smaland (designated by Huddleston 1984 and syn. by Telenga 1941).

Ascogaster jaroslawensis Kokujev 1895: 86. Holotype female, USSR: 'Jaroslaw' (syn. by Huddleston 1984). Shenefelt 1973: 824; Tobias 1986: 304 (as a valid species).

Ascogaster variipes; Telenga 1941: 322.

Diagnosis.—Antenna with 32-36 flagellomeres, slightly dilated medially (females); ocellar triangle obtuse, ocelli almost on line; face (Fig. 14) generally rugose-punctate, all hairs downwards; clypeus with its apical border transversely impressed, without medial tooth or excision; mandibles with a deep semicircular depression at base; notauli distinct, foveolate, rest of mesonotum punctate except posteriorly areolate-rugose; mesopleuron coarsely rugose so that precoxal suture not easily distinguished; propodeum completely areolate-rugose; hind coxa strongly transversely strigate; carapace short, oval, deep in lateral view, ventral opening of carapace short, distinctly in front of apex.

Specimens Examined.—SHANDONG PROVINCE: 2 females, Lao-shan, 800 m.

Additional Specimens Examined.—Lectotype of *varipes* Wesmael, female, BELGIUM: Brussels (IRSNB). Lectotype and paralectotypes of *varipes* Wesmael, BELGIUM: 2 females, 3 males (IRSNB).

Hosts.—Shenefelt (1973) listed many host records. However, much of this information is of little value because of doubt about the accuracy of identification of the parasite species involved (see Huddleston 1984).

Distribution.—China (Shandong Province), Korea, "USSR" and many other European countries (see Huddleston 1984).

Remarks.—This species is characterized on account of the semicircular depression at the base of the mandibles, the strongly strigate hind coxa, the characteristics of the clypeus and the shape of the carapace. The two female Chinese specimens examined here differ from the type series of *varipes*

Wesmael in having a rugose-punctate face instead of a finely areolate-rugose face as in the type series.

Ascogaster yunnanica Tang and Marsh, new species

Male.—Length of forewing 2.7 mm, of body 3.3 mm.

Head.—Antenna incomplete, 1st flagellomere about 3.0 times as long as broad, 2-6th flagellomeres 2.0-2.5 times as long as broad. Temple constricted behind eyes, slightly shorter than eye in dorsal view. Occiput deeply concave. Ocelli small OO = 4.0 OD; ocellar triangle acute, ocelli not on line. Frons behind antenna moderately depressed, smooth. Eyes slightly protuberant, glabrous without distinct setae. Malar space short. Gena in face view strongly constricted. Face slightly convex, finely and sparsely punctate, about twice as broad as high, the hairs on the upper part of face pointing upwards. Clypeus slightly protuberant, more sparsely punctate than face, apical border straight without flange or tooth.

Mesosoma.—Pronotum projecting little in front of mesonotum, deep foveate dorsolaterally. Notauli foveolate, coalescing posteriorly in a fine areolate-rugose area; rest of mesonotum punctate. Precoxal suture shallow foveate anterodorsally, indistinct posteroventrally; rest of mesopleuron smooth posteroventrally, punctate anterodorsally. Propodeum not distinctly divided into dorsal and posterolateral surfaces, strongly rugose but with no dentates. Hind coxa smooth. Vein r of forewing about twice as long as 3-RS.

Metasoma.—Carapace very long, CL/CW = 2.5, oval in dorsal view, deeper and not so strongly flat in lateral view, areolate-rugose, but sparsely punctate apically. Ventral opening of carapace long, at apex of carapace.

Color.—Black; all legs yellow except hind coxa mostly black, hind femur and tibia apically and tarsi infuscate; palpi yellow-brown.

Female.—Unknown.

Holotype Male.—YUNNAN PROVINCE: Kunming, III-30-81, J. H. He. Deposited in ZAU.

Host.—Unknown.

Distribution.—China (Yunnan Province).

Remarks.—Morphologically this species is similar to *townesi* from which it differs not only in the characters mentioned in the key but also in the smaller body and the less flat carapace.

Etymology.—The species name is in reference to the type locality.

ACKNOWLEDGEMENTS

We thank the following people for loan of types and much of unidentified specimens or for providing valuable information: C. van Achterberg (The Netherlands), A. Austin (Australia), H. F. Chao (FAC), X. X. Chen (ZAU), L. Y. Chou (TARI), P. Dessart (IRSNB), J. H. He (ZAU), T. Huddleston (BMNH), K. Maeto (UEI), I. Nauman (Australia), J. Papp (HNHM), D. J. Preston (BM), M. J. Sharkey (CNC), S. R. Shaw (Wyoming), G. N. Shida (BM), M. Suwa (UEI), D. Wahl (AEIG), J. Y. Wang (ZRI). We also thank C. M. Liu (FAC) for help with translations of some Russian papers. The senior author offers special thanks to Prof. H. F. Chao for his continued helpfulness and encouragement and to Chunying for her patience and understanding. This work was partly supported by a grant to Y. Q. Tang by the National Educational Commission of the People's Republic of China.

LITERATURE CITED

- Achterberg, C. van. 1976. A preliminary key to the subfamilies of the Braconidae (Hymenoptera). *Tijdschrift voor Entomologie* 119: 33-78.
- Achterberg, C. van. 1988. Revision of the subfamily Blacinae Foerster (Hymenoptera: Braconidae). *Zoologische Verhandlungen* 249: 1-324.
- Achterberg, C. van. 1990a. Illustrated key to the subfamilies of the Holarctic Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Mededelingen* 64: 1-20.
- Achterberg, C. van. 1990b. Revision of the western Palaearctic Phanerotomini (Hymenoptera: Braconidae). *Zoologische Verhandlungen* 255: 1-106.
- Baker, C. F. 1926. Braconidae-Cheloninae of the Philippines, Malaya, and Australia. *The Philippine Journal of Science* 31: 451-489.
- Boyce, H. R. 1936. Laboratory breeding of *Ascogaster carpocapsae* Viereck with notes on biology and larval morphology. *Canadian Entomologist* 68: 241-246.
- Cox, J. A. 1932. *Ascogaster carpocapsae* Viereck, an important parasite of the codling moth and the oriental fruit moth. *Technical Bulletin of the New York State Agricultural Experiment Station* 188: 1-26.
- Fahringer, J. 1934. *Opuscula Braconologica, Palaearktische Region* 2: 321-594.
- Fullaway, D. T. 1919. New genera and species of Braconidae mostly Malayan. *Journal of Straits Branch, Royal Asiatic Society* 80: 39-61.
- Harris, R. A. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology, California Department of Food and Agriculture* 28: 1-31.

- He, J. H., X. X. Chen and Y. Ma. 1989. The Braconid (Hymenoptera) parasites of *Adoxophyes orana* Fischer von Rosterstamm (Lepidoptera: Tortricidae) from China. *Acta Agriculatae Universitatis Zhejiangensis* 15 (4): 437-439.
- Huddleston, T. 1984. The Palaearctic species of *Ascogaster* (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History) (Entomology)* 49: 341-392.
- Kainoh, Y. 1986. Mating behavior of *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae), an egg-larval parasitoid of the smaller tea tortrix moth, *Adoxophyes* sp. (Lepidoptera: Tortricidae) I. Diel patterns of emergence and mating, and some conditions for mating. *Applied Entomology and Zoology* 21: 1-7.
- Kainoh, Y. 1988. Some factors influencing sex ratio in *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* 23:35-40.
- Kainoh, Y., T. Hiyori and Y. Tamaki. 1982. Kairomone of the egg-larval parasitoid of the smaller tea tortrix, *Adoxophyes* sp. (Lepidoptera: Braconidae). *Applied Entomology and Zoology* 17: 102-110.
- Kainoh, Y., T. Nemoto, K. Shimizu, S. Tatsuki, T. Kusano and Y. Kuwahara. 1991. Mating behavior of *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae), an egg-larval parasitoid of the smaller tea tortrix, *Adoxophyes* sp. (Lepidoptera: Tortricidae) II. Identification of a sex pheromone. *Applied Entomology and Zoology* 26: 543-549.
- Kainoh, Y. and Y. Tamaki. 1982. Searching behavior and oviposition of the egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* 17: 194-206.
- Kainoh, Y. and S. Tatsuki. 1988. Host egg kairomones essential for egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae) I. Internal and external kairomones. *Journal of Chemical Ecology* 14: 1475-1484.
- Kainoh, Y., S. Tatsuki and T. Kusano. 1990. Host moth scales; a cue for host location for *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* 25: 17-25.
- Kainoh, Y., S. Tatsuki, H. Sugie and Y. Tamaki. 1989. Host egg kairomones essential for egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae) II. Identification of internal kairomone. *Journal of Chemical Ecology* 15: 1219-1229.
- Kamano, Y., K. Shimizu, Y. Kainoh and S. Tatsuki. 1989. Mating behavior of *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae), an egg-larval parasitoid of the smaller tea tortrix, *Adoxophyes* sp. (Lepidoptera: Tortricidae). *Applied Entomology and Zoology* 24: 372-378.
- Kawakami, T. 1985. Development of the immature stages of *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae), an egg-larval parasitoid of the smaller tea tortrix moth, *Adoxophyes* sp. (Lepidoptera: Tortricidae). *Applied Entomology and Zoology* 20: 380-386.
- Kawakami, T. and Y. Kainoh. 1985. Host discrimination and competition in the egg larval parasitoids, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* 20: 362-364.
- Kawakami, T. and Y. Kainoh. 1986. Host specificity of the egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae) among five tortricid and one noctuid species. *Applied Entomology and Zoology* 21: 8-14.
- Papp, J. 1989. Braconidae (Hymenoptera) from Korea XI. *Acta Zoologica Hungarica* 35(3-4): 295-326.
- Quicke, D. L. J. and C. van Achterberg. 1990. Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandlungen* 258: 1-95.
- Rosenberg, H. F. 1934. The biology and distribution in France of the larval parasites of *Cydia pomonella* L. *Bulletin of Entomological Research*, 25: 201-256.
- Shaw, M. R. and T. Huddleston. 1991. Classification and biology of braconid wasps (Hymenoptera: Braconidae). *Handbooks for the Identification of British Insects* 7 (11): 1-126.
- Shaw, S.R. 1983. A taxonomic study of Nearctic *Ascogaster* and a description of a new genus *Leptodrepana* (Hymenoptera: Braconidae). *Entomography* 2: 1-54.
- Shenefelt, R. D. 1973. *Catalogus Hymenopterorum (Nov. ed. part 10 Braconidae)*, 6:813-936. s'Gravenhage.
- Sonan, J. 1932. Notes on some Braconidae and Ichneumonidae from Formosa with descriptions of 18 new species. *Transactions of the Natural History Society of Formosa* 22: 66-86.
- Szépligeti, G. V. 1905. Exotische Braconiden aus den Aethiopischen, Orientalischen und Australischen Regionen. *Annales Musei Nationalis Hungarici* 3: 25-55.
- Szépligeti, G. V. 1908. Braconidae und Ichneumonidae. *Die Fauna Sudwest-Australiens* 1(9): 317-324.
- Telenga, N. A. 1941. Insects Hymenoptera, Family Braconidae, Subfamily Braconinae (continued) and Sigalphinae. *Fauna SSSR* 5 (3): 1-466.
- Tobias, V. I. 1986a. New species of Subfamily Cheloninae (Hymenoptera: Braconidae) from the Far East of the USSR. *Trudy Zoologicheskogo Instituta Akademiyi Nauk SSSR* 159: 3-17 (in Russian).
- Tobias, V. I. 1986b. *Guide to the insect of European part of the USSR Hymenoptera Opredelitel Faune SSSR*, 3 (4): 1-500 (in Russian).
- Tobias, V. I. 1988. Two new species of Braconidae of the subfamily Cheloninae (Hymenoptera) from the protected territories of the Lituianian SSR. *Acta Entomology Lituianian* 9: 89-94.
- Walker, A. and T. Huddleston. 1987. New Zealand chelonine braconid wasps (Hymenoptera: Braconidae). *Journal of Natural History* 21: 339-361.
- Watanabe, C. 1937. A contribution to the knowledge of the Braconid fauna of the Empire of Japan. *Journal of the Faculty of Agriculture Hokkaido Imperial University* 42 (1): 1-188.
- Watanabe, C. 1967. Description of a new species of the genus *Ascogaster* Wesmael and notes on synonym of *Apanteles* species (Hymenoptera: Braconidae). *Insecta Matsumurana* 29(2): 41-44.
- Wesmael, C. 1835. Monographie des Braconides de Belgique. *Nouveaux Memoires de l'Academie Royale des sciences et belles-lettres de Bruxelles* 9: 1-252.
- Yoneda, Y. 1978. A new species of the genus *Ascogaster* Wesmael (Hymenoptera, Braconidae) from Japan. *Kontyu* 46: 291-296.
- Zettel, V. H. 1990. Eine Revision der Gattungen der Cheloninae (Hymenoptera, Braconidae) mit Beschreibungen neuer

Gattungen und Arten. *Annales Naturhistorisches Museum Wien* 91(B): 147-196.

NOTE ADDED IN PROOF

The following paper came to our attention after our manuscript was sent to the printer: Chen Jiahua, Huang Juchang and Wu Zhishan. 1994. Notes on two new species and six new records of the genus *Ascogaster* Wesmael from China (Hymenoptera: Braconidae: Cheloniinae). *Journal of the Fujian Agricultural College (Natural Sciences Edition)* 23(1):51-57. Although we were not able to study the specimens used by Chen et al., we have made comments below on each species mentioned by them based on a translated version of their paper.

Ascogaster albitarsis Sonan. The characters mentioned in their key are not significant to separate this species from *reticulatus* based on our study (see discussion under *reticulatus*).

Ascogaster arisanica Sonan and *Ascogaster bidentula* Wesmael. During our study we examined the type material of *arisanica*, *bidentula* and *atamiensis* (synonym of *bidentula*). All of the material we examined under the name *arisanica* agreed with the type but none agreed with types of *bidentula* or *atamiensis*. Furthermore, we found that the characters used by Chen et al. and Huddelston (1984) are not reliable in distinguishing *bidentula* and *arisanica* (see our discussion of *arisanica*).

Most of the material examined by Chen et al. of *bidentula* and *arisanica* was collected at the same locality and same date; thus we suspect that their material is probably *arisanica*. This problem is further complicated by the fact that *atamiensis* was recorded from China by Fahringer (1938, *Ark. Zool.* 30:3) and Shenefelt (1973). Obviously this species complex needs to be studied further.

Ascogaster consobrina Curtis and *Ascogaster infacetus* Chen and Huang. The new species described in Chen et al., *infacetus*, will run to *consobrina* in our key. Fig. 1B in Chen et al. which is an illustration of the mesopleuron is not clear. Thus, we must reserve comment on this species until the type can be observed.

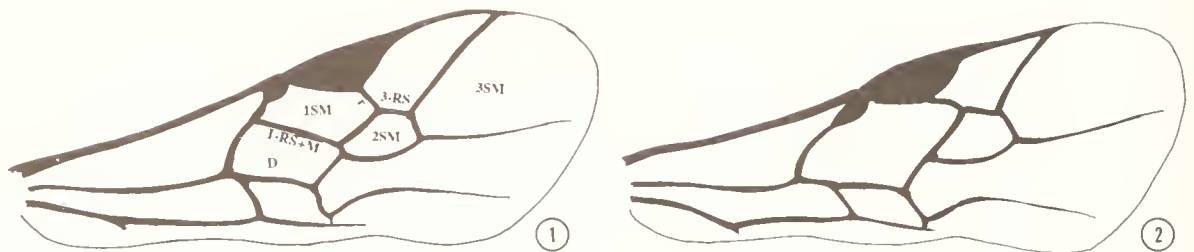
Ascogaster longicornis Huddleston. We treated this species as a synonym of *formosensis* based on type examination.

Ascogaster perkinsi Huddleston. See notes under *wuyiensis* below.

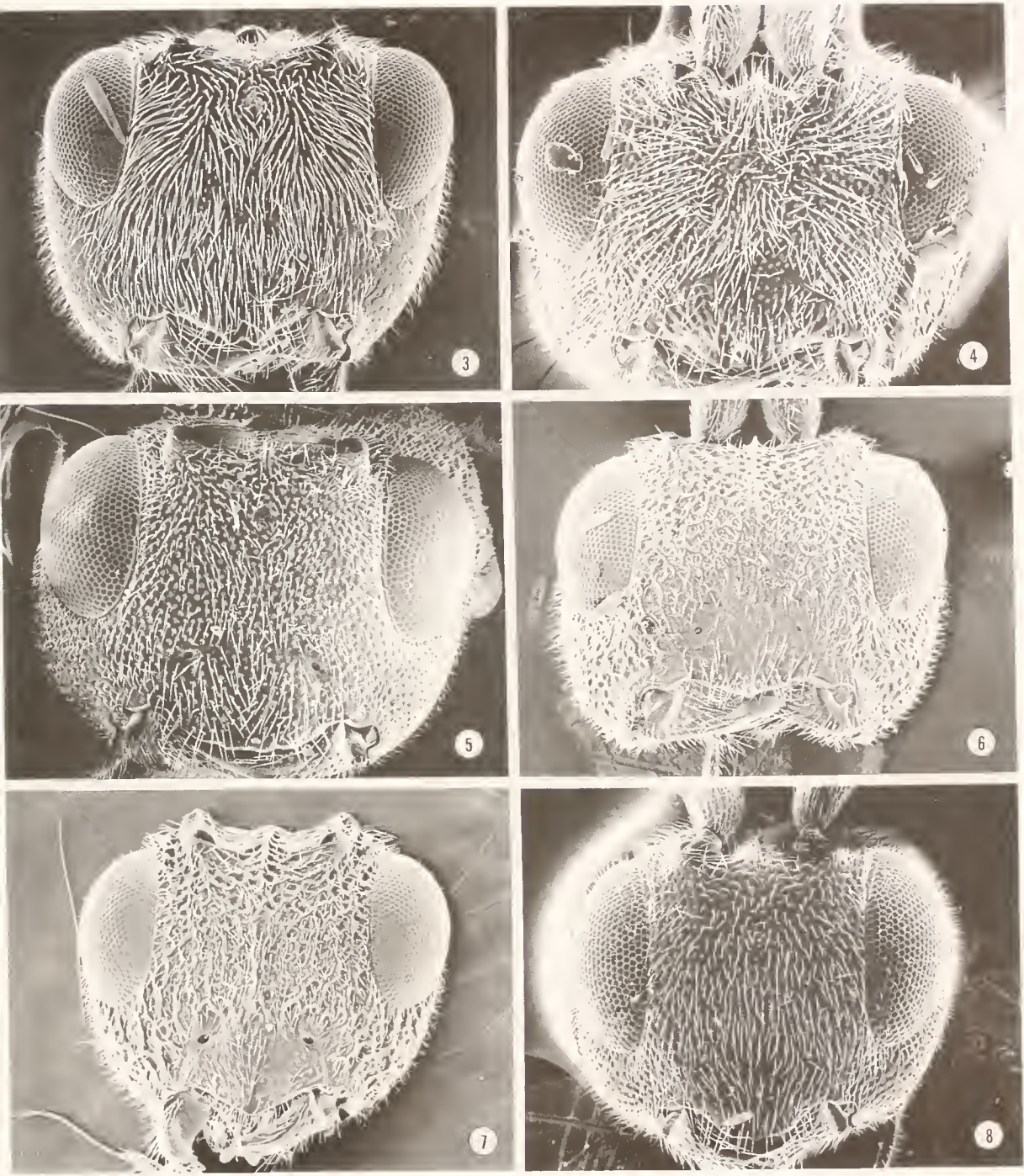
Ascogaster reticulatus Watanabe. Although this species was mentioned in their key, it was not discussed in the text. Thus, we must see their specimens before deciding upon the relationship of this species and *albitarsis*.

Ascogaster rufidens Wesmael. We did not find this species in any of the material that we studied. Again, their material should be studied before we confirm this species is in China.

Ascogaster wuyiensis Chen and Huang. This species will run to *perkinsi* in our key based on the description in Chen et al., and the color of the clypeus and the shape of the yellow mark at the base of the carapace may be only variation in *perkinsi*. We described a new species, *lini*, which is related to *wuyiensis* and *perkinsi*. The validity of these three species must wait until specimens of *wuyiensis* are examined.



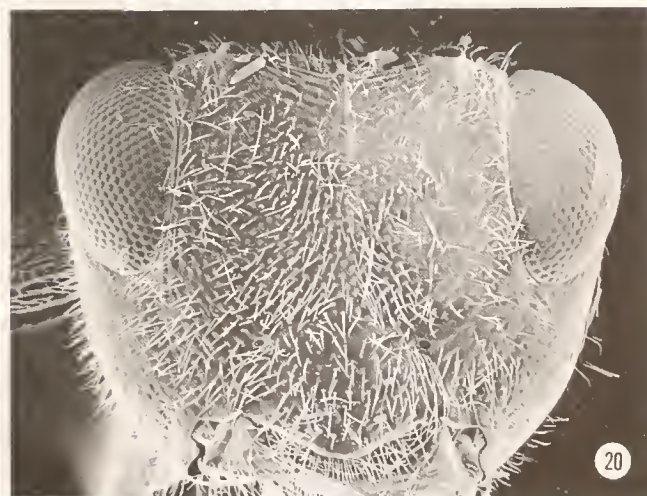
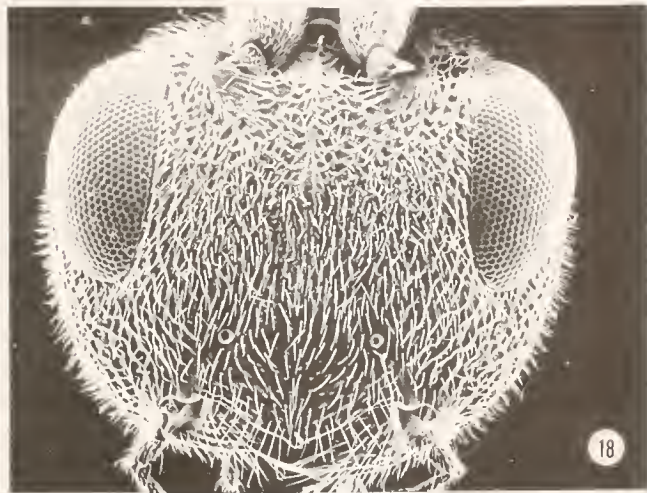
Figs. 1-2. Fore wings, somewhat diagrammatic. 1, *Ascogaster*. 2, *Chelonus*. SM=submarginal cells; D=discal cell.



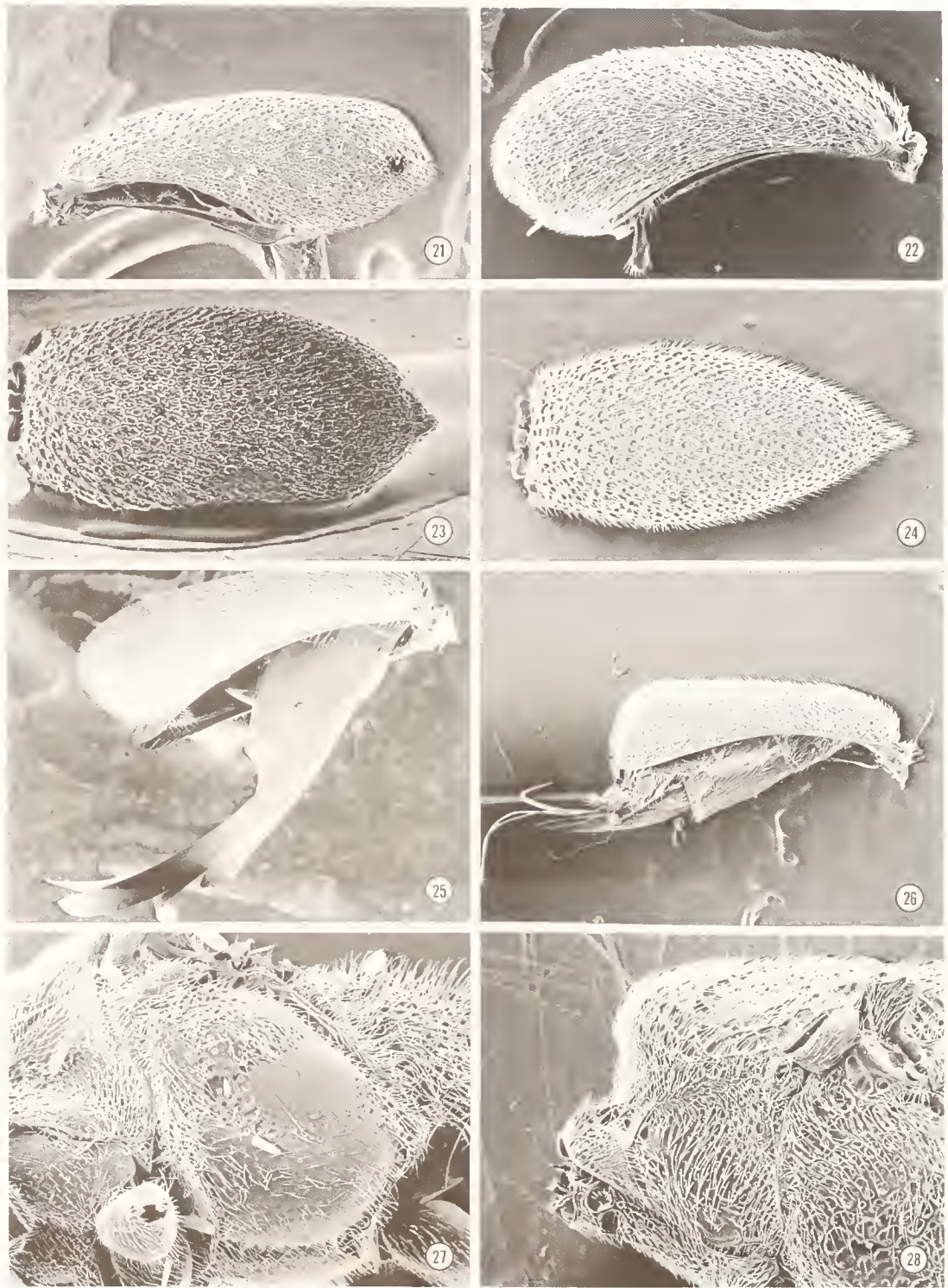
Figs. 3-8. Faces of *Ascogaster* species. 3, *arisanica* Sonan. 4, *dimorpha* n. sp. 5, *formosensis* Sonan. 6, *grandis* n. sp. 7, *fullawayi* (Baker). 8, *setula* n. sp.



Figs. 9-14. Faces of *Ascogaster* species. 9, *lini* n. sp. 10, *perkinsi* Huddleston. 11, *semenovi* Telenga. 12, *townesi* n. sp. 13, *rugulosa* n. sp. 14, *varipes* Wesmael.



Figs. 15-20. Heads of *Ascogaster* species. 15-16, *hei* n. sp.: 15, dorsal view; 16, face. 17-18, *quadridentata* Wesmael: 17, dorsal view; 18, face. 19, *armatoides* n. sp. 20, *consobrina* Curtis.



Figs. 21-28. Morphology of *Ascogaster* species. 21-26, metasomal gaster: 21, *grandis* n. sp.; 22, *perkinsi* Huddleston; 23, *acutus*

Systematics of *Pseudomethoca areta* (Cameron): Sex association, description of the male and a gynandromorph, and a new synonymy (Hymenoptera: Mutillidae).

DIOMEDES QUINTERO A. AND ROBERTO A. CAMBRA T.

Museo de Invertebrados G.B. Fairchild, Universidad de Panamá, Estafeta Universitaria, Panamá, República de Panamá;
(DQA) Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948.

Abstract.—A gynandromorph of *Pseudomethoca areta* (Cameron, 1895) is described, and previously published cases of gynandromorphism in Mutillidae are reviewed. Sex association permits recognition of the undescribed male of *P. areta*. We place *Pseudomethoca panamensis* (Cameron, 1895) in New Synonymy with *P. areta*.

Resumen.—Se describe un individuo ginandromorfo de *Pseudomethoca areta* (Cameron, 1895) y se presenta un resumen de casos previamente descritos de ginandromorfía en Mutillidae. Se lleva a cabo la asociación sexual y se describe al macho de *P. areta*, hasta ahora desconocido. *Pseudomethoca panamensis* (Cameron, 1895) se coloca como Nueva Sinonimia de *P. areta*.

INTRODUCTION

Mutillids are solitary parasitoid wasps that exhibit great sexual dimorphism, making sex associations difficult. The New World genus *Pseudomethoca* Ashmead illustrates this problem; only one-fifth of its 103 described species are known from both sexes. Distinctly fewer sex associations have been obtained for Neotropical than for Nearctic species of *Pseudomethoca*. Seventeen out of 45 Nearctic species known (37.8%) have both sexes recognized (Krombein, 1992). Of the remaining 28 species, 20 are known only from females, and eight only from males. In contrast, only four of some 58 Neotropical species of *Pseudomethoca* are known from both sexes (6.9%) (Nonveiller, 1990; Cambra & Quintero, 1992). Of the remaining 54, 46 are known from females only, and eight from males only. Success in associating the sexes will facilitate future biological work on the group and will solve some of the annoying taxonomic prob-

lems. We suspect that only about one-third of the species of *Pseudomethoca* in the Neotropics have been described. Previous taxonomic work on *Pseudomethoca* was done by Mickel (1924, 1935, revision of North American species; 1952, key to females of Guyanan species), Schuster (1945, key to Caribbean species), and Krombein (1992).

Gynandromorphy is a developmental phenomenon useful for associating the sexes in some extremely dimorphic animals, including mutillids (Mickel 1928, 1936, 1952; Bischoff 1931). Unfortunately, gynandromorphs are rare in Mutillidae. After examining more than 15,000 mutillid specimens, we have discovered only two gynandromorphs. A review of the literature revealed only six previously published cases (Table 1). We report here the second known Neotropical mutillid gynandromorph. We recently discovered a gynandromorph of *Timulla labdace* Mickel, from Panama, that will be described in a separate publication.

***Pseudomethoca areta* (Cameron)**

Figs. 1 - 4

Sphaerophthalma areta Cameron, 1895: 332, pl. 14, fig. 12, female. Bugaba, Chiriqui Province, Panama, Champion col., BM(NH), London, Type 15.822, examined; *Pseudomethoca areta*: Cambra & Quintero, 1992: 474.

Sphaerophthalma panamensis Cameron, 1895: 334-35, female. Bugaba, Chiriqui Province, Panama, Champion col., BM(NH), London, Type 15.833, examined; *Pseudomethoca panamensis*: Cambra & Quintero, 1992: 475. NEW SYNONYMY.

Diagnosis.—In Mickel's revised key (1935) it runs to *P. vanduzei* Bradley in couplet five. The male of *P. areta* differs from *P. vanduzei* as follows: posterior half of tegula bent downward so as to form a posterior face at a sharp angle with the dorsal surface (in *P. vanduzei* the tegula is uniformly convex, without a posterior face); anterior margin of clypeus in *P. areta* is bidentate (it lacks teeth in *P. vanduzei*); mandibles tridentate at the tip in *P. areta* (bidentate in *P. vanduzei*); integument of abdomen mostly ferruginous in *P. areta* (totally black in *P. vanduzei*). *Pseudomethoca areta* is endemic to Panama, and *P. vanduzei* is present in the southeastern United States (Krombein, 1979).

Description.—Integument black, except apex of tergum one and abdominal segments two to six, orange. Head large, subrectangular in dorsal view, as wide as thorax, clothed with long, erect and recumbent white pubescence; row of six to eight long, erect, dark hairs near inner margin of eyes; posterolateral angles of head not dentate. Mandibles tridentate distally; clypeus strongly bidentate medially on the cephalic margin; disk of clypeus densely punctate. Scape with a strong longitudinal carina beneath; first flagellomere equal in length to second. Front, vertex and genae coarsely and confluent punctate. Antennal scrobes and genae not carinate. Ocelli small, distance between eye margin and lateral ocelli equal to approximately five times the greatest diameter of the latter.

Pronotum, mesonotum and scutellum with close, more or less confluent punctures, punctures about the size of those on head. Propodeum strongly and coarsely reticulate dorsally and posteriorly. Tegula punctate throughout; posterior part of tegula bent downward so as to form a posterior face at a sharp angle with the dorsal surface. Humeral angles of pronotum without any

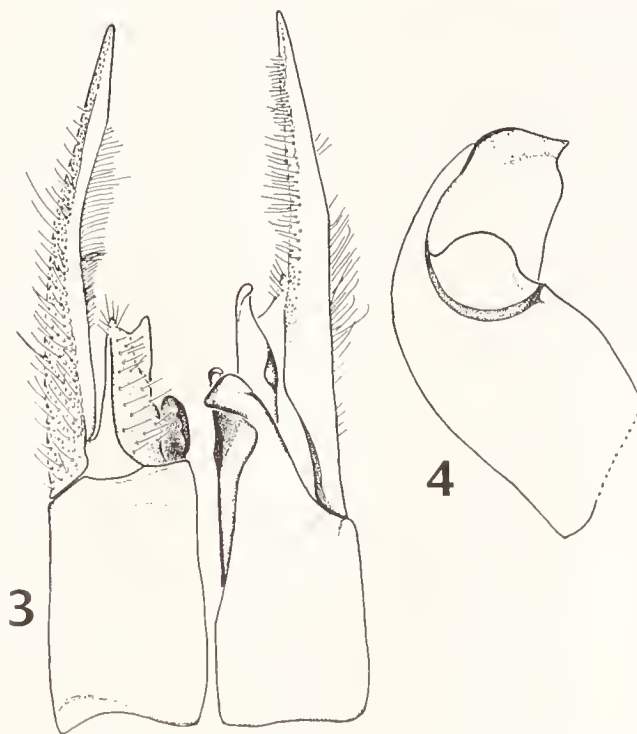
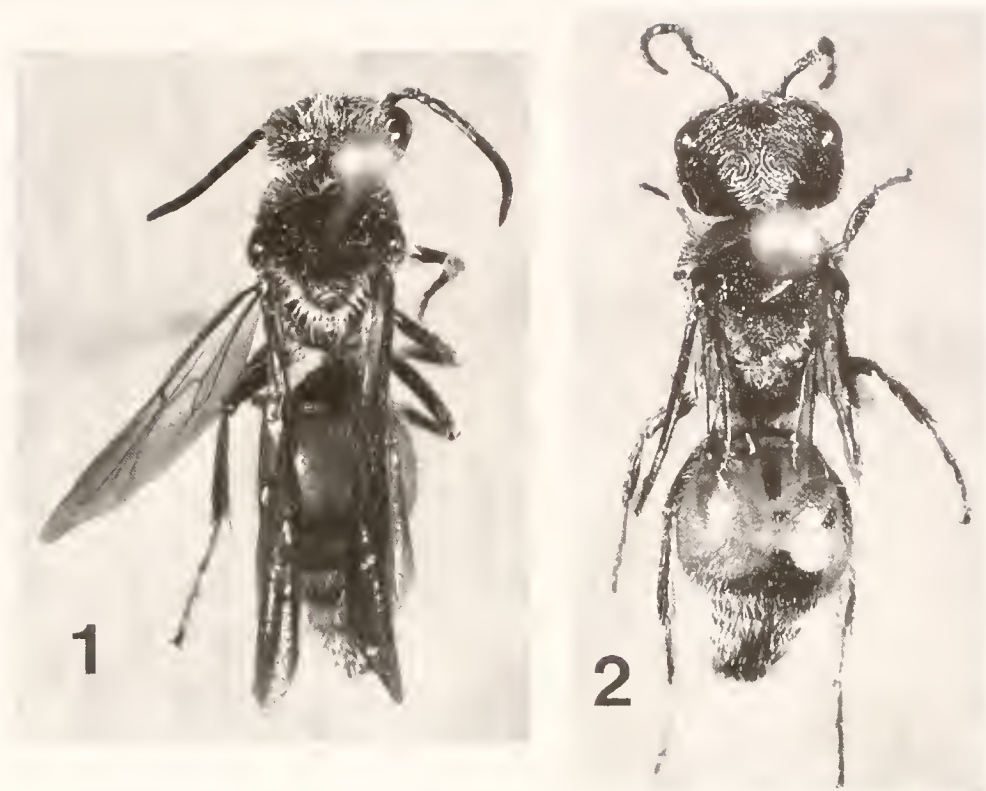
evidence of a carina. Propleura and mesopleura with close punctures; metapleura smooth, without punctures; sides of propodeum with only a few scattered punctures. Pronotum, scutellum, metanotum and dorsal face of propodeum, clothed with sparse, long erect white pubescence; mesonotum clothed with sparse black pubescence; tegula clothed with intermixed, black and white pubescence; metapleura and sides of propodeum almost bare, with only sparse white micropubescence.

Anterior and intermediate coxae without teeth or keels; posterior coxa with a keel on inner margin. Legs clothed with sparse white pubescence. Calcaria pale.

Abdomen with segment one completely sessile with second. Terga one and two with small, separated punctures, except the apical margins with close punctures; terga three to six with small, close punctures. Pygidium rugose. Felt line 0.6 x as long as lateral margin of tergum two. Sternum one almost smooth, with only a few, sparse punctures, and with a low, median longitudinal carina on anterior two-fifths. Sternum two with sparse, moderate punctures. Sterna three to six with close, moderate punctures. Posterior margin of hypopygium evenly convex. Tergum one clothed with sparse, long erect, white pubescence. Terga two to six with sparse long erect, orange pubescence, the apical margins with a band of dense, recumbent, orange pubescence. Last tergum clothed with black pubescence. Sterna one to six clothed with white pubescence, except lateral margins of sterna two to four, with orange pubescence. Last sternum clothed with white pubescence and a few intermixed fuscous hairs. Wings infuscated, especially apically; forewing with two well defined submarginal cells and traces of a third. Body length: 10.6 mm.

ALLOTYPE Male Information.—PANAMA: Darién Province, Cruce de Mono, Estación INRENARE, 8 Feb 1993 (yellow trap). R. Cambra T., J. Coronado, Museo de Invertebrados "G. B. Fairchild", Universidad de Panamá (MIUP).

Additional Material Examined.—PANAMA: Darién Province, Cruce de Mono, Estación INRENARE, R. Cambra, J. Coronado, 144 females and 27 males, 8 Feb - 4 Mar 1993, deposited in MIUP, NMNH-Smithsonian Institution, University of Minnesota Insect Collection, and BM(NH). Body length varies in males from 8.3 to 11.0 mm, in



Figs. 1-4. *Pseudomethoca areta*. 1. Male allotype, dorsal habitus. 2. Gynandromorph, dorsal habitus. 3. Male genitalia, split drawing, dorsal = right; ventral = left. 4. Penis valve, side view.

females from 7.8 to 11.1 mm.

Comments on Sex Association and New Synonymy.—Sex association is based on observations of males courting and mating with females in the field, and has been corroborated in the laboratory with mating experiments. Courtship is very brief, lasting 15-40 seconds, and consists of bursts of rapid vibrations of the wings and antennae, interspersed by short hopping flights. The male climbs onto the female and grasps her neck with his mandibles and attempts to mate with her. We have not seen heterospecific courtship or mating in *Pseudomethoca*. Erroneous heterospecific sex associations may be made if containers or outdoor sites become contaminated by pheromones released from a female of a different species that recently occupied that site (personal observations).

Males of *Pseudomethoca areta*, like those of the genotype and males of numerous other species of *Pseudomethoca* we have examined, have a strong longitudinal carina beneath the scape. Therefore, we consider erroneous Casal's (1965) observation that males of the ill-defined genus *Darditilla* Casal (genotype is only male known, and 35 other species, known only from females) differ from those of *Pseudomethoca* in having a carina beneath the scape, said to be absent in the latter. The male genitalia of *P. areta* are symmetrical (Fig. 3), as are those of all other Neotropical sphaerophthalmine males we have examined, and phoretic mating is absent in this group. In contrast, the Neotropical mutilline males of *Timulla* (*Timulla*) present strongly asymmetrical genitalia and phoretic matings (Cambra & Quintero, 1992). The asymmetry in the male genitalia possibly functions to provide a better hold, or grasp, of the female while airborne.

Cameron's types of *areta* and *panamensis* are both from Bugaba, and we found them to be identical; the name *areta* has page precedence over that of *panamensis*. *Pseudomethoca areta* is closely related to *P. hecate* (Gerstaecker, 1874), from Costa Rica, differing only in the integumental coloration of the vertex and dorsolateral areas of the thorax. We suspect that they are the same species. To confirm the synonymy we need to examine Gerstaecker's type specimen and to compare the genitalia of males sexually associated with *hecate* females with those of the males described here.

Gynandromorph Individual of *Pseudomethoca areta* Fig. 2

Description.—Head identical to that of a normal female, without a trace of male characters. Thorax and legs identical to those of a normal male, without a recognizable trace of female characters. The anterior wings have abnormally thin, translucent venation; they are torn along their posterior half, and we suspect were never functional. Abdomen with six segments, as in the female. First tergum completely male. Second tergum a mosaic: right half with coloration and pubescence of male and female; left half is completely male-like. Third tergum, right half with female characteristics only; left half is a mosaic with integument coloration and pubescence both of male and female. Abdominal segments four to six are female only. Second sternum with right half female and left half male, same as other sterna, except for sternum three, identical to that of a female. Body length: 11.1 mm.

Data and comments on the gynandromorph.—The gynandromorph individual was collected on 26 February 1993, at 10:00 AM, in the general locality of the allotype. When we first noticed it, the individual was walking over dry leaves on the ground. Shortly afterward, we watched a male arrive, flying upwind, attracted by what we thought was a normal female. The male quickly attempted to mate but encountered indifference on the part of the female-like individual. Female mutillids are known to attract winged males by means of wind-dispersed pheromones (see Cambra & Quintero, 1993). The upwind arrival of the male suggests that the gynandromorph individual was secreting female pheromones. The abnormally thin and quite battered forewings, suggest that the animal was unable to fly, although it had perhaps attempted to. The specimen exhibits anterior/posterior division of male and female components, as well as mosaic segments, a type of gynandromorphy not previously described for mutillids (see Table 1).

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute (STRI), particularly Ira Rubinoff, for providing research facilities. We are grateful to the British Embassy in Panama, in particular Ambassador Thomas H. Malcomson, for securing travel funds to England for R.A.C.; to the Entomology Department personnel of the Natural History Museum, London, BM(NH) for providing R.A.C. with working facilities and assistance during his visit. We also thank Indra Candanedo and Roberto Arango, Instituto Nacional de Recursos Naturales Renovables, who aided us with permits and logistics in the Darien National Park. This project was financed in part by Vicerectoria de Investigación y Postgrado, Universidad de Panamá, Fund No. 1-4500-91-12. Our thanks to Karl V. Krombein, Smithsonian Institution, Annette Aiello and David W. Roubik, STRI, and an anonymous reviewer, for reading and making comments on the manuscript, James Coronado, now at STRI, for providing very valuable help in the field, and to Angel Aguirre, STRI, for bibliographic assistance and location of references on gynandromorphs.

LITERATURE CITED

- Bischoff, H. 1931. Der typus der *Mutilla dubia* F.—ein gynander. *Mitteilungen deutschen entomologischen gesellschaft* 2(4): 54-56.
- Cambra, R. A. and D. Quintero A. 1992. Velvet ants of Panama: distribution and systematics (Hymenoptera: Mutillidae), pp. 459-478. In: Quintero A., D. & A. Aiello (eds.) *Insects of Panama and Mesoamerica: Selected studies*. Oxford University Press, Oxford.
- Cambra, R. A. and D. Quintero A. 1993. Studies on *Timulla* Ashmead (Hymenoptera: Mutillidae): New distribution records and synonymies, and descriptions of previously unknown allotypes. *Pan-Pacific Entomologist* 69(4): 296-310.
- Cameron, P. 1895-1896. Hymenoptera, vol. 2. *Biologia Centrali Americana*, pp. 262-360, plates 13-14.
- Casal, O. H. 1965. *Darditilla* nuevo género Neotropical de Sphaerophthalminae (Hym. Mutillidae). *Eos*, Madrid, 41: 9-18.
- Dalla Torre, C. G. and C. Friese. 1899 (1898). Die hermaphroditen und gynandromorphen Hymenopteren. *Berichte des naturwissenschaftlich - Medizinischen Vereins in Innsbruck* 24: 1-96.
- Gerstaecker, C. E. 1874. Mutillarum Americae meridionalis indigenarum synopsis systematica et synonymica. *Archiv für Naturgeschichte* 40: 41-77.
- Krombein, K. V. 1979. Family Mutillidae, pp. 1276-1314. In: Krombein, K. V. et al., eds. *Catalog of Hymenoptera in America North of Mexico*, Vol. 2. Smithsonian Institution Press, Washington, D.C.
- Krombein, K. V. 1992. Host relationships, ethology and systematics of *Pseudomethoca* Ashmead (Hymenoptera: Mutillidae, Andrenidae, Halictidae and Anthophoridae). *Proceedings of the Entomological Society of Washington* 94(1): 91-106.
- Maeklin, F. W. 1856. Om hermafroditism bland insekterna, samt beskrifning öfver en i Helsingfors funnen hermafrodit af *Mutilla obscura* Nyl. öfver. af *Finska Vetenskaps-Societens Förhandlingar* 3: 106-112.
- Mann, W. M. 1915. A gynandromorphous mutillid from Montana. *Psyche* 22: 178-180.
- Mickel, C. E. 1924. A revision of the mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* occurring in America North of Mexico. *Proceedings of the United States National Museum* 64(15): 1-51.
- Mickel, C. E. 1928. Biological and taxonomic investigations on the mutillid wasps. *United States National Museum Bulletin* 143: 1-351.
- Mickel, C. E. 1935. Descriptions and records of mutillid wasps of the genera *Myrmilloides* and *Pseudomethoca* (Hymenoptera: Mutillidae). *Transactions of the American Entomological Society* 61: 383-398.
- Mickel, C. E. 1936. New species and records of Nearctic mutillid wasps of the genus *Dasymutilla*. *Annals of the Entomological Society of America* 29: 29-60.
- Mickel, C. E. 1952. The Mutillidae (wasps) of British Guiana. *Zoologica* 37(3): 105-150.
- Nonveiller, G. 1990. *Catalog of the Mutillidae, Myrmosidae and Bradynobaenidae of the Neotropical region including Mexico (Insecta: Hymenoptera)*. SPB Academic Publishing bv, The Netherlands, 150 pp.
- Schuster, R. M. 1945. A new species of *Pseudomethoca* (Mutillidae) from the West Indies. *Bulletin of the Brooklyn Entomological Society* 40: 7-8.
- Wheeler, W. M. 1910. A gynandromorphous mutillid. *Psyche* 17: 186-190.

Table 1. Previously published cases of gynandromorphy in Mutillidae

Species	Type	Wing & tegula	Country	Ref.
<i>Mutilla europea obscura</i>	bilateral, right f, left m	+	Finland	Maeklin 1856 DallaTorre & Friese 1899
<i>Dasymutilla cypris</i> [=hora]	head, thorax, abdom. segm. 5-7 m; 1-4 f	+	USA	Mickel 1928
<i>Dasymutilla gloriosa</i> [=reperticia]	not described	?	USA	Mickel 1936
<i>Dasymutilla vestita</i> [=euchroa =fulvohirta]	decussated, head half: right m, left f; thorax & abdomen: right f; left m	0	USA	Mann 1915
<i>Pseudomethoca frigida</i> [=canadensis]	bilateral, right m, left f	+	USA	Wheeler 1910
<i>Traumatomutilla dubia</i>	head, thorax, 1st abdom. segment m, rest abdomen mosaic	+	Am. Mer. [Guyana]	Bischoff 1931 Mickel 1952

Abbreviations: f, female; m, male; +, well developed; 0, absent.

Additions and Corrections to Volume 2, Number 1, 1993

Publication date: the correct date of publication for Volume 2, Number 1, is November 17, 1993.

All "≥", "≤" and "≈" signs were inadvertently left out of the text in the following two articles resulting in a significant loss of information. The affected text is as follows:

Davidson, D. W. and D. McKey, "The evolutionary ecology of symbiotic ant-plant relationships," pp. 13-83.

P. 14, column 2, line 42	“(N ≈ 8)”
P. 14, column 2, line 43	“(N ≈ 6)”
P. 14, column 2, line 44	“(N ≈ 4)”
P. 14, column 2, line 46	“(N ≈ 5) and “(N ≈ 6)”
P. 15, column 1, lines 11, 12	“(N ≈ 8), (N ≈ 7) and (N ≥ 5)”
P. 15, column 1, line 35	“(N ≈ 50-60 ant-plant species)”
P. 15, column 1, line 36	“(N ≈ 20)”
P. 15, column 1, line 37	“(N ≈ 15)”
P. 15, column 1, lines 38, 39	“(N ≈ 12 species) and (N ≥ 6)”
P. 15, column 1, line 40	“(N ≈ 15)”
P. 15, column 1, line 42	“(N ≈ 3)”
P. 15, column 2, line 6	“(N ≈ 23)”

Additional corrections are as follows:

- P. 69, Appendix 1: reference to Manriquez & Dirzo 1990 should read "Iborra-Manriquez & Dirzo 1990."
- P. 70, Appendix 1: entry for *Barteria* should read "... HFOWE^b Y Z ..."
- P. 74, Appendix 1: entry for *Maieta* should read "... B;D; Vasconcelos 1990, 1991, IP; Herre et al. 1986"
- P. 78, Appendix 1: entry for *Cordia* should read "... ^{U,P,R}Iy Y,i^l GH ..."

Ward, P. S., "Systematic studies on *Pseudomyrmex* acacia-ants," pp. 117-168.

P. 121, column 2, line 30	"PLI2 ≥ 0.77"
P. 121, column 2, line 45	"worker PLI ≥ 0.71, queen PLI ≥ 0.64"
P. 122, column 1, line 36	"HW ≤ 0.85"
P. 122, column 1, line 37	"HW ≥ 0.85"
P. 122, column 1, line 41	"PL/HW ≥ 0.71"
P. 122, column 2, lines 8-9	"CI ≥ 0.94 and/or HW ≥ 0.96"
P. 122, column 2, line 15	"SL/HL ≥ 0.22"
P. 122, column 2, line 16	"SL/HL ≤ 0.21"
P. 130, line 33	"CI ≈ 1.12"
P. 130, line 35	"CI ≈ 0.80"
P. 132, line 40	"SL/HL ≤ 0.21"
P. 132, line 42	"SL/HL ≥ 0.22"
P. 133, lines 4-5	"CI ≥ 0.94 and/or HW ≥ 0.96"
P. 133, column 1, line 8	"MD8/MD9 ≈ 0.70"
P. 133, column 1, line 11	"MD4/MD5 ≈ 0.74"
P. 135, column 2, line 4	"worker REL ≤ 0.50, queen REL ≤ 0.48"
P. 135, column 2, lines 5-6	"worker PLI ≤ 0.71, queen PLI ≤ 0.63"
P. 135, column 2, lines 29-30	"queen PLI ≈ 0.65, queen PL/HL ≈ 0.49"
P. 145, column 1, lines 26-27	"REL ≤ 0.45, REL2 ≤ 0.56, EL/LHT ≤ 0.61"

P. 145, column 1, line 30	"FCI \approx 0.055"
P. 145, column 2, lines 7-8	"worker PWI3 \geq 0.50, worker PPWI \leq 1.30"
P. 146, column 2, line 10	"CI \approx 0.61"
P. 146, column 2, line 12	"LHT/HW \approx 1.12"
P. 152, column 2, lines 14-15	"(\leq 0.10 mm)"
P. 155, column 1, line 10	"REL \approx 0.66"
P. 157, column 1, lines 20-21	"PLI \approx 0.55"
P. 157, column 2, line 12	"MD8/MD9 \approx 0.70"
P. 157, column 2, line 17	"MD4/MD5 \approx 0.65"
P. 158, column 1, lines 7-8	"PWI3 \approx 0.60"
P. 158, column 1, line 41	"REL \approx 0.65"
P. 158, column 1, lines 42-43	"MFC \approx 0.02"
P. 158, column 1, line 44	"CI \approx 0.85"
P. 159, column 1, line 3	"CI \approx 1.12"

Additional corrections are as follows:

P. 163, Table 2, column 31: *Pseudomyrmex nigrocinctus* and *P. particeps* should be "1", not "0" for character 31.

P. 121, column 1, line 41: for "public domain software" read "Shareware software".

P. 131, line 34: for "Figs. 10, 34" read "Figs. 11, 34".

Kazenas, V. L. and B. A. Alexander, "The nest, prey, and larva of *Entomosericus kaufmani*", pp. 221-226. Nearly all references to illustrations should be corrected as follows:

P. 221, column 2, line 19: for "Fig. 2" read "Fig. 4".

P. 221, column 2, line 23: for "Fig. 3" read "Fig. 6".

P. 223, column 1, lines 7-8: for "Fig. 4" read "Fig. 7".

P. 223, column 1, line 13: for "Figs. 5, 8" read "Figs. 8, 11".

P. 223, column 1, line 22: for "Fig. 8" read "Fig. 9".

P. 223, column 1, line 28: for "Figs. 5, 8": read "Figs. 8, 11".

P. 223, column 1, lines 29-30: for "Figs. 10, 11" read "Figs. 2, 3, 8".

P. 223, column 1, line 31: for "Figs. 5, 6" read "Figs. 5, 8".

P. 223, column 1, line 37: for "Fig. 6" read "Fig. 5".

P. 223, column 2, line 3: for "Fig. 7" read "Fig 10".

INSTRUCTIONS FOR AUTHORS

General Policy

The *Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are unlikely to be accepted unless a strong case is evident, such as importance in economic entomology or with concurrent biology or ecology. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level.

All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript.

The language of publication is English. Summaries in other languages are acceptable.

Format and Preparation

Three copies of each manuscript, including copies of illustrations, should be submitted on letter size or A4 paper, double spaced, with at least 25 mm margins on all sides. On the upper left of the title page give name, address and telephone and fax numbers of the author to whom all correspondence is to be sent.

The paper should have a concise and informative title, followed by the names and addresses of all authors. The sequence of material should be: title, author(s), abstract, text, acknowledgments, literature cited, appendix, figure legends, figure copies (each numbered and identified), tables (each numbered and with heading). Each of the following should start a new page: (1) title page, (2) abstract, (3) text, (4) literature cited, (5) figure legends, (6) footnotes.

Following acceptance of the manuscript, the author should provide the editor with two copies of the manuscript accompanied by a copy on diskette using DD, double sided computer diskettes - IBM compatible MS DOS 5.25 inch or IBM and Macintosh 3.5 inch diskettes. (Authors who do not have access to a computer should submit three copies of the manuscript.) The paper may be submitted in most PC and Mac word processor programs such as Microsoft Word, FullWrite Professional, WordPerfect, WriteNow, Nisus, MacWrite, or MacWrite II; it is important that the manuscript also be formatted as an ASCII or TEXT file. If possible, all words that must be italicized should be done so, not underscored. Use of the words male and female is preferred to sex symbols. Tables may be formatted in a spread sheet program such as MS Works or MS Excel. Text should be double spaced typing, with 25 mm left and right margins. Tables should be put in a separate file. Diskettes should be accompanied by the name of the software program used (e.g., WordPerfect, Microsoft Word). Authors should keep backup copies of all material sent to the Editor. The Society cannot be responsible for diskettes or text mislaid or destroyed in transit or during editing.

Illustrations should be planned for reduction to the dimension of the printed page (15.3 X 22 cm, column width 7.5 cm) and allow room for legends at the top and bottom. Do not make plates larger than 14" X 18" (35.5 X 46 cm). Individual figures should be mounted on a suitable drawing board or similar heavy stock. Photographs should be trimmed, grouped together and abutted when mounted. Figure numbers should be on the plate, but it is strongly recommended that names be included after the numbers (e.g., Fig. 2, *texanus*). Include title, author(s) and address(es), and illustration numbers on back of each plate. Original figures need not be sent until requested by the editor, usually after the manuscript has been accepted. Reference to figures/tables in the text should be in the style "(Fig. 1)" "(Table 1)". Measurements should be in the metric system.

All papers must conform to the *International Code of Zoological Nomenclature*. The first mention of a plant or animal should include the full scientific name including the authority. Genus names should not be abbreviated at the beginning of a sentence. In taxonomic papers type specimens must be clearly designated, type depositories must be clearly indicated, and new taxa must be clearly differentiated from existing taxa by means of keys or differential diagnoses. Authors are required to deposit all type material in internationally recognized institutions (not private collections). Voucher specimens should be designated for specimens used in behavioral or autecological studies, and they should be deposited similarly.

Acceptance of taxonomic papers will not require use of cladistic methods; however, authors using them will be expected to specify the phylogenetic program used (if any), including discussion of program options used. A data matrix should be provided. The number of parsimonious cladograms generated should be stated and the reasons for the one adopted. Lengths and consistency indices should be provided.

References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For papers in press, use "in press," not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely.

Charges

Publication is free to members of the International Society of Hymenopterists. At least one author of the paper must be a member. Reprints are charged to the author and must be ordered when returning the proofs; there are no free reprints. Author's corrections and changes in proof are also charged to the author. Color plates will be billed at full cost to the author.

All manuscripts and correspondence should be sent to:

Paul M. Marsh, Editor
P. O. Box 384
North Newton, Kansas 67117
(316) 284-0990



HECKMAN
BINDERY, INC.
Bound-To-Pleas®
FEB 00
N. MANCHESTER, INDIANA 46962

SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01058 9539